



OPEN Anthropogenic stressors of black clam distribution in Kochi backwaters on the Indian west coast

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The black clam (*Villorita cyprinoides* Gray, 1825) is the most commercially important clam in India and the major share of its landing (around 25,000 tonnes/year) comes from Kochi backwaters (KBW), the largest estuarine system on the west coast of India, where approximately 4000 fishermen harvest them year-round. This study based on recent and historical data sets, comprehended how multiple anthropogenic stressors impact the black clam distribution in the KBW. In the first part, a recent data set from an extensive hydrographic and sediment sampling from 22 locations in the central and southern sections of the KBW during the Pre-Monsoon (March), Southwest Monsoon (July), and Northeast Monsoon (December) was introduced to demarcate the most conducive salinity and sediment textural conditions of black clam. Black clam in the KBW prefer midstream and upstream regions with mesohaline to oligohaline conditions and sand-dominant substratum, but their current distribution is shaped by multiple anthropogenic stressors, notably the consequence of the installation of the Thannermukkom Barrage (TB) in 1975 to prevent saltwater intrusion for paddy cultivation. The combination of current and historical data, supplemented with literature, demonstrates that TB generated various stressors on the natural distribution, resulting in a decrease in the abundance of black clam in the KBW. This includes (a) shrinkage and relocation of their most preferred salinity zones (mesohaline) for spawning from the south of TB (Vembanad) to the north of TB, (b) the increased siltation due to stagnancy in the Vembanad caused by TB increased the contribution of finer particles especially clay in the bottom substratum, which is less preferred over sand by black clam and (c) the opening and closing of the TB shutters cause salt shock causing vast mortality of black clam on both sides of TB. Secondary stressors of TB are affected by (a) poor water quality, eutrophication, and massive spread of hyacinth mats, making it difficult for local fishermen to exploit the black clam resource, and (b) overexploitation of the black clam in certain areas due to shrinkage in the total area and relocation of the conducive spawning environment in KBW.

Keywords Black clam, *Villorita cyprinoides*, Kochi backwaters, Salinity, Sediment texture, *Eichhornia*

The mollusc/bivalve black clam, *Villorita cyprinoides* Gray, 1825 is the most abundant clam species in the Kochi backwaters (KBW) of around 70 km alongshore extent, contributing up to 75% of the total clam production in India¹. This clam occurs in the entire submerged zones of the KBW (Vembanad Lake System), but its highest abundance occurs upstream^{2,3}. Black clams are harvested for their meat, and their shell is used commercially for cement, calcium carbide, sand lime bricks, distemper, glass, rayon, paper, sugar, medicines, pesticides, chicken feed, and so on^{2,3}. They are being collected extensively from the wild and thousands of fishermen rely on them for their livelihood and employ multiple ways to exploit the resource including (a) handpicking in shallow waters below 0.5 m depth, (b) detecting the presence of clams by the feet in slightly deeper water (< 1.15 m depth) and then collect them in containers, (c) diving underwater in deeper waters and collect them by hand and (d) by using hand rake with a pole attached (kolli) from the canoe. Since black clam is an indispensable resource to the local community upstream of the KBW, fisherman societies exist there to manage the utilization of the resource. Several studies on black clams are available from the KBW since the 1970s, mostly presenting their ecobiology, occurrence, distribution, and utilization aspects^{2–8}. One of our very recent studies⁹ based on black clam larvae abundance in the KBW showed the following (a) black clam is a continuous breeder with two spawning peaks during March–May and October to February periods, and (b) mesohaline salinity (5–18) is the most conducive

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for the peak spawning and larval production of black clam and (c) flow restriction by TB have adverse impact on the distribution and production of black clam⁹. A summary of the most relevant information in the past studies is presented in Table 1, which shows that mesohaline is the most conducive condition for black clam production in the KBW.

Largely, seasons in the study domain are classified mainly based on monsoonal wind and rainfall into (a) Pre-Monsoon [(PRM) February to May], (b) Southwest Monsoon [(SWM) June to September] and Northeast Monsoon [(NEM) October to January]. The KBW has a long history of human interventions through widespread reclamation, and alteration of the hydrological balance through the installation of barrages and activities associated with human settlements and urbanisation of many towns and cities along its banks^{10,11}. Studies showed that extensive land reclamation was the major human intervention of the KBW in India's pre-independence period (before the 1950s), while it was the establishment of several industries and saltwater barrages in the post-independence period¹¹. In 1975, a hydraulic barrage was constructed at Thannermukkom in KBW, 45 km south of the Kochi inlet, to prevent saltwater intrusion into the upstream Kuttanad region mainly to promote multiple cropping of paddy every year. When TB is closed during the PRM and NEM, the KBW has two isolated parts and the downstream and midstream behave polyhaline and mesohaline, while the upstream Vembanad region remains oligohaline to limnetic status. The alarming concern is that as the TB separates the KBW into two during non-monsoon periods, it introduces ecological degradation, due to the alteration of the salinity regimes and flushing characteristics. This change was found to be awful in the south of TB in the Vembanad, where the survival and the abundance of many endemic and migratory organisms are severely affected^{5&12}. It is known that the Vembanad region, which had highly productive clam beds before the establishment of TB, has become barren and caused the severe dislocation of thousands of clam fishers^{2,7&12}. Fundamentally, salinity and sediment texture are the two most significant environmental variables controlling the distribution of benthos in estuaries^{13,14}. However, there is a general lack of information about the possible long-term changes in sediment texture in the KBW where black clam production was high before TB.

One of our recent studies showed how human interventions in the KBW promoted eutrophication and massive proliferation of water weeds especially in the upstream Vembanad region causing vertical and horizontal shrinkage of the system through increased siltation and faster ecological succession¹¹. It was observed that the inherently fragile KBW was harmed by extensive and long-term reclamation, the construction of saltwater barrages, and many landfill roads serving as coastal dams, creating water stagnation. Given these contexts, we hypothesize that, while alterations in salinity distribution caused by TB could be a primary stressor on the decline of black clam in the KBW especially in the Vembanad, there are multiple other stressors in operation on the black clam, since there exists multiple levels of environmental degradation due to altering the flushing characteristics of the system. Therefore, this study focuses on (a) understanding the current distribution and ecology of black clams in the KBW based on a recent data set having extensive coverage during the three different seasons, and (b) investigating the multiple anthropogenic stressors of black clam that adversely affected their distribution in the KBW especially in the upstream Vembanad region.

Materials and methods
Study area

The estuaries on the west coast of India are in general referred to as monsoonal estuaries as most of the river discharge in a year occurs during the 4-month duration of the SWM and then the total runoff is significantly larger than the estuarine volume¹⁵. Kochi backwaters (KBW) also referred to as the Vembanad Lake System is the largest monsoonal estuary along the west coast of India located between 9° 30'-10° 10' N and 76° 15'-76°

SL.No	References	Salient observations
1	Sivankutty Nair (1975)	This original study before the installation of TB showed that purely freshwater conditions are not conducive to the growth and abundance of black clams during the SWM. It was noted that the growth and production of black clams are either retarded or arrested in the KBW during the SWM when freshwater completely dominates the system
2	Pillai (1991)	Due to the closure of TB from January–May, the ecological imbalances it pauses lead to a low abundance of black clams in various regions of the KBW especially in the Vembanad region
3	Vinuchandran and Damodaran, (2000)	This study based on the specimens collected from the KBW presented the osmoregulatory aspects of black clam. The study showed that though the survival of black clams was reported up to 27 salinity in experimental conditions, they appear to be surviving better up to 15 salinity in the natural conditions and this was evident in the intracellular osmotic parameters considered in the study
4	Laxmilatha and Appukkuttan (2002)	This review study on black clam in the KBW presented the following points (a) black clam is an active breeder that reaches its peak in February–April and November–December. (b) Dredging operations impacted the clam fisheries by smothering silt, which constricted off clam beds and disrupted seed settling. (c) Water hyacinth (<i>Eichhornia crassipes</i>) and African weed (<i>Salvinia auriculata</i>) infested certain areas of the lake with thick mats, causing a 2–3 month disruption to clam fishing every year
5	Arun (2005)	This doctoral study, based on the experimental cages showed how TB impacted the ecology of the KBW, especially in the Vembanad for the black clam bed. Studies showed that the optimum salinity for spawning of black clams is about 10–12 and a change in salinity is the most important factor that triggers spawning. The study presented the view that construction and periodical opening and closing of TB adversely affect the ecology of the KBW, especially in the Vembanad for clam beds
6	Suja and Mohammed (2010)	This review cum field survey-based study showed that in nearly all the landings of black clams in India, about 25,000 tons (t)/year are harvested from the KBW. Nearly 4000 fishermen harvest the black clams year-round. The stocks of black clams seem to be declining slowly in the Vembanad region because of the salinity alterations caused by TB
7	Arunpandi et al., (2021)	Black clams in the KBW were found breeding throughout the year, with their larvae abundance peaks in plankton samples from March to May and from October to February. Mesohaline conditions are preferred for optimal spawning and larval production

Table 1. Salient observations in some of the past studies on black clam in the Kochi backwaters.

25' E (Fig. 1a), which is connected to the Arabian Sea through 2 inlets¹⁶. The KBW is a microtidal estuary and the nearby southeastern Arabian Sea has mixed semidiurnal tides, with two highs and two lows each day, that regularly enter and exit the KBW through the Kochi inlet in its central region and Munambam inlet in its northern region, facilitating frequent ventilation and flushing¹⁷. A strip of land of sand and alluvium deposited by six rivers: the Periyar in the north, Muvattupuzha in the central, the Achancoil, Pamba, and Manimala, and Meenachil Rivers in the south, separates the KBW from the adjacent southeastern Arabian Sea^{12&18–20}. Due to their proximity to the inlets at Kochi and Mumambam, the central and northern sections of KBW are exposed more to the saltwater incursion from the Southeastern Arabian Sea. On the other hand, the upstream of KBW in the Vembanad is notable for its vast rice (paddy) fields and peculiar topographical features. The Western Ghats mountains are the watershed that releases a large amount of freshwater and sediments into the KBW, especially during the SWM, when 70% of the annual rainfall falls in the study domain. Because of the large seasonal variations in river discharge into KBW, its flushing time varies significantly between seasons, with around 7 days during the SWM and 70 days during the Pre-SWM²¹.

Many studies showed that KBW has truly estuarine characteristics only during the PRM and NEM with well-defined regions of polyhaline, mesohaline, oligohaline, and limnetic conditions from the inlet to the upstream^{11,18,22}. The shutters of TB (Fig. 1 b) are kept closed from the latter half of NEM (December) to the entire PRM period (up to May) each year and then opened for the entire SWM and the first half of the NEM. During the PRM, the freshwater input into the KBW decreases dramatically due to the weak river discharge in the region. As a result, a well-defined salinity gradient develops in the KBW from the downstream to the upstream²². KBW has high nutrient levels all through the year ($\text{NO}_3 > 8 \mu\text{M}$, $\text{PO}_4 > 3 \mu\text{M}$, $\text{SiO}_4 > 5 \mu\text{M}$), with very high levels ($\text{NO}_3 > 50 \mu\text{M}$, $\text{PO}_4 > 50 \mu\text{M}$, $\text{SiO}_4 > 125 \mu\text{M}$) during the SWM^{18&23,24}. The principal sources of nutrients in the KBW are believed to be the runoff from agriculture, industrial discharge, aquaculture, and

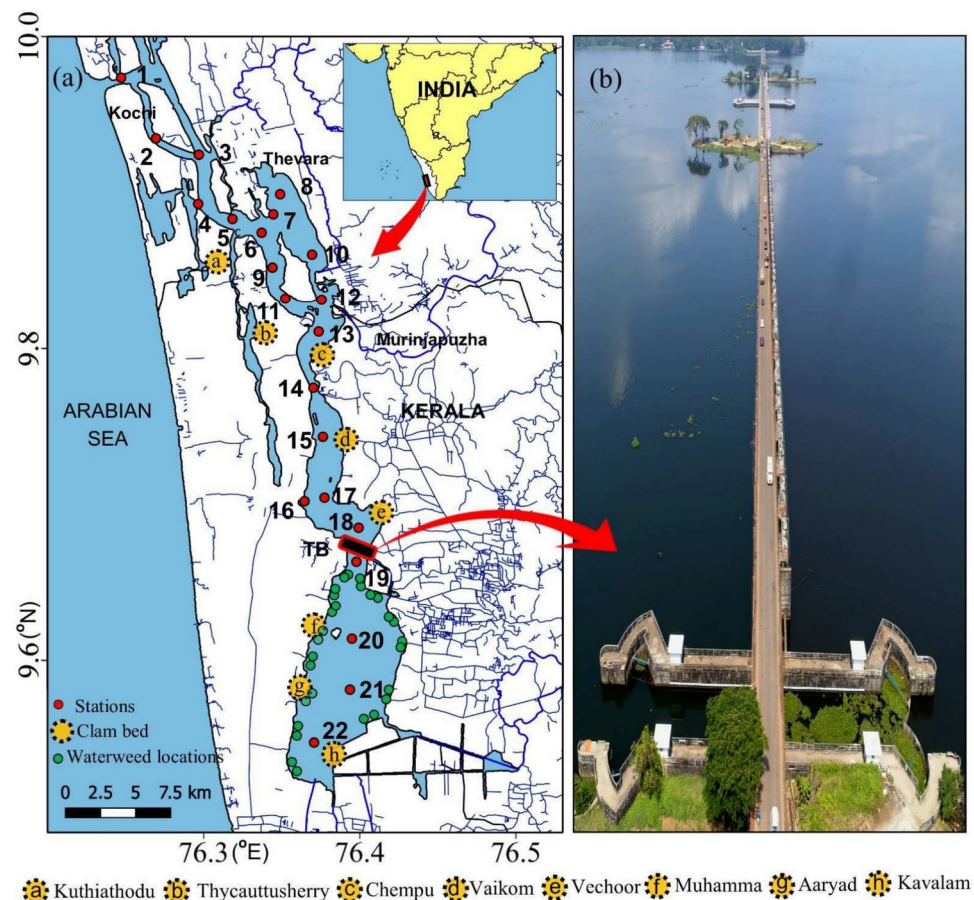


Fig. 1. (a) Study area and sampling locations. Panel (a) depicts 22 locations (red dots) from the downstream inlet region to the upstream in the Vembanad (1–22) that were sampled during PRM, SWM and NEM seasons for the hydrography, bottom substratum and macrobenthos. The green circles show the areas in the upstream Vembanad region where water weed growth was observed throughout the year. Panel (b) represents the aerial view of the Thannermukkom barrage (TB). This map (Fig. 1a) was created using QGIS v3.38.1-Grenoble (QGIS Development Team, 2017), following the attribution guidelines. QGIS Geographic Information System. Open Source Geospatial Foundation Project (<http://www.qgis.org>). QGIS software comes under GNU General Public License. Photograph (Fig. 1b) was taken by the corresponding author Dr. R. Jyothibaburjyothibabu@nio.res.in; rjyothil@gmail.com.

domestic sewage^{25–27}. Due to the eutrophic nature of the KBW, the phytoplankton biomass here is consistently high throughout the year with the nano-size fraction contributing the majority of stock and production^{28,29}.

Water stagnancy, eutrophication, and waterweed spread especially *Eichhornia crassipes* currently cause a serious ecological and socioeconomic concern in the KBW mostly in the upstream Vemband region where black clam collection has been actively practised¹¹. Ecological imbalances caused by water weeds have a profound impact on those who depend on KBW for their livelihood¹¹. Floating and submerged water weeds can compete for nutrients with phytoplankton and other native aquatic plants^{30–32}. It was noted that the extensive growth and mat formations of *Eichhornia crassipes* create hindrances to fishing gear and vessels including black clam exploitation^{28,33}. Similarly, huge mats of floating waterweed cause damage to the fishing gear, and there were even instances of fishermen getting trapped in extensive weed mats and having the fire force service come to rescue them¹¹.

Methods

Three seasonal sampling exercises were carried out in 22 locations in the KBW to measure the environmental setting and to understand the multiple human stressors on black clams. The hydrography and sediment samples were collected from the Kochi inlet (downstream) to the upstream Vembanad in the KBW during the SWM (June 2013), NEM (December 2013), and PRM (March 2014). Field sampling was carried out in 22 locations along the 50 km stretch of the KBW from the Kochi inlet downstream to the upstream Vembanad. During the current sampling, the vertical profiles of salinity at each sampling location were measured using a CTD Profiler (SEABIRD, USA). Bottom sediment was collected by Van Veen Grab, with an area of 0.04 m² and a penetration depth of 20 cm. Sediment samples were sieved using a standard mesh (0.5 mm) and the macrofauna separated were preserved with a 5% Rose Bengal-formaldehyde solution^{34,35}. After sieving the sediment, macrofauna were sorted into different groups. The macrobenthic organisms were identified up to genus/ species using taxonomic manuals^{36–42}. The taxonomic identity of the specimens was confirmed and updated using the World Register of Marine Species (WoRMS) website. After identification, macrofaunal abundance was estimated using a standard procedure⁴³. Sub-samples of sediments were also used for texture analysis using a laser diffraction particle size analyzer⁴⁴.

PRIMER V6⁴⁵ and CANOCO 4.5 (Ter Braak and Smilauer⁴⁶) software were used to perform the statistical analysis of the data in the current study. Following dataset standardization, PRIMER V6 software was used for an Euclidian distance-based group average method of cluster analysis to determine the average linkage of locations depending on salinity. Bottom salinity was considered to define the grouping of locations since it is evident from the literature that it is the most significant environmental factor influencing the abundance of black clams in the KBW. The study sites were then divided into several salinity levels according to McLusky's⁴⁷ classifications: limnetic (salinity < 0.5), oligohaline (salinity 0.5–5), mesohaline (salinity 5–18), polyhaline (salinity 18–30), and euhaline (salinity > 30). Additionally, the Bray–Curtis similarity index-based group average linkage method of cluster/SIMPREF overlaid non-metric multidimensional scaling (nMDS) was carried out on the abundance of macrobenthos and black clam using PRIMER V6 software to group the areas with similar features⁴⁵. The relationships between the environmental and biological variables were analyzed using RDA (CANOCO 4.5) (Ter Braak and Smilauer⁴⁶), which describes the multiple correlation analyses between parameters. The environmental variables were centred and standardized before the RDA ordination model was fitted. The ordination significance was tested with Monte Carlo permutation tests (499 unrestricted permutations) ($p < 0.05$). The results of the RDA are presented in Triplots wherein, the sampling locations are represented by points and biological and environmental parameters by arrows. The relative orientation of the parameter arrows represents their inter-relationship. Parameter arrows closely oriented in the same direction possess a significant positive correlation and those that are distantly and oppositely oriented represent a significant negative correlation⁴⁸. To determine how the salinity distribution pattern in the KBW changed overall before and after TB, the data from the current investigation were compared with the salinity data provided by Haridas⁴⁹ et al. Since Haridas⁴⁹ et al. used seven locations to represent the current study region, only the seven locations sampled in the current study that best matched the historical data were taken into consideration for the comparison. Similarly, the current sediment texture data was compared with historical data⁵⁰ to mark the change in the bottom substratum due to the establishment of TB. Also, as a benchmark for future studies and to draw a comprehensive understanding of the multiple human stressors on black clams in the KBW, a synthesis of all past studies from the study region also has been attempted in this study.

Results and discussion

Seasonal hydrography

The vertical distribution of salinity in the KBW during different seasons is presented in Fig. 2. The spatial distribution in salinity in the KBW showed seasonal variations with widespread polyhaline to mesohaline conditions during the PRM, polyhaline to oligohaline conditions during the NEM, and oligohaline to limnetic conditions during the SWM. It was very clear that the near inlet locations during the PRM and NEM behaved like an extension of the adjacent EAS while during the SWM the entire KBW behaved like a freshwater lake^{27&51}. It is also evident in Table 1 that the salinity is the most important environmental variable that governs the black clam abundance in the KBW, so based on the salinity, the sampling locations were clustered, which showed different clusters during the three seasons based on their similarity/dissimilarity (Fig. 3). During the PRM, the intense saltwater incursion through the inlet and weak river discharge from the upstream, caused a wide range of salinity regimes in the KBW resulting in the segregation of the sampling locations into four clusters. These clusters of locations represented the inlet, near inlet, midstream, and upstream. The inlet region (Cluster 1) consisted of locations 1–3, which had euhaline to polyhaline salinity (av. 28.72 ± 1.84). The near inlet region

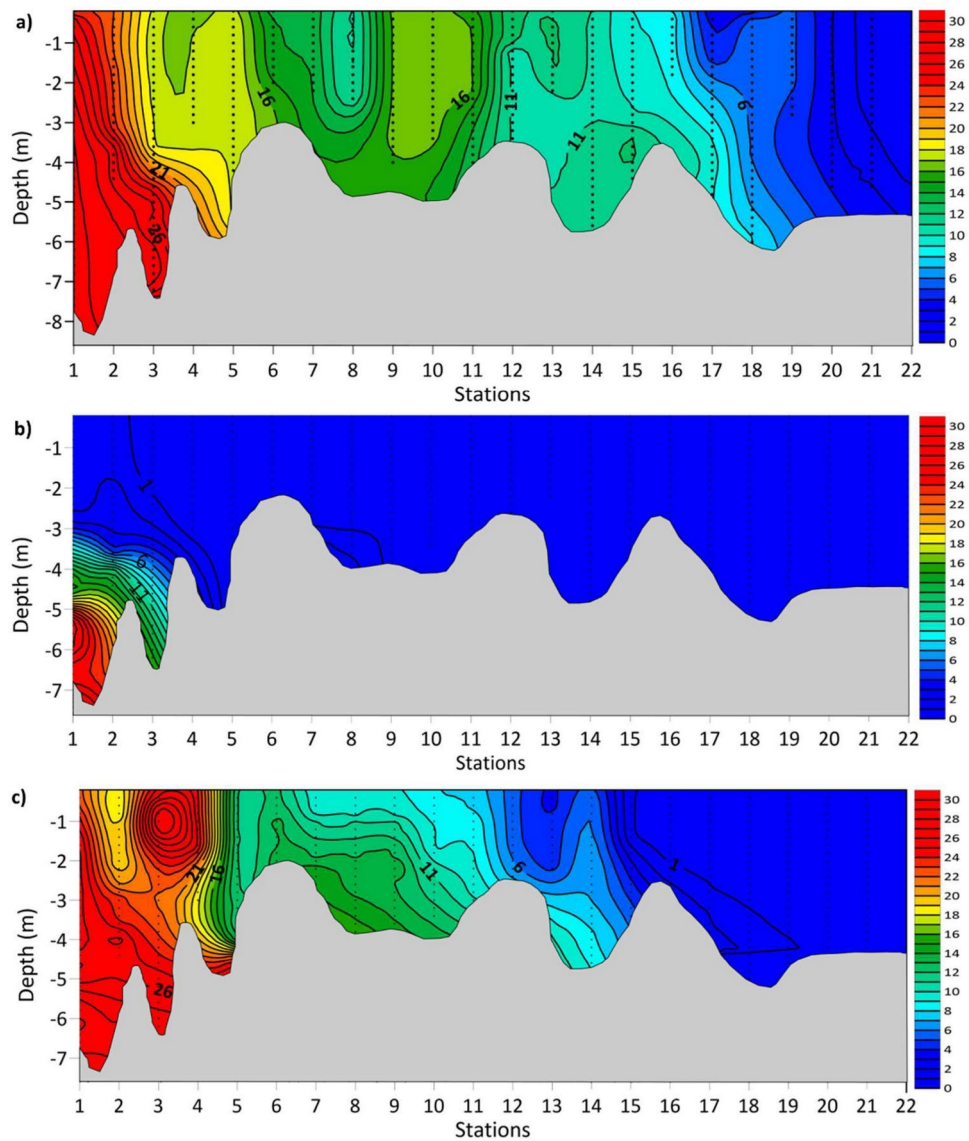


Fig. 2. Vertical distribution of salinity during (a) PRM (b) SWM (c) NEM. The vertical dotted lines depict the orientation of CTD measurements carried out in the study and each dot in the vertical lines represents a data point at 0.2 m intervals. Plots are made in Surfer, V 16. (Golden Software, USA; <http://www.goldensoftware.com/>).

(Cluster 2) was composed of locations 4–13, which had predominantly mesohaline salinity ($\text{av. } 15.17 \pm 2.14$). The midstream region (Cluster 3) was represented by locations 14–16, which had mesohaline salinity ($\text{av. } 11 \pm 0.99$). The upstream region (Cluster 4) consisted of locations 17–22 having mesohaline to oligohaline salinity ($\text{av. } 4.41 \pm 1.02$). The SWM was characterized by a completely different hydrographical setting in the KBW due to heavy river discharge upstream as around 70% of the annual rainfall occurs during that time. As a result, the saline water incursion into the KBW through the Kochi inlet was very weak during the period and hence salinity was found only in inlet locations at that time. Hence during the SWM, the inlet locations in cluster 1 had polyhaline salinity ($\text{av. } 22.38 \pm 8.41$), and all the rest of the locations in cluster 2 in the midstream and upstream had limnetic conditions (salinity $\text{av. } 0.13 \pm 0.03$). The true estuarine feature of the KBW was recovered by the NEM and zones of euhaline to the limnetic conditions were formed at that time primarily due to the decrease in river discharge in the upstream and enhanced salinity incursion through the Kochi inlet. During the NEM, compared to the SWM, more locations near the inlet region in Cluster 1 (locations 1–4) had euhaline to polyhaline (salinity $\text{av. } 27.66 \pm 2.67$). The downstream region formed of locations 5–12 in Cluster 2 had mesohaline (salinity $\text{av. } 13.78 \pm 5.19$) conditions and the midstream and upstream regions in Cluster 3 (locations 13–22) had oligohaline to limnetic conditions ($\text{av. } 1.35 \pm 0.85$). Supplementary Table 1 presents a quantitative summary of environmental and biological variables measured during the three different seasons.

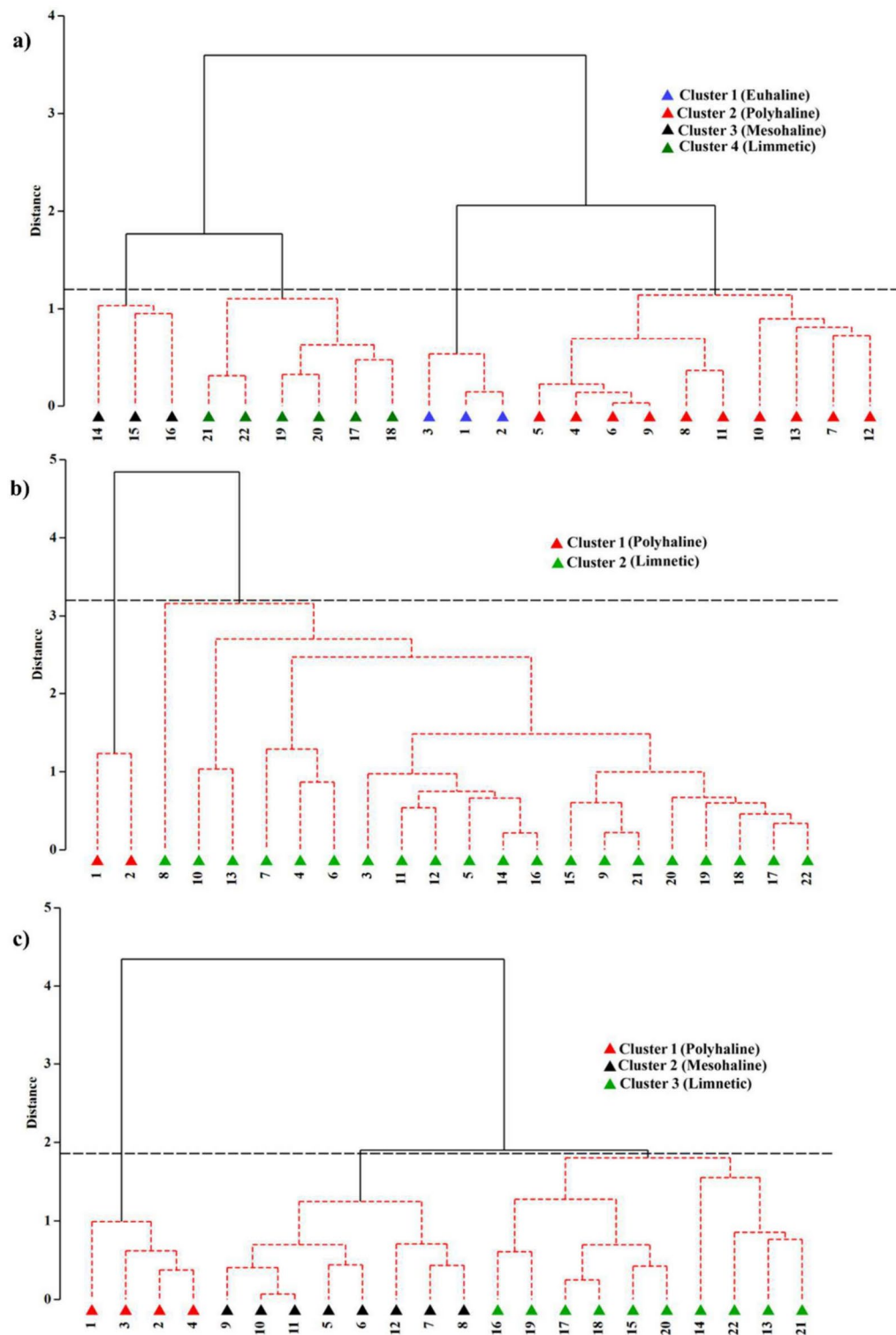


Fig. 3. Euclidean distance-based group average clustering representing the segregation of locations based on salinity (a) PRM, (b) SWM, (c) NEM. Colour codes of clusters and their salinity specifics during different seasons are represented in respective panels. This analysis was done in PRIMER V7 (<http://www.primer-e.com/>).

Bottom sediment texture and siltation

Temporal and spatial variations in sediment texture are presented in Fig. 4. In general, sand and silt (%) dominated the KBW in varying proportions during the PRM and SWM whereas sand and clay were predominant during the NEM. During the PRM, locations in clusters 1 and 4 were silty or sandy silt, and clusters 2 & 3 were sandy

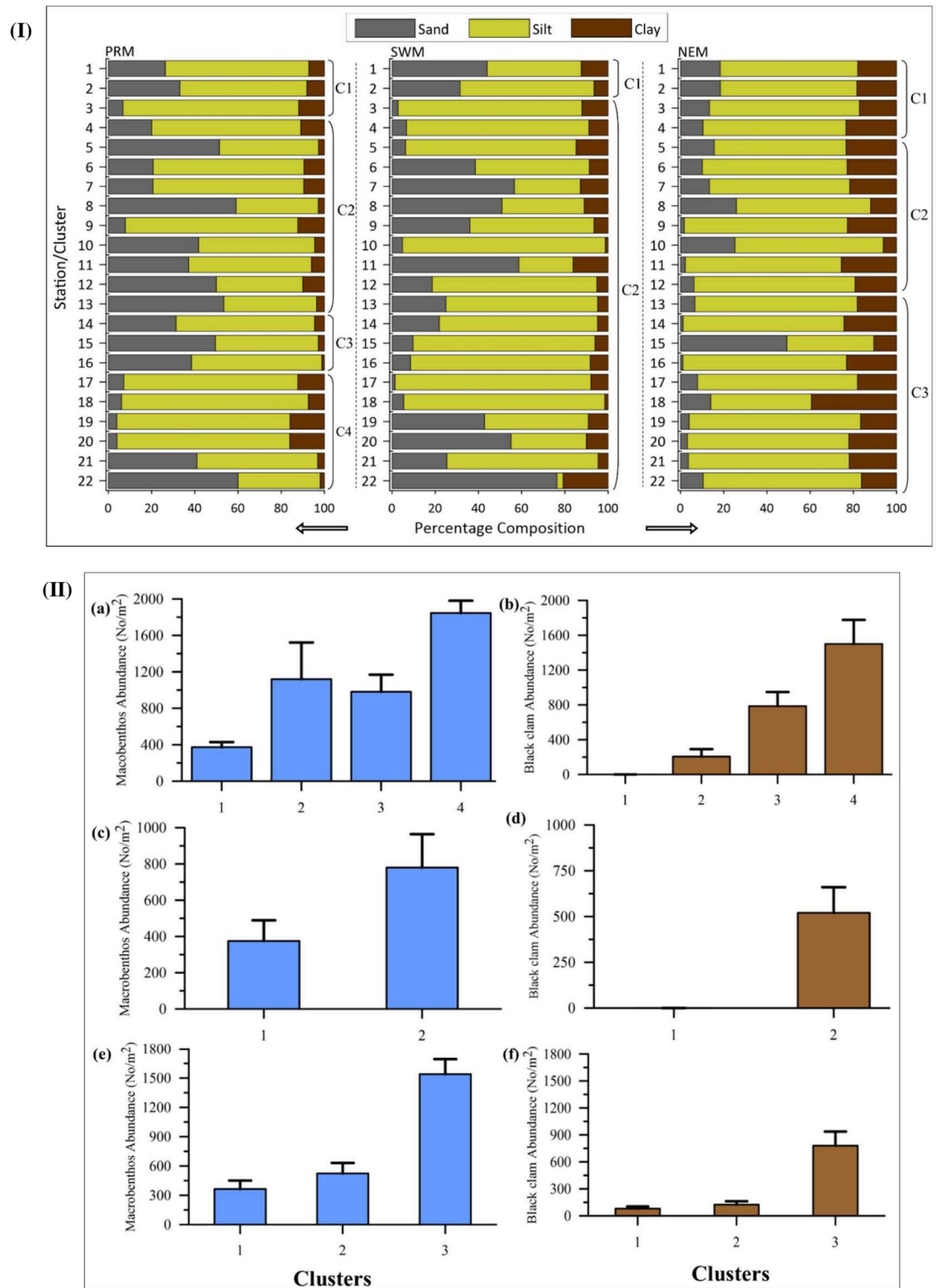


Fig. 4. (I) Texture of the bottom substratum (%) during the PRM, SWM and NEM and (II) Abundance of macrobenthos and black clam in clusters of locations during (a & b) PRM, (c & d) SWM, and (e & f) NEM. Kindly note that the scales on the y-axis are not uniform in different panels. Figure 4 (I & II) are made in Grapher, V 7.2. (Golden Software, USA; <http://www.goldensoftware.com/>).

silt. During the SWM, cluster 1 locations in the inlet were silty sand, while it was sandy silt in all the remaining locations (cluster 2). On the other hand, during the NEM, locations in all clusters were predominantly clayey silt. Numerous rivers from the Western Ghats discharge freshwater into the KBW, especially during the SWM. Due to the narrow sea inlets and the microtidal nature of the KBW, flushing is a relatively slow process here favouring

heavy siltation^{52–57}. The total annual sediment yield from the rivers into the KBW is estimated to be 32 million tonnes/year, which significantly decreased the mean depth of the KBW over the last 8 decades from 6.7 m to 4.4 m^{58–60}. The depth of the KBW has reduced over time owing to excessive sedimentation, as evidenced by a considerable decline in its water-holding capacity from 2.4 km³ in 1960 to 0.6 km³ in 2000 (Padmakumar 2002, 2019; Ramani et al., 2010). Reclamation and flow restriction through barrages contributed significantly to the siltation of the KBW in the Vembanad region, and it has been shown that if the siltation continues at its present rate, the KBW will disappear in 50 years, transforming into extensive swamps^{58,59}.

Benthos composition and distribution

Macrobenthos community in the KBW was composed of polychaetes, tanaidacea, bivalves, gastropods, decapods, and harpacticoids. Polychaete was the dominant macrobenthic group regardless of the seasons, with the major families Terebellidae, Nephtidae, Nereididae, Capitallidae, and Onuphidae. Many studies in the past too showed Polychaeta as the most predominant macrobenthic group in the KBW followed by bivalves, and gastropods^{61–66}. The dominant species of polychaetes found in the current study were *Capitella capitata* Fabricius, 1780, *Heteromastus similis* Southern, 1921, *Parheteromastus tenuis* Monro, 1937, *Prionospio cirrobranchiata* Day, 1961, *Prionospio cirrifera* Wirén, 1883, *Pagurapseudopsis kochindica* Pandiyarajan & Biju, 2017, *Pagurapseudopsis gymnoptobia* Barnard, 1935, *Ctenapseudes Indiana* Pandiyarajan & Biju, 2017, *Ctenapseudes chilensis* Chilton, 1924, and *Tanais* sp. Macrobenthic abundance during all three seasons is presented in Fig. 4, which has been statistically represented in the nMDS plots in Supplementary Fig. 1. Cluster/SIMPROF overlaid nMDS plots show spatial grouping of locations based on macrobenthos abundance (SIMPROF $P < 0.05$). Stress levels < 0.1 in nMDS plots indicate a significant grouping of locations. Seasonally, the macrobenthic abundance was the highest during the PRM and the lowest during the SWM. During the PRM, the highest abundance of macrobenthos was found upstream in Cluster 4 (av. 1845 ± 135 No.m⁻²). Higher abundance was also found in Cluster 2 in the downstream (av. 1120 ± 402 No.m⁻²) and Cluster 3 in the midstream (av. 982 ± 187 No.m⁻²) (Fig. 4a). Macrofauna abundance during the SWM was the seasonal lowest with relatively high abundance found in locations in Cluster 2 (av. 780 ± 184 No.m⁻²) that represented the rest of the region other than the inlet locations in Cluster 1 (av. 375 ± 114 No.m⁻²) (Fig. 4c). Macrofauna abundance during the NEM was the highest in Cluster 3 locations in the upstream (av. 1540 ± 153 No.m⁻²) followed by the Cluster 2 locations in the midstream locations (av. 524 ± 107 No.m⁻²), Cluster 1 locations in barmouth region (av. 364 ± 87 No.m⁻²) (Fig. 4e). Regardless of seasons, cluster 1 inlet locations had the lowest macrofauna abundance. The general trend in the current study corroborated with many past studies on the seasonal distribution of macrobenthos showing a marked decline in macrobenthos during the SWM^{25,61&64}. Desai and Krishnankutty⁶¹ also showed that the recolonization of macrobenthos after their sharp decline during the SWM occurs during the early NEM and then their maximum abundance during the PRM.

Black clam seasonal abundance and distribution

The seasonal abundance and distribution of black clams in the KBW are shown (Fig. 4, Supplementary Table 1), which is represented in terms of nMDS plots in Supplementary Fig. 1. nMDS plots with cluster/SIMPROF overlays that show the spatial grouping locations (SIMPROF $P < 0.05$) according to the abundance of black clams. The significant grouping in nMDS plots is indicated by stress values less than 0.1. The spatial pattern of variation in black clam abundance values was represented by overlaying them as bubbles. Black clam (bivalve) was the third abundant group in the macrobenthic community. The trend in the seasonal abundance of black clam was very similar to the total macrobenthos with their highest abundances during the PRM followed by the NEM. Their seasonal lowest abundance was found during the SWM when the entire KBW was heavily influenced by the enormous river discharge. During the PRM, their highest abundance was found in the midstream locations in Cluster 4 (av. 1500 ± 277 No.m⁻²), followed by the midstream locations in Cluster 3 (av. 786 ± 165 No.m⁻²) followed by the downstream locations in Cluster 3 (av. 206 ± 85 No.m⁻²) (Fig. 4b). The lowest seasonal abundance of black clams was found during the SWM with a relatively high abundance in Cluster 2 (av. 520 ± 140 No.m⁻²) representative of the rest of the locations other than the inlet area (Fig. 4d). During the NEM, their highest abundance was in Cluster 3 locations in the upstream (av. 780 ± 157 No.m⁻²), followed by Cluster 2 locations in the midstream (av. 125 ± 37 No.m⁻²) & Cluster 1 locations in the inlet region (av. 80 ± 24 No.m⁻²) (Fig. 4e). Suja and Mohamed³ viewed that the black clam production in the KBW declined over the last many decades and attributed it to the long-term hydrographical changes in the KBW, which appears to be reasonable as the current study also observed a significantly lower population density of black clams as compared to the abundance recorded many decades ago which ranged from 2860 to 4620 No.m² (Rasalam and Sebastian⁶⁷). The filter-feeding black clams normally feed algae, bacteria, and zooplankton. However, a high load of fine sediments (clay) may inhibit the filter-feeding process^{68,69}, which in turn reduces the growth of clams in the mid-estuary during the SWM.

Studies showed that sexual maturity in black clams attains at a length of 11–15 mm and their reproductive stages generally include the undifferentiated stage (adult), early gametogenesis, late gametogenesis, mature, partially spent, and fully spent^{7,9&70}. Studies also showed that the spawning peaks of black clams in the KBW occur twice a year, in NEM and a PRM^{3&7}. Based on the larval abundance in the KBW, Arunpandi et al⁹ showed that the black clam is a continuous breeder as their larvae were found all through the sampling during the different seasons. This observation was supported by the current study since all the size classes of the black clams were found in the KBW regardless of seasons (Fig. 5 a). It was also observed in the current field sampling that all size classes of black clam have been commercially exploited especially upstream of the KBW regardless of season as the heaps of the shells of different size classes were a usual feature in the adjacent landing places (Fig. 5b–e). The percentage contribution of different size classes of black clams in different clusters of locations is presented in Fig. 5 (f–h) & Supplementary Table 2. The largest percentage contribution was from the size class 9–16 mm

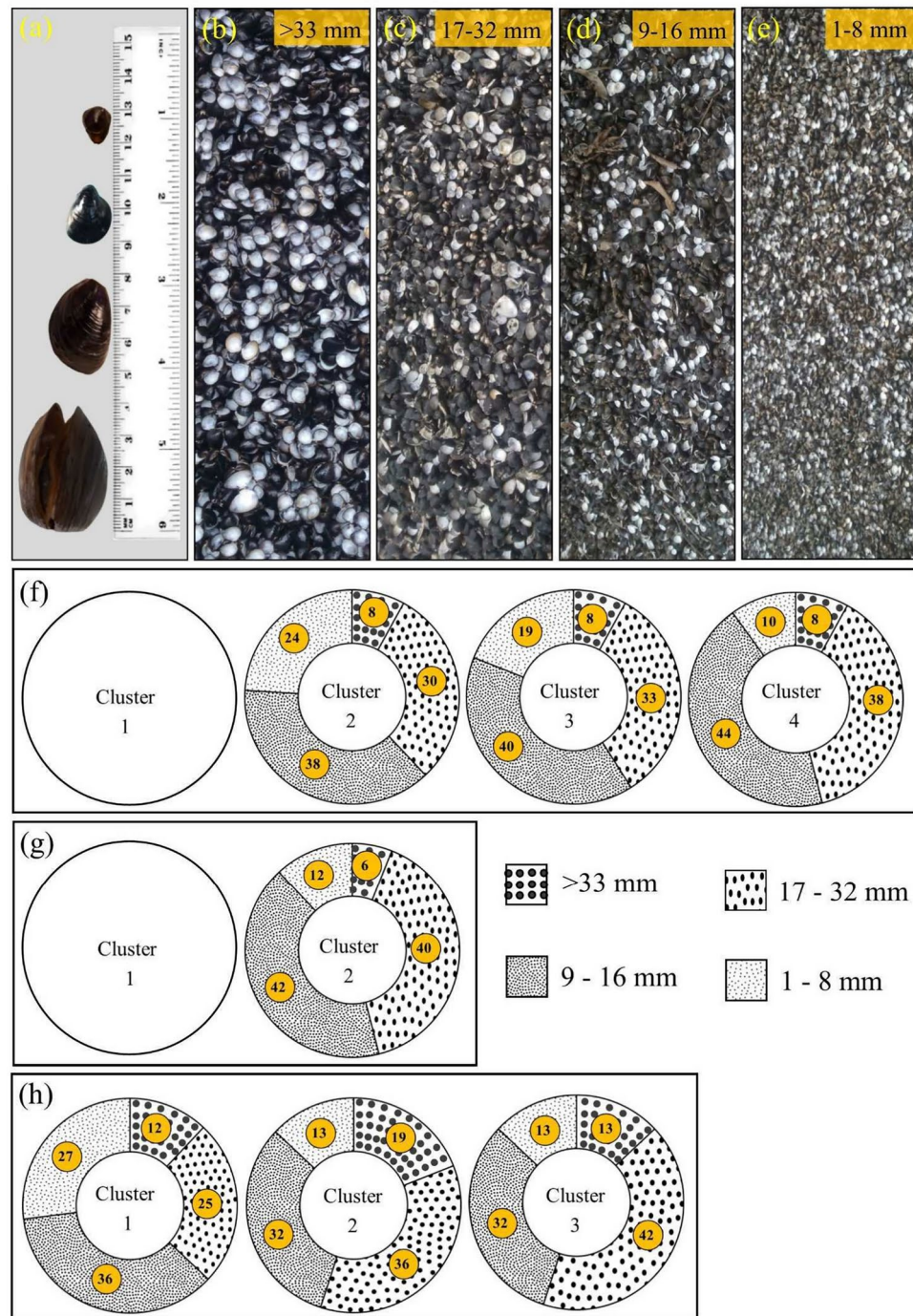


Fig. 5. Panel (a) different size classes of black clam, panels (b-e) heaps of shells of different size classes landed on the banks during the field sampling. The percentage contribution of different size classes of clams in sampling locations during the (f) PRM, (g) SWM and (h) NEM. Photograph (Fig. 5a-e) was taken by the corresponding author Dr. R. Jyothibabu; rjyothibabu@nio.res.in; rjyothi1@gmail.com. Plots (Fig. 5f-h) are made in Grapher, V 7.2. (Golden Software, USA; <http://www.goldensoftware.com/>).

and 17–13 mm regardless of seasons. The immature 1–8 mm size class of black clam was found to be higher during the PRM and NEM periods probably the result of their peak spawning during those periods. Similarly, the largest size class (> 33 mm) was found more abundant during the NEM compared to the PRM and the SWM.

Preferred ecological condition of Black clam

Because the salinity and the bottom sediment texture are the principal environmental variables controlling macrobenthic/ black clam abundance in estuaries^{68,69}, here we demarcate the most optimal levels of these variables for black clam in the KBW. The multiple correlations of salinity and sediment texture with the abundance of

macrofauna and black clams in the KBW regardless of seasons and during the three different seasons have been presented as RDA plots in Fig. 6. RDA explains the interrelationships between hydrographical parameters and biological parameters. RDA results were presented as the Triplot. The sum of all canonical eigenvalues was 0.457. Eigenvalues represent the percentage of influence of the environmental parameters (salinity, sediment texture) on the distribution of biological parameters⁴⁸. This study results represent salinity and sediment texture and explain the 45.7% variations of the Macrobenthos and black clam distribution in the study area. The first two axes represent 98.8% of the species and environment correlation. The attribution model result of salinity was overlaid to represent the distribution of biological variables (black clam abundance) related to salinity. Attribution models confirmed that black clam distribution is closely related to salinity and their high proportions are in mesohaline conditions. The RDA in panel (a) regardless of seasons showed salinity, clay, and silt parameters axes oriented towards the right side of the plot whereas, the axes of sand, macrofauna, and black clam were oriented towards the left side of the plot. What is clear in this panel is the increased abundance of macrofauna and black clams towards a high percentage of sand and oligohaline to mesohaline salinity (salinity < 10). To understand the seasonal features more clearly triplot representations of different sections have been presented in subsequent panels (b–e). As stated before, a true estuarine feature exists in the KBW only during the PRM and NEM wherein well-defined zones of euhaline, polyhaline, mesohaline, oligohaline, and limnetic conditions prevail along the system from the inlet to the upstream regions. It is clear in the current study and literature that PRM and NEM

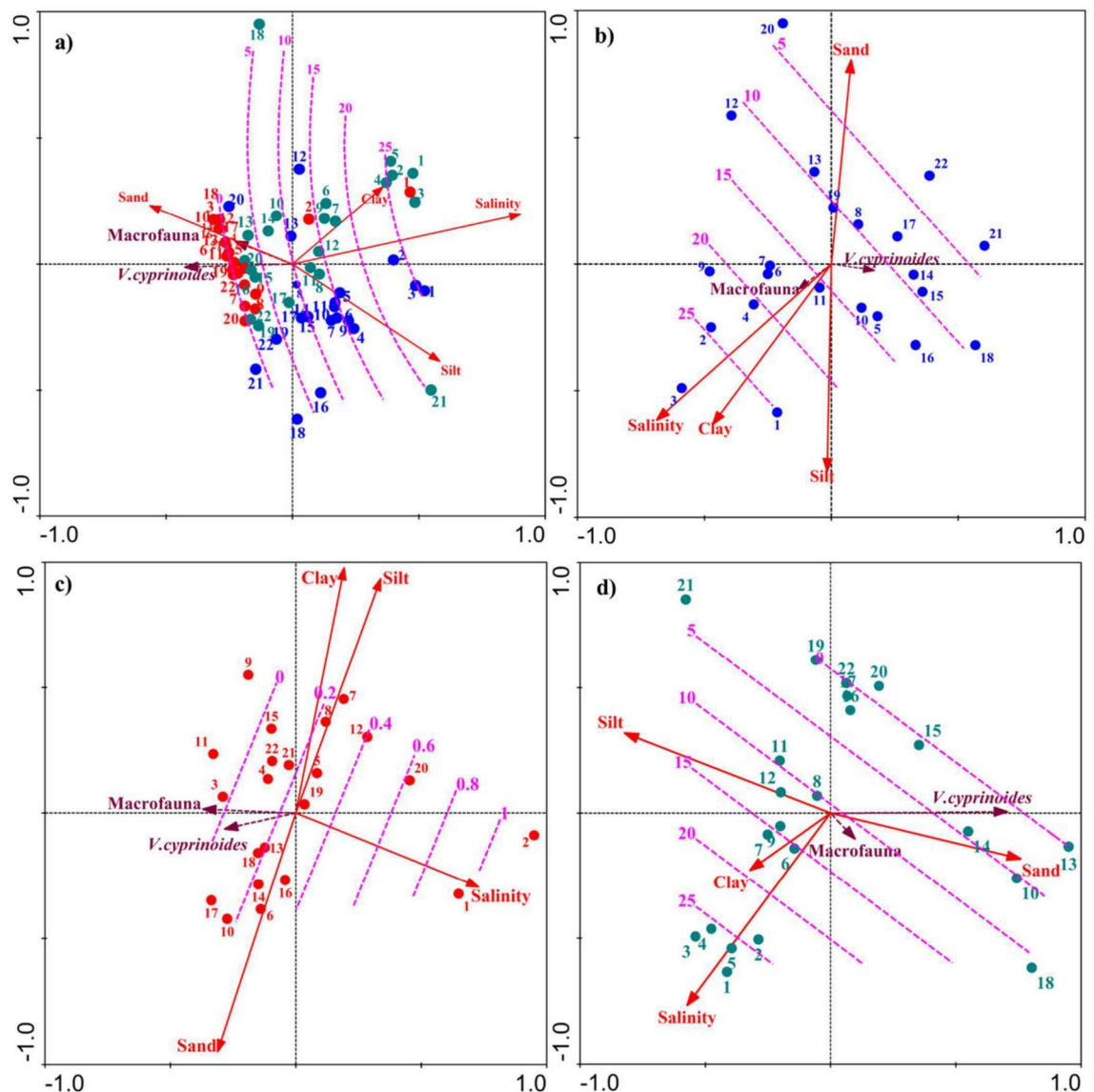


Fig. 6. RDA Triplots showing the ecological linkage of macrobenthos and black clam with salinity and sediment texture in the KBW. Panels (a) regardless of seasons (b) PRM, (c) SWM and (d) NEM. The different coloured circles in panel (a) correspond to sampling during the three different seasons presented in panels (b) to (d). Plots are made in by CANOCO 4.5 plot using the standard procedure of the Leps, J. & Smilauer, P.S46 (<http://www.microcomputerpower.com/default.html>).

are the most conducive seasons for the proliferation of macrobenthos in general and black clam in particular as their abundance during these seasons is found to be much higher than the SWM^{3&69}. In the RDA Triplot for the PRM, the axis of salinity was oriented on the left side along with increasing gradients of silt and clay representing mostly the downstream locations (Fig. 6b). The gradient axis of sand and silt were positioned in the opposite directions slightly on the right side and left side of the Triplot, respectively. The increasing gradient axis of macrobenthos was oriented on the left-hand side of the plot closely aligned to the salinity and clay axes. On the other hand, the axis of black clam was oriented to the right side of the plot almost equally aligned towards sand and silt axes and locations with mesohaline conditions.

During the SWM, the KBW was completely occupied by freshwater except in the Kochi inlet locations due to heavy rainfall and river discharge. The salinity axis was oriented to the right side of the Triplot towards inlet locations 1 & 2 (Fig. 6c). The axis representing the sand in the bottom sediment was oriented slightly on the left side of the plot whereas axes of clay and silt were oriented slightly towards the right-hand side. The axes representing the abundance of macrobenthos and black clam were oriented to the left, more closely aligned to the sand dominant, and locations with oligohaline to limnetic conditions. The affinity of macrobenthos and black clams towards limnetic conditions during the SWM appears to be the result of the intense physical forcing of the river discharge which transforms almost the entire KBW into a freshwater lake^{22&51}. This has been corroborated by the lowest seasonal abundance of macrobenthos and black clams in particular observed in the current study in the KBW during the SWM and also in many past studies as well^{22&51}. In the triplot representing the NEM, the increasing gradient axis of salinity was oriented towards the right side of the plot (Fig. 6d). The axes representing the clay and silt were also oriented in the same direction, whereas the axis representing the sand was towards the opposite side of the salinity axes on the left side of the Triplot. The axes of the total abundance of macrobenthos and black clams were oriented on the right side of the Triplot, indicating their general preference for the sand-dominant bottom substratum. During the PRM and the NEM when the KBW was truly estuarine, black clams showed their salinity preferences are from mesohaline to oligohaline regions with sand-dominant sediment texture. Among these two, the distribution of black clams showed their enhanced preference towards oligohaline conditions, whereas the total macrofauna was more closely aligned to the mesohaline conditions.

Based on the current and historical data before the establishment of TB, the long-term trend in the changes in salinity and bottom sediment texture in the KBW is presented here. The general trend in the spatial variations in salinity distributions in the KBW during different seasons before and after the installation of TB is presented in Fig. 7. It is very clear that the salinity intrusion into the KBW drastically decreased after the establishment of TB regardless of seasons, in other words, the salinity front receded much to the downstream since the commissioning of TB in 1975. This feature was the most prominent during the PRM when mesohaline salinity levels were found even up to the extreme south Vembanad before the establishment of TB. These salinity levels receded to the south in the midstream due to the establishment of TB. The change in the composition of the bottom substratum in the KBW after the establishment of TB is presented in Fig. 8, where a comparison of the current NEM data with the one before the establishment of TB is presented. A notable change in the bottom sediment after the establishment of TB in the KBW was an increase in clay content in place of sand which was the second dominant component before the establishment of TB. This was very clear in upstream Vembanad where sandy silt and silty sand prevailed before TB, which were transformed into clayey silt after TB. This can be directly linked to the stagnancy and the decrease in the dynamicity (low energetic condition) of the KBW caused by the functioning of TB⁵⁰. It is well established that, in general, the particle size of sediments is larger in sedimentary deposits in high-energy environments while fine-grained sediments tend to erode in high-energy environments and get deposited in low-energy environments. Fast-flowing water and waves let larger materials settle and get deposited first while finer materials are carried away and deposited in calmer environments which are low-energy environments⁷².

Multiple anthropogenic stressors of black clam

Environmental modifications of natural water flow restrictions through barrages could adversely affect the clam production potential and slowly affect their drastic decline in aquatic systems^{73,74}. Undeniably, the establishment of TB in 1976 adversely impacted and altered the black clam abundance distribution in the KBW^{3,7&9}. A summary of the general understanding of the ecology of the black clam in the KBW reflected in some of the past studies is shown in Table 1. Similarly, a comprehensive assessment has been presented on how TB introduced multiple stressors on black clam distribution in the KBW a summary of which is presented in Fig. 9.

- (a) Salinity is the major factor determining black clam distribution in the KBW^{3,7,9&64}. Spatial changes in salinity in the KBW caused by TB are the primary human stressor on the decline of black clams in the KBW especially in the upstream Vembanad. How the salinity distribution trend changed spatially due to the establishment of TB is presented in Fig. 7. At large, the establishment of TB significantly decreased the saline water intrusion into the KBW through the Kochi inlet, especially during the PRM. As a result, the mesohaline to oligohaline salinity levels in the upstream Vembanad (southern) region before TB have been relocated much towards the midstream after the TB. The current study also corroborates the earlier view that completely freshwater conditions are not conducive for black clam production in the KBW and most of their harvest takes place in salinity zones from 2 to 10 ppt^{3,7&9}. Sivankutty Nair⁴, showed that the growth of black clams is either retarded or arrested during the SWM and this feature was well reflected in the current sampling as well, as their lowest abundance in the KBW was recorded during the SWM when the system behaved like a freshwater lake due to the enormous freshwater discharge. High freshwater input and heavy siltation can lead to mass mortality of clams⁷⁵. Studies showed that the optimum salinity for spawning of black clams is about 10–12 and a change in salinity is the most important factor that triggers spawning^{3,7&9}. Considering the above observations, it can be comprehended to understand how the closure of TB during

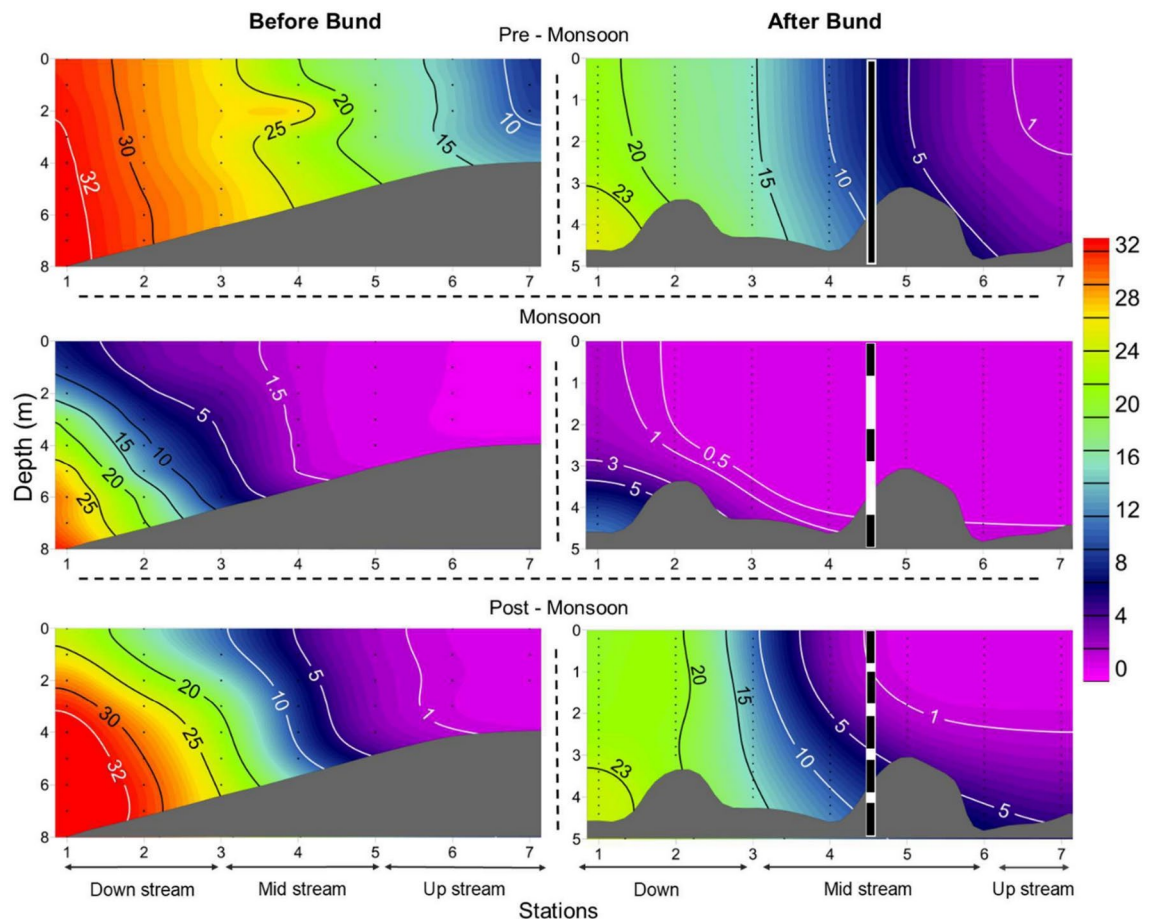


Fig. 7. Altered salinity regimes in the KBW due to the establishment of TB. Salinity distribution before TB (Haridas et al., 1975) and after TB (current study) are presented. The vertical dotted lines represent the seven sampling locations considered for this long-term comparison and each dot in the vertical lines represents a data point. Plots are made in Surfer v16. (Golden Software, USA; <http://www.goldensoftware.com/>).

the PRM and NEM influences the black clam stock in the Vembanad upstream. The closing of the shutters of TB after the monsoon prevents the entry of saline waters into Vembanad upstream, while it increases the salinity on the northern side of the TB. This causes restrictions in the natural formation of the extended mesohaline region in the upstream Vembanad, most ideal for the black clam spawning. This eventually causes a low spawning rate and production of larval black clam and thereby a decline in adult black clam stock in the upstream Vembanad.

- (b) The texture of the bottom sediment is another important environmental variable that governs the black clam distribution in aquatic systems^{68,69}. Recently, Arunpandi et al.⁹, explained the process of spawning and spat fall of black clams in the KBW and showed how the spat fall and subsequent development of black clam beds are being formed. After completion of the larval development, and pediveliger stage black clams settle into the bottom and the young clams in the bottom would naturally prefer a conducive bottom substratum. The current study showed that black clam prefers sand-dominant bottom sediments regardless of season (Fig. 8). The filter-feeding black clams normally feed algae, bacteria, and zooplankton⁷⁶. It is known that fine particles accommodate more organic matter, and thus they inhibit the filter-feeding process, which in turn, reduces the growth of black clams. The long-term change in the sediment texture in the KBW showed an increase in the contribution of clay material and a decrease in the contribution of sand and this can be attributed to the low-energy conditions created by TB. Low-energy conditions support increased settling of finer clay particles in the KBW which is less conducive for the proliferation of black clam compared to the sand. It is known that the Vembanad region, which had highly productive clam beds before the establishment of TB, has become barren after the establishment of TB and caused the severe dislocation of thousands of clam fishers^{2,5&7}. The black clam prefers a mesohaline/limnohaline and sand-dominant substratum for optimum growth and survival. The TB has prevented the salinity entry to the southern part of the estuary, thus depriving of the above conditions for the clam growth. Concluding the preceding account, it can be concluded that the major shift in the clam beds from the Vembanad to the midstream of the KBW after the establishment of TB is a combined effect of the northward spatial shift of mesohaline regimes and sand dominant bottom. These conducive conditions of black clam co-occur extensively and more frequently over seasons in the midstream compared to the upstream Vembanad after the establishment of TB.

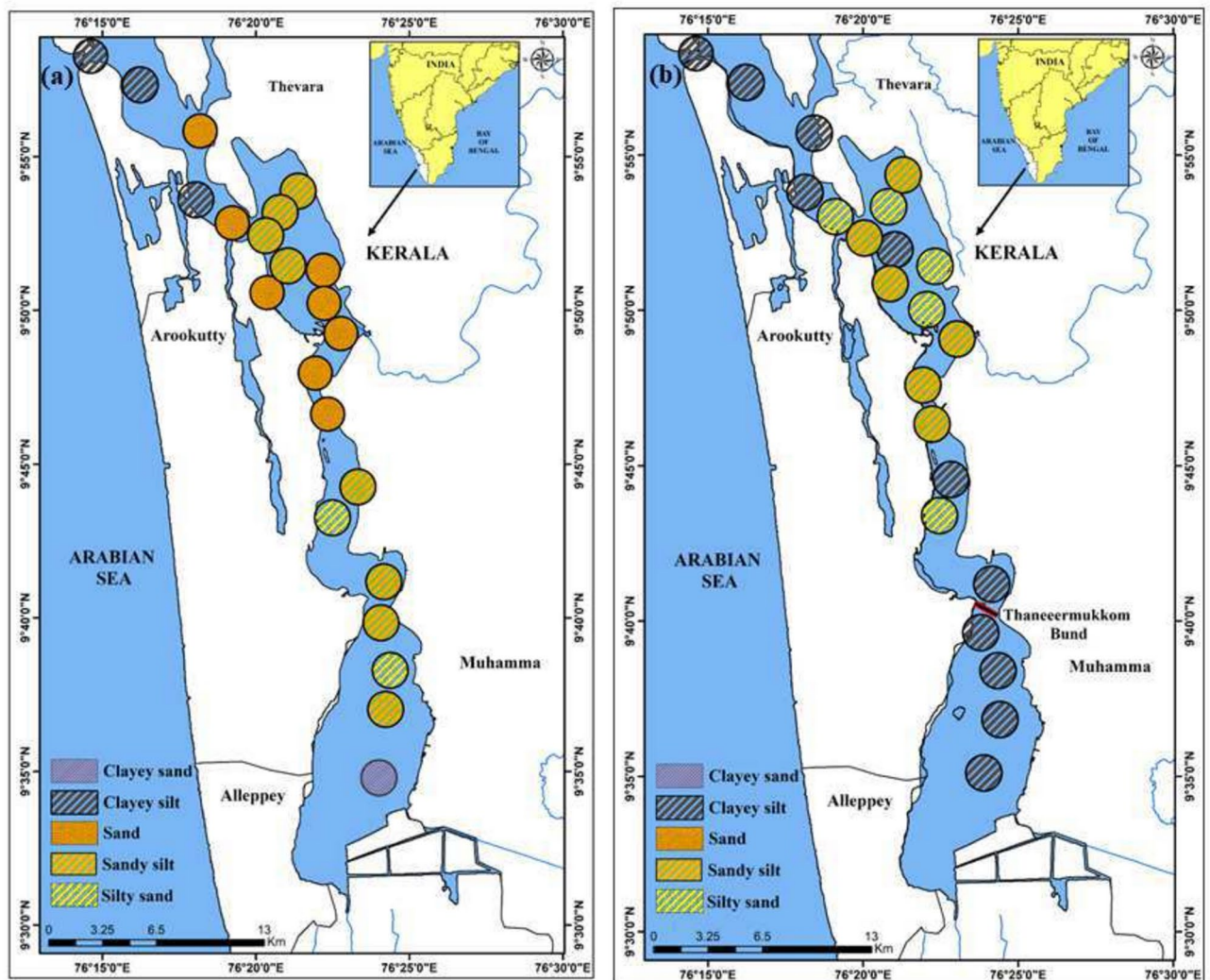


Fig. 8. The sediment texture in the KBW during the NEM (a) before TB (Murthy & Veerya, (1972) and (b) after TB (current study). This map (Fig. 8) was created using QGIS v3.38.1-Grenoble (QGIS Development Team, 2017), following the attribution guidelines. QGIS Geographic Information System. Open Source Geospatial Foundation Project (<http://www.qgis.org>).

- (c) The closure of TB from January to May every year changes the natural salinity distribution and results in drastic ecological degradation in the Vembanad, affecting the distribution and survival of the living resources. Also noted that the opening and closing of the shutters of TB exert salinity shock and massive mortality of black clams in the KBW. The opening of the TB shutters causes salinity shock to the black clam living on both sides of the barrage, and it is harmful to black clams as they are sensitive to sudden changes in the salinity of an environment⁷¹. The black clam has wide tolerance and the ability to survive from freshwater to salinity around 20 when they are acclimatised with gradual variations in salinity as is the case of their distribution in the KBW during different seasons. It was observed that black clam survives in a stressful condition in freshwater and high saline conditions in Kochi as indicated by their stunted growth during such conditions^{4,7&8}. However abrupt changes in salinity regimes on both sides of TB due to the closing and opening of the shutters cause massive mortality on both sides of TB^{7&9}. Some industrial wastes pollute areas in the southern region and also sewage pollution from urban and semi-urban townships along the banks of KBW causes pollution through inferior water quality. Frequent mechanized dredging activities result in the suspension of finer sediments causing the smothering of clam beds and affecting settlement of seed in these areas.
- (d) The spread of water weeds in several areas of the KBW hampers the black clam exploitation for nearly 2–3 months each year^{2,3}. Recently, Jyothibabu et al., (2022) reviewed the anthropogenic causes of eutrophication and the massive spread of water weeds in the KBW (Supplementary Fig. 2). This study pointed out the following relevant points (a) Over many decades, the KBW experienced large-scale flow restrictions through the construction of barrages, spillways, and numerous landfilled roads, all of which eventually contributed to stagnation and eutrophication, (b) there are numerous non-point nutrient sources in the KBW

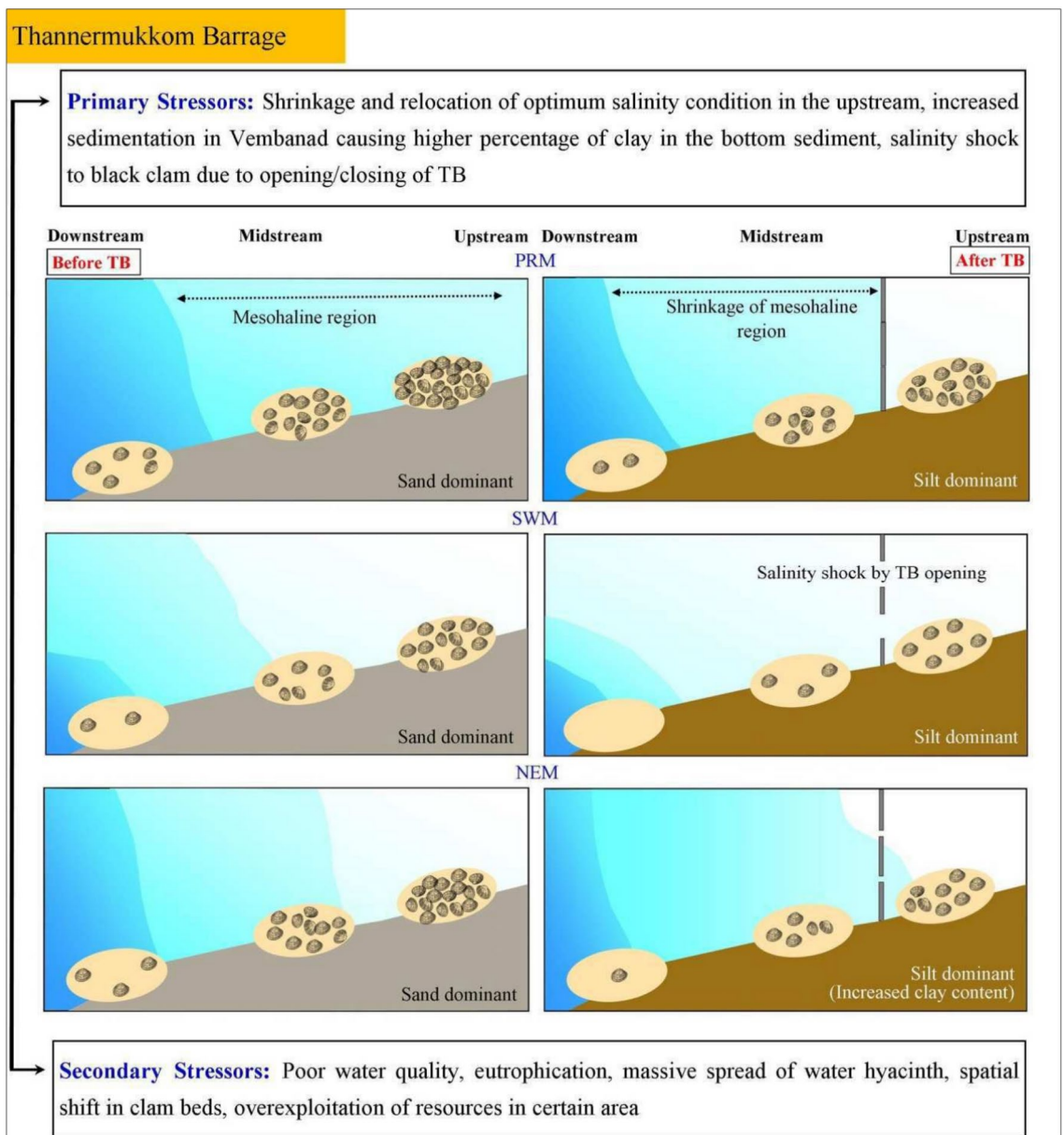


Fig. 9. A schematic of the multiple stressors of black clam due to the introduction of TB in the KBW. This image was drawn using GIMP 2.10.38. GIMP software comes under GNU General Public License.

associated with agriculture, municipal and domestic sewages and (c) the numerous land-filled roadways constructed across the low lying areas associated with KBW increase the stagnancy and eutrophication. The human-caused flow restrictions eutrophication in the KBW over the years created a favorable environment for the water weed growth (Jyothibabu et al., 2021). Water weeds flourish in the Vembanad region due to the prevailing limnetic to oligohaline conditions over the seasons. They spread to the entire stretch of the KBW during monsoon, when the shutters of TB are kept open. The studies showed that the dense beds of floating macrophytes can negatively impact aquatic invertebrate and fish communities by reducing light penetration into the water column and inhibiting gas exchange between the water's surface and the atmosphere^{77–80}.

- (e) There is a general lack of regulation to arrest the exploitation of juvenile clams and the overexploitation of certain clam beds in the KBW. Suja and Mohammed³ showed the lack of effective government regulations to conserve the fishery of black clams in the KBW, except for the general instruction given that juvenile clams should not be exploited. Also, the above instruction to conserve young ones is only lightly enforced as there is no administration set up in place to monitor and implement the management instructions. The black clam areas were once open to all fishermen, but gradually local groups have been trying to keep other fishermen out of their harvesting areas, and the fishery in the lake is becoming more compartmentalized. Even though widespread overexploitation signs of black clams in the KBW have not been reported³, the

exploitation of juvenile black clams in many areas is alarming. However, a recent population characteristics study of black clams in the KBW by Aswathy and Parvathi⁸¹, based on population parameters as a tool to determine their exploitation status, showed their overexploitation in the midstream of the KBW. During the field sampling of the current study, we witnessed heaps of shells of juvenile clams landed on the shore for commercial use (Fig. 5 d & e). Also dumping of juvenile clams for the decomposition of meat and subsequent retrieval of shells for the lime industry leads to pollution which is environmental/health hazard and the incompletely putrefied meat is a matter of grave concern². Another practice noticed in some areas is the transplantation / semi-culture wherein fishermen collect the spat and young ones of black clams from areas of their dense settlement and transplant them to places (near their homes/homesteads) where no spat fall has occurred. This practice of fishermen is mainly to facilitate the harvesting/ picking of black clams at the time of their choice and they believe that this practice helps to prevent the destruction of the baby clams due to the effluents released from shrimp peeling sheds and areas where fishing is hampered by clogging of weeds². Essentially, all these practices are different dimensions of human stressors on the black clam resource in the black clam distribution in the KBW.

The rest of the world must be taken into consideration to observe similar conditions where saltwater barrages affect the natural distribution of living resources. In this context, it is important to consider Bice et al, who examined the negative impacts of tidal barriers on the fish community in estuaries worldwide, including those in the US, Australia, and the Netherlands, as well as the remediation initiatives that are presently taking place in these areas. Although the ecological effects of barrages vary depending on their design, purpose, and geographic location, the aforementioned study supported many of the findings made in the current study and showed that they generally affect fauna through three main mechanisms: (a) direct obstruction of movement; (b) loss of upstream tidal flux and estuarine habitats; and (c) modification of downstream estuarine habitats due to altered tidal flux and decreased freshwater flows.

The overall environmental degradation of KBW and some of the remedial measures to protect the system have been presented in one of the most recent publications from our research group that dealt with water weed proliferation¹¹. This study showed that the operation of TB installed in the VBL should be re-examined holistically in light of the strong scientific evidence supporting the detrimental ecological effects they cause. The barrage is unquestionably a major contributing element that redistributes the salinity regimes in the system and acts now as an environmental stressor in some regions causing decline and spatial shift in the availability of fauna. It is impractical to remove the barrages at this time because they serve as bridges and roads that allow transportation between otherwise disconnected regions and provide some crucial services to the local population, such as preventing saline water intrusion into upstream freshwater reservoirs and paddy fields^{82–85}. A group of specialists that examined salinity and flood control scenarios in the VBL in 2011 proposed that it is possible to keep the TB shutters open daily for a set amount of time. Allowing the natural saline water intrusion and tidal flushing is a very constructive idea, that will also help to the reestablishment of the natural clam beds in the upstream south of TB. The required levels of salinity intrusion that should be permitted to enhance the black clam population upstream of the TB should be determined scientifically based on long-term data sets.

Conclusion

This study presented the distribution and ecology of black clams in the KBW and assessed the multiple anthropogenic stressors acting on them. The black clam was found widespread in the KBW and they generally prefer the midstream and Vembanad in the upstream having mesohaline to oligohaline salinity and sand-dominant bottom substratum. Perennial clam beds in the KBW were found in the midstream region where the conducive environmental conditions of salinity and bottom substratum prevailed. Many researchers in the past showed a drastic reduction in black clam production in the upstream Vembanad of the KBW after the establishment of TB. We showed here that the spatial shift of the conducive salinity and substrate conditions of black clam to the midstream from the upstream Vembanad is responsible for it. This is caused by TB which creates a significant spatial shift in the distribution of salinity when it is closed. Based on the literature, an assessment of the current hydrography and sediment texture data with those before the establishment of TB revealed the existence of multiple anthropogenic stressors on black clam distribution in the KBW, especially in the upstream Vembanad which include (a) a considerable shrinkage of the mesohaline condition that is conducive for black clam spawning, (b) change in the bottom conditions with an increase in the percentage of clay after the establishment of TB (c) the salinity shock and massive mortality of black clam on both sides of TB during opening and closing of the TB shutters. Several secondary stressors of TB on black clam are caused by poor water quality, eutrophication, and massive spread of hyacinth mats and all these contribute to the decline in black clam production and their overexploitation in certain areas.

Data availability

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request through the Director, CSIR- NIO, Goa.

Received: 10 September 2024; Accepted: 13 February 2025

Published online: 15 May 2025

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Acknowledgements

The authors thank the Director, CSIR- National Institute of Oceanography, Goa for facilities and encouragement. We thankfully acknowledge all our colleagues in CSIR- NIO, RC—Kochi, India, who helped in carrying out the fieldwork. This work was initiated as a part of the OCEAN FINDER program of CSIR-NIO, India under the leadership of Dr. A.C. Anil. This is CSIR-NIO Contribution 7424

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Funding

This work was funded by CSIR as a part of the OCEAN FINDER program of CSIR-NIO, India.

Declarations

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-025-90573-4>.

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