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Drivers of change in the epifaunal assemblages associated with intertidal macro-algae at the Mangrove site south Safaga, Egypt, Red Sea

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ABSTRACT

The present study aimed to study the effects of intertidal habitat complexion on algae-epifaunal communities in the poly-zoned coastal mangrove site south Safaga on the Egyptian Red Sea coast. The study focuses on the effects of main intertidal primary habitats along with the facilitation of habitat cascades on the focal/inhabited organisms, which represented here by algae-epifaunal organisms. The intertidal main primary zones (habitats) in the study area including 1- outer mangrove tree zone, 2- inner flat back reef area, and 3- A sand lagoon in between the previous two zones. However, different algae species that either stand-alone or mixed by other algae species in patches were considered here as secondary habitat-formers.

Results indicated that a total of 64 epifaunal species were recorded in different intertidal macro-algae habitats and such faunal diversity and abundance affected mainly by the primary habitat in which approximately 50% of the current epifaunal species showed specificity to only one primary habitat. Results also detected that habitat facilitation was strongest when the secondary habitat-former was most functional for the epifaunal organisms in feeding and hiding from predators. The present study suggested that such effects of secondary habitat formers on the algae-epifaunal diversity are depending essentially on the primary habitat construction and its zone characteristics. In consistence, the results suggested that predation effort is the main factor controlling the distribution of algae-associated organisms depending on how far such organisms can benefit from the special shape and construction of each algae habitat-unit in protection and hiding from predators.

INTRODUCTION

The Red Sea is characterized by the presence of more than one ecosystem within its coastal areas. These ecosystems included the most famous coral reef, sea grass, and mangrove in addition to sandy and rocky beaches **(El-Nagar *et al.*, 2017)**. Among all these different types of ecosystems and habitats, a vast number of marine species were found to be associated with a single and/or multiple habitats. The most repeated habitat among those ecosystems is the seaweed habitat **(Abdel Razek *et al.*, 2014, Hellal *et al.*, 2017, Shaban *et al.*, 2016).**

Understanding the assemblages of organisms is based on the quantitative description of patterns of distribution and abundance of species **(Underwood *et al.*, 2000; Pereira *et al.*, 2006** and **Shaban & Abdel-Gaid, 2019)**. The boundaries in an ecological level are often attributed to climatic conditions (**Wardell-Johnson & Roberts 1993** and **Shaban & Abdel-Gaid, 2019**) or antagonistic relationships of competition and predation (**Hersteinsson & McDonald 1992**). Furthermore, food preference and habitat complexity may also play an important role in the distribution and abundance of marine organisms **(El-Naggar *et al.*, 2019** and **Mona *et al.*, 2019).**

A habitat cascade is a common example of a facilitation cascade **(Mouritsen, 2004** and **Altieri *et. al.*, 2007)** where indirect positive effects on focal organisms are mediated by successive formation or modification of biogenic habitat. A habitat cascade is composed of at least three organisms: the main habitat and a secondary habitat-former or modifier and a focal organism that utilizes the secondary habitat-former or modifier. Secondary habitat-formers can be attached to entangled around or embedded within the primary habitat-former **(Altieri *et. al.*, 2007; Thomsen *et al.*, 2010).**

Mangrove and algal communities occur closely associated with each other in the environment by different habitat complexity patterns; either the algae attached by pneumatophores of the mangrove **(Proches & Marshall, 2002)** or attached to the mangrove sediment substrate **(Wee & Corlett, 1986** and **Sen & Naskar 2002).** Nutrients come from Mangrove area enrich the adjacent coastal zone by seaweeds which become denser and variable in some cases **(Alongi, 2002).**

The area of the grey mangrove, *Avicenna marina*, stands protected area located at 17^{th} km south Safaga city in the Egyptian Red Sea coast. It is considered **a** clear example of habitat complexity in which many different marine habitats placed close each together in very small area comprising mangrove tree, mangrove pneumatophores and mangrove mudflat. This unique ecosystem will be added here to the usual Red Sea coastal ecosystems including Red Sea coral reef barrier and its flat back-reef in addition to sand lagoon lie between back reef and mangrove stand **(Dworschak & Pervesler, 1988)**. So, the present study aimed mainly to study the effect of the variability of primary intertidal habitat (especially when mangrove habitat circumstances added to the coastal system) on the structure, abundance and diversity of algae-associated epifauna.

According to different previous studies, algal specific shape and texture in addition to algal composition (in algae patches) play an important role in algae epifaunal assemblage structure and dynamics **(Edgar & Klumpp, 2003** and **Shaban, 2012)**. Therefore, the present study aimed also to study the mangrove coast primary habitat variability as well as the algae composition, as the algae-formers cascade habitats, on the focal epifaunal animals in terms of their diversity and abundance.

MATERIALS AND METHODS

Study area

The present study was conducted at the mangrove stand protected area about 17 km south Safaga city, which include three successive habitat sectors (**Fig. 1**). The sectors including (from the outer to the inner):

(A): mangrove stand area (34^0 00′ 43.3″ E and 26^0 36′ 55.3″ N), consists of about tens of the grey mangrove *Avicenna marina*, trees (moderate in size and each one surrounded by a dense respiratory roots with fine sand to muddy soil in between).
(B): Sandy lagoons sectors (34^0 00′ 44.5″ E and 26^0 36′ 55.4″ N), whereas such lagoons consists either due to the irregular back reef end line or due to the enlargement of any Mangal tree naked area.
(C): Back reef area (34^0 00′ 48.9″ E and 26^0 36′ 55.2″ N), its relatively wide and flat structure lie before reef crest and in turn reef slope.

Water temperature, salinity and pH were measured instantly in the field at the collection time according to standard methods. However, determination of organic matter in sediment was carried out, by loss on ignition according to **Kumada (1988)**. Average values for each previous parameter were determined for each primary habitat sector and presented in **Table (1)**.

Sampling, Sorting, and Identification

Algae samples were collected in spring 2019 to figure out the effects of different habitat variables on the structure of algae-epifaunal communities. The sampling was done during low tide at each predefined marked habitat sectors. Fifteen algae variables were sampled belonging only three algae species: *Cystoseira*, *Saragassum and Padina* algae species. Sampling in each main habitat sector also comprising the mixture samples with two and three mixed-algae species (found very close and entangled). Algae samples were cut off manually from the hard substrate and were then placed within a plastic bag. Generally, the size of each collected algal sample weighed around 400 g, and at least 3 samples from each individual habitat sector was taken at the same time rang. The collected samples were re-opened again, and 10% of seawater formaldehyde plus 1% Eosin was add and labeled.

In the Laboratory, the collected samples were poured into a 1L glass beaker. The plastic bag of the sample was washed by seawater twice and then once by tap water. After that, the formalin-seawater was poured on the sieve with mesh size 0.5 m (500 μm) for filtering and then the retained associated fauna was caught. Repeat three times (wash and filter) to retain all associated fauna. Each algae sample was weighed per gram for the nearest decimal value for wet weight (W.W.). By using binuclear stereomicroscope, all fauna species were sorted and counted. Epifauna were identified to the nearest possible taxa using the available literatures (for Mollusca: **Rusmore-Villaume, 2008; Zuschin *et al.*, 2009; Janssen *et al.*, 2011;** for Echinodermata: **Clark & Rowe, 1971; Guille *et al.*, 1986;** for Crustacea: **Barnard & Karaman, 1991 a&b; Brusca & Brusca, 1990; McLaughlin & Dworschak, 2001; Ravichandran & Kannupandi, 2007; Lowry & Myers, 2009; Al-Zubaidy & Mhaisen, 2014;** for Annelida: **Rouse, 1990; Wehe & Fiege, 2002** and **Maciolek & Blake, 2006).**

Data analysis

Algae-associated epifaunal community structure (epifaunal groups' percentages and species composition) were calculated and presented for different primary and former habitat variables. Following, occurrence and abundance for epifaunal-recorded species in different primary and algae former habitat were compared in order to figure out primary and former habitat effects on epifauna in terms of faunal diversity and abundance.

Diversity detected by species richness as an absolute number of species at each habitat variable while Shannon wiener index was calculated to compare fauna diversity among different habitat units with the consideration of their associated species abundance.

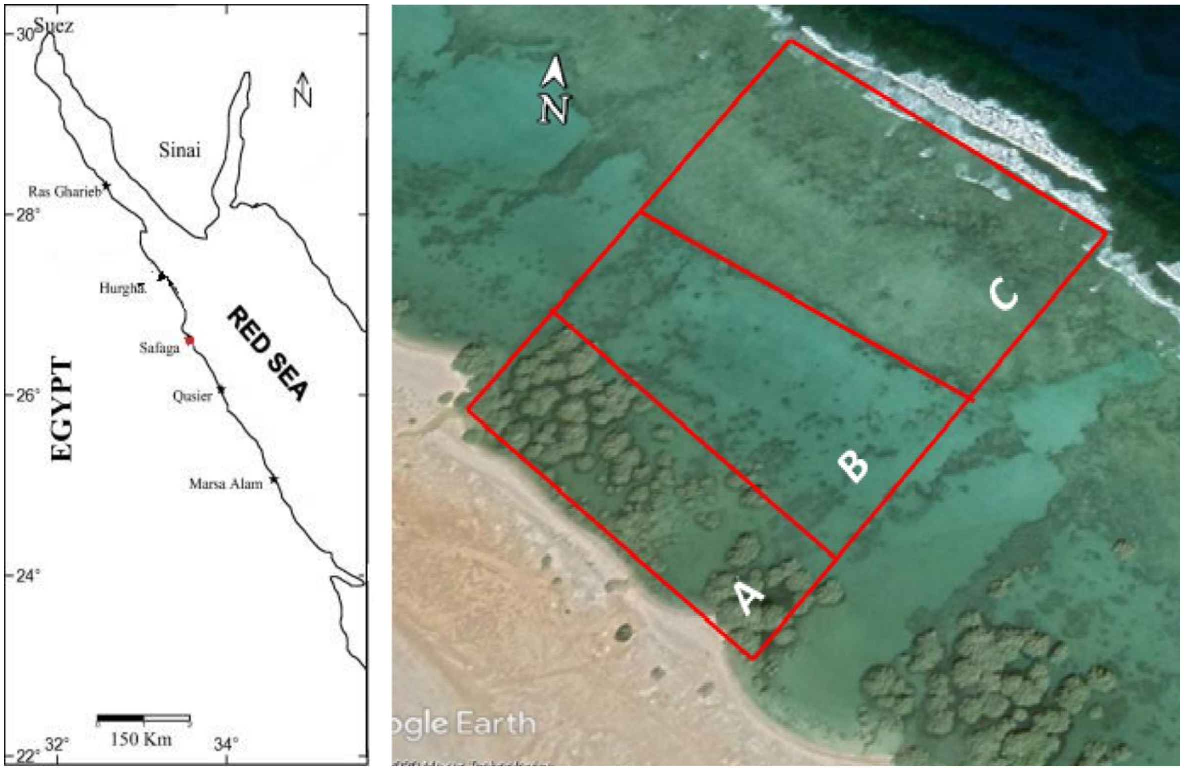

Fig. 1. Detailed map of the study area, at mangrove Safaga site (South Safaga, Red Sea, Egypt) showing main coastal primary habitat zones; (A) Mangrove Stand, (B) Sand Lagoon and (C) Back Reef.

Table 1. GPS readings and the environmental measurements of each primary habitat zone in the study area.

Zone	GPS	Temp (C^0)	PH	Salinity (‰)	Organic cont. (%)
Mangrove stand	26^0 36′ 55.3″ N 34^0 00′ 43.3″ E	26.7	8.5	41.1	16.4
Sand Lagoon	26^0 36′ 55.4″ N 34^0 00′ 44.5″ E	25.5	8.7	41.3	4.1
Back Reef	26^0 36′ 55.2″ N 34^0 00′ 48.9″ E	27.5	8.8	41.6	2.6

RESULTS

Changes in the average environmental measurements of different primary habitat zones/sectors in study area are represented in **Table (1)**. Data indicated that there are slightly differences in temperature, pH and salinity at three zones. Average environmental measurements (temperature, pH and salinity values) at back reef area (BR) are slightly higher than its average values in mangrove area (M) and sand lagoon area (SL). Meanwhile, average organic content percentage at M area (16.4 %) was markedly higher than such values at SL area (4.1 %) and BR area (2.6 %).

The total number of the recorded epifaunal species in all different algae samples was 64 species belonging to four major phyla including Annelida, Crustacea, Mollusca and Echinodermata. Phylum Mollusca is the most diverse taxa, represented by 24 species (37.5 %), of which 19 species belonging to class Gastropod and 5 species belonging to class Bivalvia. Phylum Annelida come in the second rank containing 20 species (31.3%) mostly belonging to one class Polychaeta, except only one species from class Oligochaete. Phylum Crustacea comes next with 18 species (28.1%) and phylum Echinodermata comes last (3.1%) and represented by only two species; *Aquilonastra burtoni* and *Ophiocoma scolopendrina* **(Table 2)**.

In particular, 53.1 % of recorded species (34) were represented in low total abundance number from one to less than 10 individuals. However, the rest of recorded species (30 species representing 46.9 %) occurred with moderate to high total-abundance (10 to 208 individuals). However, only three species (2 amphipods, *Ampithoe ramondi* and *Ceradocus sp.;* one polyachete species, *Hesionides gohari)* occurred with total abundance exceed 100 individuals **(Table 2).**

A large fluctuation of the organic content percentage is an indication for the fluctuation in nutrient supply of this area, and it is accompanied by a comparable distribution of their algae-associated epifauna. As a consequence, results detected that every single primary habitat harbors their specific algae-associated fauna; whereas 10 faunal species (of total 64) occurred only in mangrove soil zone (M); the same species number occurred only on sand lagoon zone (SL) and 13 faunal species occurred only in back reef area (BR). However, 16 species are recorded in two primary habitat zones; 4 species occurred on (SL) ∩ (M), 4 species occurred on (BR) ∩ (M), 8 species occurred on (SL) ∩ (BR). Meanwhile, 15 species are recorded in all 3 zones (M) ∩ (SL) ∩ (BR) **(Table 3).**

Faunal composition data showed that the primary habitat type as well as the algae type or algae species composition (in mixed seaweed patches) affected species richness and groups-contributions **(Fig. 2)**. By the way, the primary habitat will affect too much than the other factors to extend f the absence of entire groups which may be marked when their algae primary habitat changes. It should be noted in *Cystosera* algae samples, all 4 represented groups were recorded in (BR) primary habitat and it reduced to 3 groups in (M), with the absence of echinoderms, which reduced again to only 2 groups in (SL), with the absence of echinoderms and annelids. The same phenomena are observed also in *Padina* samples with the complete absence of echinoderms and mollusks in (SL) primary habitat.

The previous findings reflect the stronger effect of primary habitats not only on the occurrence of focal species but also on its diversity as it is shown in **Fig. (3A)** which compare between species richness within single algae samples among different primary habitats). Primary habitat also affects the epifaunal abundance **(Fig. 4A)** if we also ignore the mixed patches. It should be noted that primary habitat effects on algae epifauna diversity and abundance are much stronger than the effects of algae specificity (in single species patches) and algal synergism (in mixed-species patches) as it showed in **Figures (3, 4** and **5).**

Table 2. Occurrence and Abundance of algae-epifaunal species in different algal habitat samples among 3 different primary habitats: mangrove (M), sand lagoon (SL), back reef (BR), *Cystoseira*(Cs), *Saragassum* (Sg)and *Padina* (Pd).

Group/ species	***Sp.* code**	**Single algae habitat**									**2- Algae Mix**			**3- Algae Mix**		
		Cystoseira			***Saragassum***			***Padina***			**Cs.Sg**	**Cs.Sg**	**Cs.Sg**	**Pd.Cs.Sg**	**Pd.Cs.Sg**	**Pd.Cs.Sg**
		M	**SL**	**BR**	**M**	**SL**	**BR**	**M**	**SL**	**BR**	**M**	**SL**	**BR**	**M**	**SL**	**BR**
Polychaeta																
Dorvilleaangolana	P1							36							10	
Onuphiseremita	P2							54							5	
Hesionidesgohari	P3	3				47			30	16	5		11	30		
Oxydromus sp.	P4				2											
Nephtys sp.	P5					9		54	30							
Ceratonereis mirabilis	P6							36								
Heteronereis sp.	P7	3							24	8			5	24		
Nereis vexillosa	P8															7
Perinereisnuntia	P9			3			2					5		18		
Syllides sp.	P10					8								6		
Decamastusgracilis	P11				6	9										
cossuralongocirrata	P12				2				7						8	5
Clymenura sp.	P13	1				9			12		1				5	
Axiothellaobockensis	P14				3	6			6						8	
Ophelia borealis	P15														5	
Ophelia sp.	P16					15										
Scoloplos (Leodamas) chevalieri	P17														3	
Cirratuluscirratus	P18	1														
Terebella sp.	P19								8							
Oligochaeta																
Tubificoidesswirencowi	Olg			3												
Amphipoda																
Ampithoeramondi	Am1	5		40	4		15	54			11		37	8	13	20
Jassa sp.	Am2			10	1	2	2			5	6	2	16			33
Ceradocus sp.	Am3	21		20			20	54	10		8	5			5	
Parelasmopussuluensis	Am4				11		12		6	8				11	10	20
Leucothoe sp.	Am5			20		4	5			22			21		8	
Lysianassa sp.	Am6												4			
Isopoda																
Gnathiaafricana	Is1			50					4							
Idotea sp.	Is2				1									11		
Decapoda																
Paguristes sp.	De1				9											
Alpheus sp.	De2			20		6		36	5				26			
Athanopsisaustralis	De3	21		16	2		5						11			13
Galathea sp.	De4			50	1					2		1				

Pyromaia sp.	De5		3	1	1		1			2						1
Brachycarpus sp.	De6						2	36					16			
Nectocarcinus sp.	De7				2									2		3
Thalamitasima	De8									6						
Chlorodiella sp.	De9	3									3				3	1
Leptostraca																
Nebalia sp.	Le			15						2			8			
Gastropoda																
Conus virgo	Ga1								4		2	1	1			
Cerithium sp.	Ga2									2						
Diala sp.	Ga3								1							
Epitonium sp.	Ga4															3
Smaragdia sp.	Ga5								1							
Longchaeusturritus	Ga6	1														
Pyramidella sp.	Ga7															1
Pseudodiala acuta	Ga8															3
Vanikoro sp.	Ga9								1							
Anachis sp.	Ga10				7											3
Mitrellamaestratii	Ga11															4
Mitrella sp.	Ga12									2						
Vexillum tusum	Ga13	1			2		1		2	2						3
Nassarius sp.	Ga14													1		
Nassariusocellatus	Ga15		2													
Ancilla lineolata	Ga16									2						
Phasianellasolida	Ga17	3									1					
samargdia sp.	Ga18				1											
Canariummatabile	Ga19		2							13	1					
Bivalvia																
Lunulicardiaretusa auricula	Bv1					2			1							
Divalinga arabica	Bv2					2										
Brachidontespharaonis	Bv3												1			
Modiolus auriculatus	Bv4		1	1					6	2		3	3			1
Cryptopectennux	Bv5										1	1				
Echinodermata																
Aquilonastra burtoni	Ec1				1											
Ophiocoma scolopendrina	Ec2			1			17		24	3		22	3			
Diversity	**11**	**4**	**14**	**17**	**12**	**11**	**8**	**19**	**16**	**10**	**8**	**14**	**9**	**12**	**16**	**11**
Abundance	**63**	**8**	**250**	**58**	**119**	**82**	**357**	**181**	**92**	**40**	**40**	**163**	**111**	**82**	**121**	**63**

Results also indicated that predation effort is the other direct factor affecting the distribution of algae-associated epifauna. This was likely as the special shape and construction of each algae species is important in protecting and hiding from predators. In the sandy lagoon zone, the most exposed zone to predators, *Padina* single algal species, with wide leaf-like shape, has the highest diversity value and accommodates 19 species. Among them 7 species belonging to phylum Annelida, 4 were crustaceans, 7 were molluscs, and one species belongs to Echinodermata **(Table 2, Fig. 3B)**. On the other hand, 3 algal-mix species comprised 12 species of which 7 and 5 species were annelids and crustaceans, respectively. However, 2 algal-mix species have the lowest diversity of species and included only 8 species. Single *Padina* harbor the highest abundance of individuals inhabited sand lagoon zone being 181 individuals (out of them, 23 individuals were annelids, 45 individuals were crustaceans, 20 individuals were molluscs and 3 individuals were echinoderms). Meanwhile, the number of individuals recorded at 2-mix and 3-mix species being, 40 and 82 individuals respectively **(Fig. 5).**

Table 3. List of species representing different algae faunal species (expressed by species codes, mentioned in Table, 2) exclusively found in only one primary habitat zone: mangrove (M), sand lagoon (SL) and back reef (BR); or in only two primary habitat zones: (SL∩M, BR∩M and BR∩SL); and in all three primary habitat zones: (M∩SL∩BR).

M	SL	BR	(M) ∩ (SL)	(M) ∩ (BR)	(SL) ∩ (BR)	(M) ∩ (SL) ∩ (BR)
P4	P15	P8	P1	De3	Am5	P3
P6	P16	Olg	P2	De6	Is1	P7
P18	P17	Am6	P5	De7	Bv4	P9
Is2	P19	De8	P10	Ga10	Ec2	P12
De1	Ga3	Le	P11			Am1
Ga6	Ga5	Ga2	P13			Am2
Ga14	Ga9	Ga4	P14			Am3
Ga17	Ga15	Ga7	Bv5			Am4
Ga18	Bv1	Ga8				De2
Ec1	Bv2	Ga11				De4
		Ga12				De5
		Ga16				De9
		Bv3				Ga1
						Ga13
						Ga19
10	**10**	**13**	**8**	**4**	**4**	**15**
						64

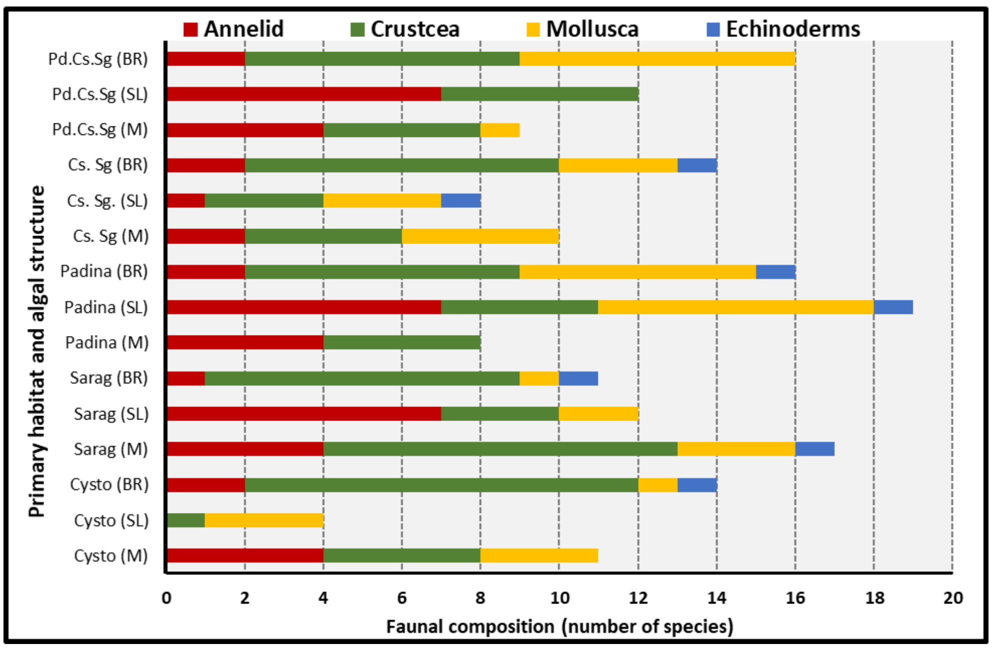

Fig. 2. Faunal composition in different algae habitat-samples: mangrove (M), sand lagoon (SL), back reef (BR), *Cystoseira* (Cs), *Saragassum* (Sg) and *Padina* (Pd).

In the nurse and muddy mangrove soil zone, filamentous overlapped *Sargassum* algae single species has the highest diversity of species and accommodates 17 species. Mollusca was the most diverse phylum inhabiting this zone by 9 species. However, 2 algal-mix species and 3 algal-mix species comprised 10 and 9 species respectively **(Fig. 3C)**. In contrast, *Padina* single algal species recorded the highest individual abundance among this zone and all studied zone by 357 individuals record (out of them, 179 individuals were annelids and 179 individuals were crustaceans). The lowest abundance value recorded in mangrove zone was in 2-mix algae with 40 individuals respectively **(Figs. 4 & 5)**. It should note that the most diverse *Sargassum* single species harbor a low abundance number being 58 individuals.

Results of back reef zone, that featured by high abundance and diversity of algae species, exhibited balanced diversity values **(Fig. 3D)** and showed that *Padina* single algal species and 3 algal-mix species have the same number of species accommodates 16 species. However, 2 algal-mix species included 14 species of which 2, 8, 3, and one species belonging to Annelida, Crustacea, Mollusca, and Echinodermata, respectively **(Table, 2** and **Fig. 3).** Regarding the abundance data, it is clear that *Cystosera* single-algae habitat has the highest abundance value in such primary habitat being 250 individual (6, 242, 1 and 1 for annelids, crustaceans, molluscans, and echinoderms, respectively), Abundance values in at 2-mix and 3-mix species were 163 and 121 individuals respectively **(Figs. 4 & 5).**

Furthermore, similarity indices between different algae secondary habitats occurred in the three primary zones **(Fig. 6)** showed low similarity values between different epifaunal samples even those that share the same algae host. The figure divided samples into two clusters with a 20.54 % similarity value. The first one included *Padina* (SL), *Sargassum* (SL), and 3 mixed algae (M) with a similarity value of 27.3 %. The second cluster incorporates four primary groups with a similarity of 22.1 %. The first group contains *Sargassum* (M) and 3 mixed algae (BR) with similarity value 48.35 %, the second group included *Padina* (M) and 3 mixed algae (SL) with similarity value 38.6 %, the third group incorporates Mangrove zone algae *Cystosera* and 2 mixed algae *Cystosera* with *Sargassum* (with highest similarity being, 51.2 %). The fourth groups contain remain algae habitat. In addition, the data separate *Cystosera* (SL) from the cluster with the lowest similarity values with the other habitat almost 5.3% respectively.

Changes in Shannon-winner diversity index value (H') among different primary and former habitats is given in **Figure (7)**. Regarding proportional abundances of species, in every in the in every habitat variable, Shannon-winner index values ranged from the highest value (H'=2.5) in *Padina* (SL) to the lowest (H'=1.32) in *Cystosera* (SL). By comparing the effect of primary habitats on the ability of single algae species to rise the (H') value, we found that mangrove (M) followed by back reef (BR) enhanced (H') values of *Sargassum* community. In *Cystosera* communities, (BR) habitat followed by (M) enhanced (H') values, while (SL) followed by (BR) enhanced it in *Padina* community. Communities of 2-mix algae patches showed increase of (H') values in Back reef habitat (H'=2.27) which decreased to (H'=1.96) in mangrove. Meanwhile, Communities of 3-mix algae patches showed increase of (H') values in back reef habitat (H'=2.39) which slightly decreased in SL (H'=2.22).

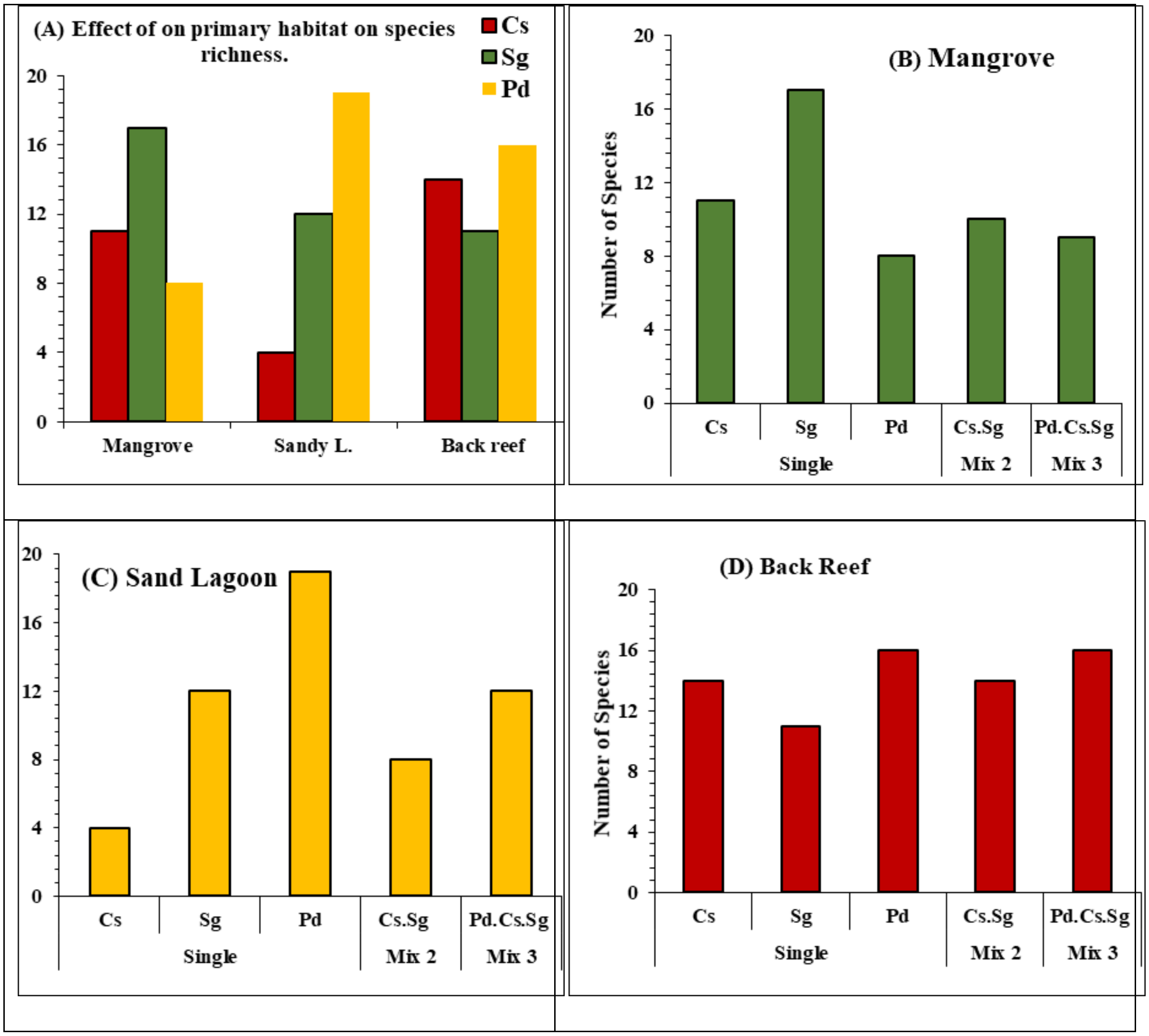

Fig. 3. Species richness (# of species) inhabiting different algae habitat-samples in different primary habitats (B) mangrove, (C) sandy lagoon and (D) back reef in addition to comparison between different single algae among different primary habitat zone (A): *Cystoseira* (Cs), *Saragassum* (Sg) and *Padina* (Pd).

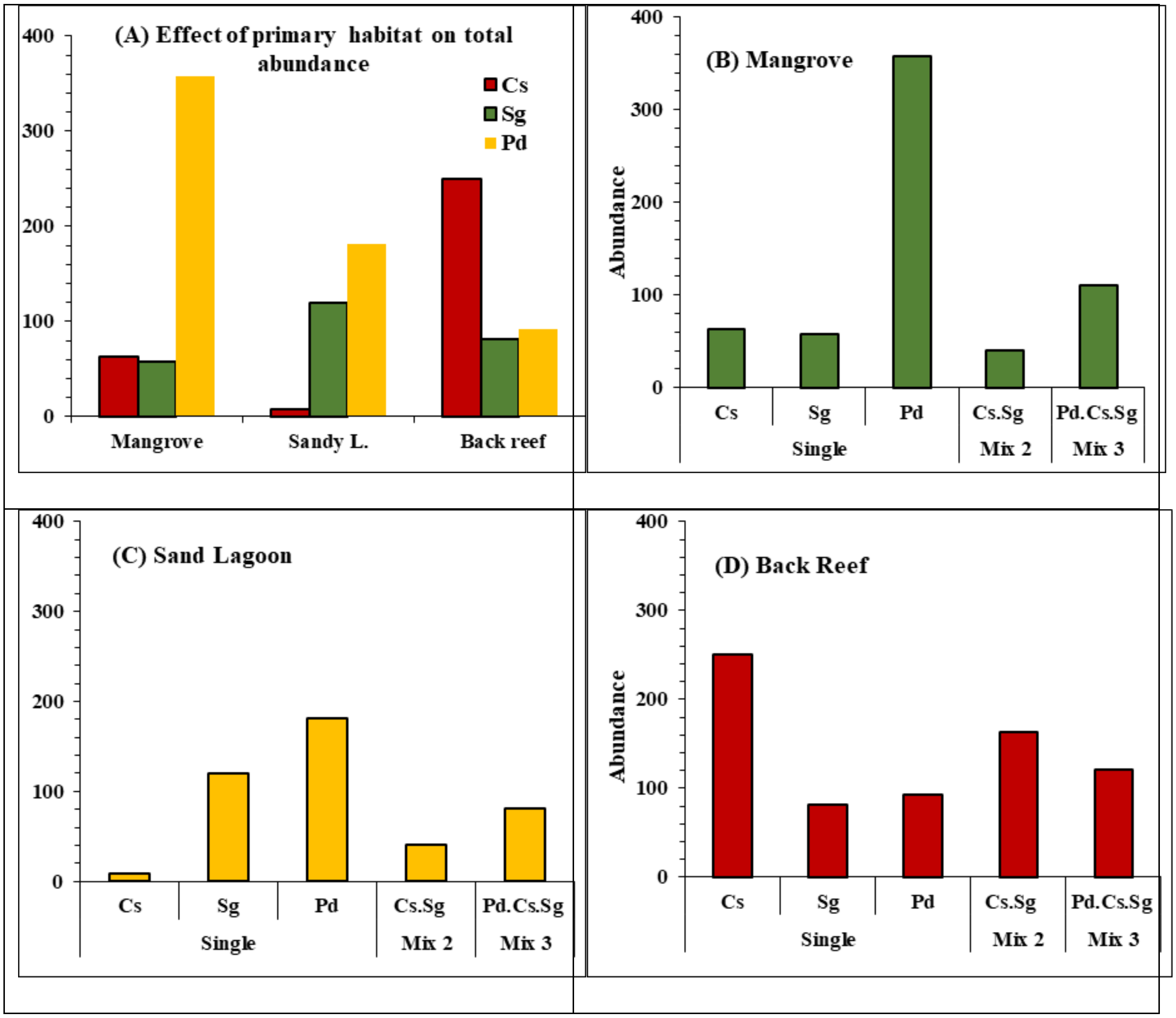

Fig. 4. Abundance variation in different primary habitats (B) mangrove, (C) sandy lagoon and (D) back reef in addition to comparison between different single (not mixed) algae secondary-habitats in different primary-habitats zone (A): *Cystoseira* (Cs), *Saragassum* (Sg) and *Padina* (Pd).

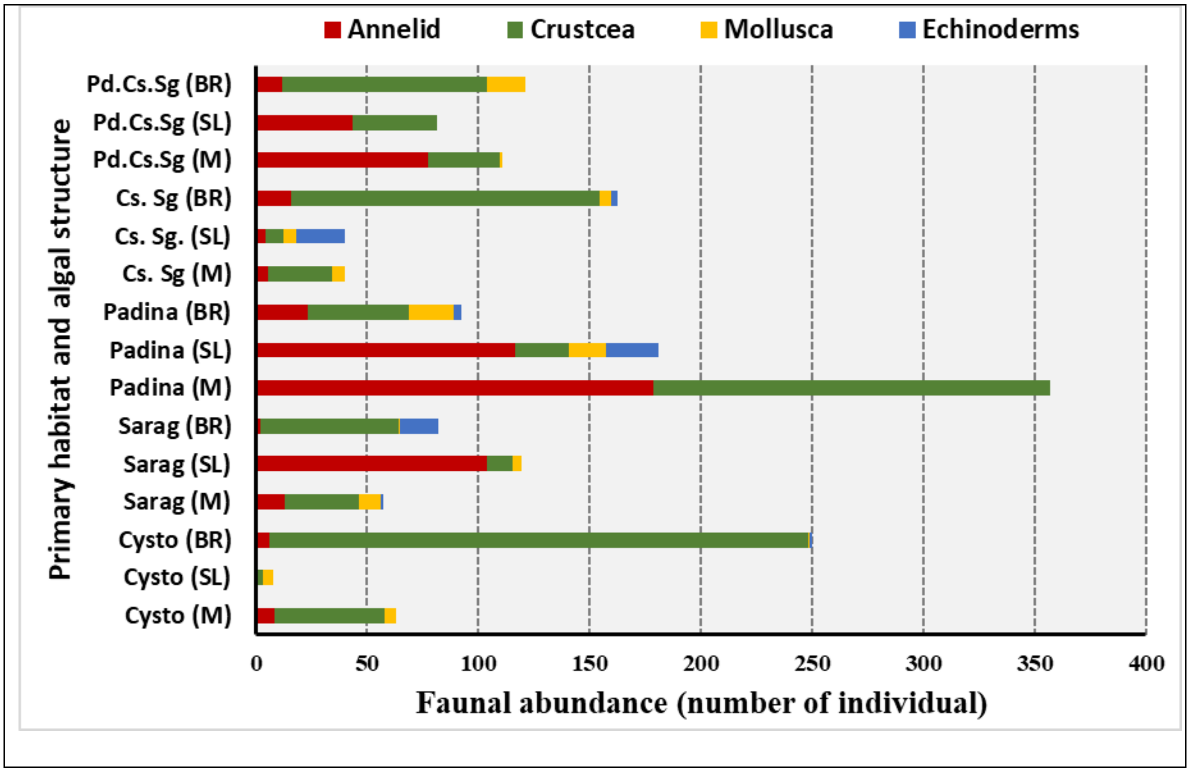

Fig. 5. Group contributions (group total number of individuals) in faunal abundance among different algae habitat-samples : mangrove (M), sand lagoon (SL), back reef (BR), *Cystoseira* (Cs), *Saragassum* (Sg) and *Padina* (Pd).

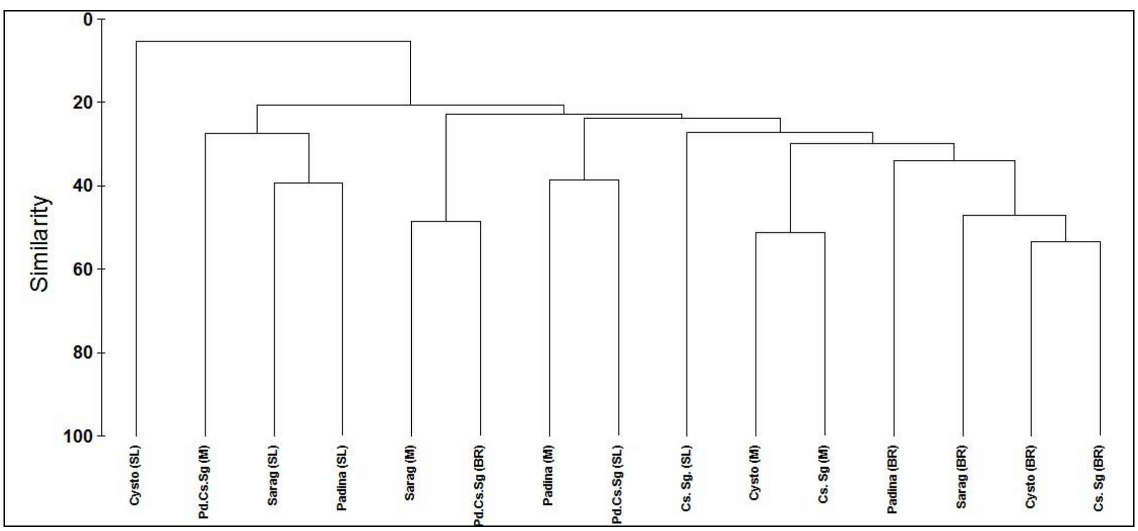

Fig. 6. Dendrogram of similarity matrix between different algae habitat-samples among different zones: mangrove (M), sand lagoon (SL), back reef (BR), *Cystoseira* (Cs), *Saragassum* (Sg) and *Padina* (Pd).

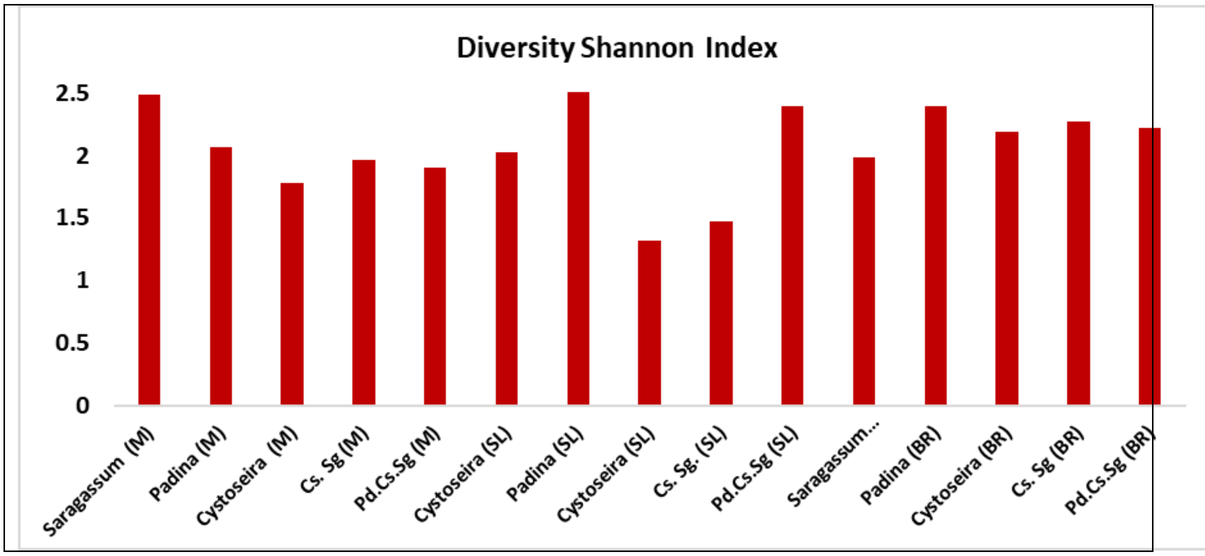

Fig. 7. Changes in Shannon winner diversity index (H') values among different primary and secondary-former habitats: mangrove (M), sand lagoon (SL), back reef (BR), *Cystoseira* (Cs), *Saragassum* (Sg) and *Padina* (Pd).

DISCUSSION

Mangrove Safaga area is given its name because of the occurrence of a well-known grey mangrove, *Avicenna marina* stand along its coastline. Habitat variety in this area is obvious and unique containing; mangrove mudflat, mangrove tree, mangrove pneumatophores, sand lagoons, flat back reef and coral reef barrier (in zones from shoreline to marine offshore side) unlike different secondary former habitats **(Dworschak & Pervesler, 1988)**. We used sampling design and census techniques for algae-associated epifaunal assemblages in three main habitats (namely, Mangrove; sandy lagoon and Back reef) in spring season to explore factors that drive changes in the composition and abundance of epifaunal assemblages in such important host habitats.

In the present study, we documented that the algae-epifaunal colonization in the intertidal habitat, at the mangrove area south Safaga, affected mainly by the special characteristics of the primary habitat. Furthermore, we suggested that the positive effects or negative of secondary habitat formers on biodiversity of algae-epifauna depending essentially on the primary habitat construction and its intertidal zonation. Also, we detected that habitat facilitation was strongest when and where the secondary habitat-former was most functional for inhabitants of marine invertebrates in terms of feeding and hiding from predators.

In mangrove ecosystem, primary productivity has usually been controlled by leaf litter fall, **(Alongi, 2009)** which contribute in soil microbial processes to increase its carbon budgets and in turn organic matter especially particularly around their respiratory roots, these processes possibly increase the amount of organic matters in adjacent coastal waters (**Feller *et al.*, 2010)**. In the present study area, average organic content fluctuation reflects the bottom soils nature which tend to be muddy in mangrove, fine sand to silty in Sand lagoon and hard bottom in back reef area. Such fluctuations express how these habitats able to make the differences between each other and these findings also reported in **Proches *et al.*, (2001)** who documented that mesofauna were considerably differed in mangrove pneumatophores habitat from those in other adjacent benthic major habitats.

Another factor should be noted her which is the exposure to wave action (which, in some way, is also related to the first organic-content influence factor) where a very slow water movement is marked in mangrove zone **(Dworschak & Pervesler, 1988; Feller *et al.*, 2010)** which increases in zones that follow toward the coral crest. The present findings included no surprises with the classic effect of marked intertidal habitat/zones that conveniently reported in many studies (for example **Mouritsen, 2004; Pereira *et al.*, 2006; El-Naggar *et al.*, 2017**). The primary habitat will affect too much than the other factors whereas some species or entire groups absence when their algae primary habitat is changed. The logical explanation here lies where nutrients/food supply as well as protection, makes every single primary study-habitat harbors their specific algae-associated fauna. Nearly 50% of algae-epifaunal species prefer only one primary habitat of which 10 epifaunal species (from total 64) were recorded only in mangrove pneumatophores zone and the same number in sand lagoon zone, meanwhile, 13 faunal species were recorded only in back reef zone. These stronger effects of primary habitats affect not only on the occurrence of focal species but also on its diversity and abundance.

The second driver of change in the current study, however, were related to habitat facilitation inside different primary habitat zones including algae identity and some other modification which in the present study is restricted synergism by 2 or 3 algae species that composed the scattered dense mixed-species algae patches. Data in the present study showed strong effects of some of these secondary habitat-formers more than others due to useful forms/modification which increase their efficiency for small invertebrates feeding and hiding away from predators. Such indirect positive effects that mediated by sequential formation or modification of secondary-formers habitat which are being known as habitat cascades effect where two co-occurring habitat-forming species control their inhabitant diversity/abundance. Such effect was essentially documented to describe habitat complexity in forests **(Cruz-Angon & Greenberg, 2005)** and also used for marine habitats such as salt marshes **(Altieri *et al.*, 2007)**, sea grass beds **(Edgar & Robertson 1992** and **Thomsen, 2010)**, mangroves **(Bishop *et al.*, 2013; Bell *et. al.*, 2014)** and mudflats **(Thomsen *et al.*, 2016**).

Thus, in the current study, results indicated that predation effort is the other direct factor affecting the distribution of algae-associated organisms depending on how far such organisms can benefits from the special shape and construction of each algae habitat unit in protecting and hiding from predators, (these like in **Edgar & Klumpp, 2003; Shaban, 2012; Gestoso *et al.*, 2012)**. In sandy lagoon zone that exposed to predators *Padina* single algal species with its wide leaf-like shape has the highest diversity value and harbor the highest abundance of individuals followed by 3 algal-mix species, containing *Padina* species itself.

Colonization structure pattern differs according to the primary habitat construction nature and characteristics in the current study as well as many other studies including **Proches *et al.*, (2001); Thomsen & McGlathery (2005); Pereira *et al.*, (2006)** and **Pfaff & Robles (2019)**. In the nurse and muddy mangrove soil zone, for example, the filamentous muddy-overlapped *Sargassum* single algae species has the highest diversity. In contrast, *Padina* single algal species recorded the highest abundance among this zone and all studied zone. Furthermore, current Shannon-winner diversity analysis which compared between (H') values in in algae samples, regarding to its inhabitant-species abundance, and indicated that some primary-secondary habitat complex will be fittest for biodiversity than others. Such combination provides more feeding and protection opportunities for large number of a small invertebrates with abundant numbers, such as *Sargassum*-mangrove and *Padina*-sandy lagoon combinations. As well as the current study, many recent studies recommended the expanding of studying the effect of habitat complexity in different marine ecosystems **(Feller *et al.*, 2010; Thomsen *et al.*, 2016; Livernois, 2019; Carmintto *et al.*, 2020; Pygas *et al.*, 2020)** rather than the classical studies, which only describe the relationship between separate habitat-level variation and their inhabitants.

CONCLUSION

The current study concludes that the epifaunal assemblage in the intertidal ecosystems is subject to the influence of habitat complexity in which it affected mainly by the special characteristics of the primary habitat and then by the facilitation cascades in these primary habitats. The habitat facilitation was effect positively on the epifaunal assemblage by increasing its diversity or increasing abundance of certain groups/species when and where the secondary habitat-former was most functional for such invertebrate inhabitants in terms of feeding and hiding from predators.

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ARABIC SUMMARY

محركات التغيير في تجمعات الفونة المصاحبة للطحالب العشبية المدية في موقع المانجروف جنوب سفاجا، مصر، البحر الأحمر

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يهدف هذا البحث إلى دراسة آثار تعقيد الموائل المدية على الفونة البحرية في مجتمعات الطحالب العشبية وذلك في موقع المانجروف الساحلي بجنوب سفاجا على ساحل البحر الأحمر المصري المعروف بتعدد بيئاته المتواجدة على مستوي النطاقات الساحلية المتوالية. هذا وتركز الدراسة على آثار الموائل المدية الرئيسية سالفة الذكر إلى جانب تأثيرالموائل الثانوية المختلفة الموجودة داخلها - بما يعرف بالتسهيلات الحيوية الناتجة عن تسلسل مستويات الموائل الى موائل فرعية متحورة - وذلك على الكائنات الحية داخل البؤرة البيئية والتي هي هنا اللافقاريات الساكنة والمصاحبة للطحالب. المناطق الأولية الرئيسية في منطقة المد والجزر بمنطقة الدراسة هي ١- منطقة أشجار المانجروف أي الطحالب الموجودة ما بين جذورها التنفسية المحيطة بها ٢- المنطقة المسطحة خلف حافة الشعاب ٣- المنطقة الرملية المنخفضة بين المنطقتين السابقتين (البحيرة ذات القاع الرملي). بينما أنواع الطحالب المختلفة (التي كانت متواجدة داخل البيئات الرئيسية سواء كانت قائمة بذاتها دون اختلاط أو متواجدة مختلطة مع بعضها البعض داخل بقع الطحالب العشبية البحرية) اعتبرت هنا بمثابة الموائل ثانوية.

هذا وقد أشارت النتائج إلى أنه في المجمل تم تسجيل ٦٤ نوعًا من اللافقاريات تسكن مختلف موائل الطحالب على كافة تنوعاتها ، كما أوضحت النتائج أن تنوع ووفرة هذه اللافقاريات في تلك المستعمرات البيئية تتأثر بشكل رئيسي بالموئل الرئيسي حتى أنه ما يقرب من ٥٠٪ من الأنواع المصاحبة للطحالب محل الدراسة الحالية قد أظهرت نوع من انواع التخصص لموئل أساسي واحد فقط. وكشفت النتائج أيضًا أن تأثير تنوع البيئات الثانوية (تسهيلات تسلسل الموائل) التي قد تؤثر بشكل ايجابي قوى على التنوع الحيوي والوفرة داخل مستعمرة الطحالب يكون مشروطا بطبيعة هذا الموئل الثانوي حيث يشترط أن يكون الموئل الثانوي أكثر وظيفية وفعالا للكائنات المصاحبة للطحالب في النواحي التي تتعلق بتغذيته أو مساعدته على الاختباء من الحيوانات المفترسة. ولكن بالنظر للنتائج يبدو أن جهد الافتراس هو العامل الرئيسي الذي يتحكم في توزيع الكائنات الحية المرتبطة بالطحالب اعتمادًا على مدى استفادة هذه الكائنات من الشكل الخاص والبناء الخاص لكل وحدة من وحدات الطحالب في الحماية والاختباء من الحيوانات المفترسة. وعلى هذا الأساس فقد استخلصت الدراسة الحالية أن التأثيرات الإيجابية لأحد الموائل الثانوية في أحد البيئات الرئيسية دون غيره على تنوع المستعمرين لموائل الطحالب يعتمد على بناء وخصائص الموائل الأولية التي ينتمي إليها وكذلك مدى موائمته لعدد أكبر من اللافقاريات سواء في تقديم الدعم في عملية تجنب الإفتراس بشكل رئيسي أو في تسهيل الحصول على الغذاء.