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Impact of warming on biofouling communities in the northern Persian Gulf

Maral Khosravi[a,b], Ali Nasrolahi[a,*], Mohammad Reza Shokri[a], Sergey Dobretsov[c,d], Christian Pansch[b]

[a] Department of Aquatic Biotechnology, Faculty of Life Sciences and Biotechnology, Shahid Beheshti University, G. C., Evin, Tehran, 1983969411, Iran
[b] Department of Marine Ecology, GEOMAR - Helmholtz Centre for Ocean Research Kiel, Düsternbrooker Weg 20, 24105, Kiel, Germany
[c] Department of Marine Sciences and Fisheries, College of Agricultural and Marine Sciences, Sultan Qaboos University, P.O. Box 34, Al Khoud, 123, Oman
[d] Centre of Excellence in Marine Biotechnology, Sultan Qaboos University, P.O. Box 50, Al Khoud, 123, Oman

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ABSTRACT

While the impact of ocean warming on single species is well described, the impact on marine biofouling communities is not well understood. Effluents of power plants have higher temperatures and can be used as natural large-scale test sites to investigate warming effects on marine ecosystems. In the present study, we evaluated the impact of elevated temperatures in the vicinity of a power plant on macro-biofouling communities in the northern coast of the Persian Gulf. The impact site was on average 2 °C warmer than the control site. Our results demonstrate a significantly different structure and composition of biofouling communities between control and impact sites. Warming led to a 1.5-fold increase in the mean coverage of biofouling communities and slightly decreased functional and species richness. Our results indicated that future warming will likely increase biofouling pressure, while decreasing diversity of communities, particularly in habitats where organisms exist at their upper tolerance limits of temperature.

1. Introduction

Biofouling is the undesirable attachment and growth of micro- and macro-organisms to submerged anthropogenic structures (Wahl, 1989). Biofouling communities are distributed on hard substrates, particularly in shallow water marine environments. Because of their fast growth rates and the ability to attach to any artificial structure, biofouling organisms have recently been a suitable model in many ecological studies (Railkin, 2004; Dürr and Thomason, 2010). In several respects, these communities are comparable with naturally-occurring hard shore assemblages and, therefore, can be used as models to study the effects of environmental changes (e.g., elevated temperatures) on their assemblage structure, species richness and abundance. In addition, biofouling can pose extensive economic problems to maritime industries e.g. shipping, fishing vessels, and recreational use (Coetser and Cloete, 2005; Maggiore and Keppel, 2007; Schultz et al., 2011; Fitridge et al., 2012). It is estimated that even a little increase in ship fouling would eventually increase the fuel consumption of ships (Evans et al., 2000). Also, from an environmental point of view, this would lead to an increase in CO_2, NO_x and SO_2 emission (Townsin, 2003), which subsequently contribute to the higher sea surface temperatures, sea level rise, water circulation change and ocean acidification (IPCC, 2007).

Warming is discussed among the most pervasive of the global present-day impacts of climate change on marine systems (Halpern et al., 2008), from genes (Reusch, 2013; Harvey et al., 2014) to the ecosystem level (Brierley and Kingsford, 2009). Furthermore, warming can facilitate the spread of non-indigenous marine fouling species (Walther et al., 2009; Kim and Micheli, 2013). It has long been revealed that warming has the potential to alter biological processes of biofouling communities, such as growth, metabolism, and reproduction (Brierley and Kingsford, 2009; Dürr and Thomason, 2010; Dobretsov et al., 2019), as well as community structure (Smale et al., 2011), which may have major economic, ecological and environmental consequences (Dürr and Thomason, 2010).

Marine organisms inhabiting the Persian Gulf are constantly exposed to dramatic fluctuations in temperature and salinity (Hume et al., 2013; Nandkeolyar et al., 2013). The Persian Gulf is the hottest sea on earth, where the sea surface temperature in summer reaches up to 35 °C while dropping to 18 °C in winter (Kleypas et al., 1999; Riegl and Purkis, 2012). Its temperature has increased 0.57 °C between 1950 and 2010 (Shirvani et al., 2015) and is projected to further increase by about 2.2 °C by 2100 (Noori et al., 2019). This water body in its present thermal condition could thus be used as a natural laboratory for testing the responses of marine organisms to warming at their thermal

* Corresponding author.
E-mail address: A_Nasrolahi@sbu.ac.ir (A. Nasrolahi).

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tolerance range (Feary et al., 2013). In such a harsh habitat, organisms might already be close to their upper thermal tolerance limit (reviewed by Somero, 2010). On the other hand, living under thermal stress for a long time may have resulted in the selection of heat-resistant lineages of the species inhabiting the Persian Gulf (Berkhout et al., 2014; Bento et al., 2016). In addition to the natural harsh conditions, this area is anthropogenically impacted with 30% of world's crude oil shipping and many sewage and desalination brine water effluents (Sheppard et al., 2010).

The extreme conditions of the Persian Gulf in line with its geological history caused a relatively low diversity of macrobentic biota in this area compared to other regions of the Indian Ocean (Sheppard et al., 1992). Many studies have been conducted on macroinvertebrates inhabiting the Persian Gulf, mostly those that are reef-associated (see Riegl and Purkis, 2012). However, only a few publications investigated biofouling communities in the Persian Gulf, including a study by Al-khayat and Al-Maslamani (2001) that identified 111 fouling species at pearl oyster beds and a study by Naser (2017) that found a total of 41 biofouling species on fiberglass tiles in a marina and a mariculture center. Besides these efforts, the identity of many biofouling species from the Persian Gulf remains unknown. To the best of our knowledge, the effect of elevated seawater temperature on biofouling communities in the area has never been studied.

In the present study, we investigated the effect of elevated seawater temperature on biofouling communities in the northern coast of the Persian Gulf over a full year cycle. We hypothesized that elevated water temperatures influence the structure and composition of biofouling communities, and increase the biofouling coverage. The main aims of this study were to investigate the effect of elevated water temperature on: 1) percent coverage of biofouling communities, and 2) structure and composition of biofouling communities stabled on inert test panels in the vicinity of the thermal effluent of a power plant.

2. Materials and methods

2.1. Study area

The experiment was conducted in the vicinity of the power plant at the northern coast of the Persian Gulf, in Bushehr Province (28°48′56.81″N, 50°52′40.48″E; Fig. 1), from July 2014 to May 2015. The 1000 MW power plant began its operation in 2012 and uses coastal seawater as heat sink. The cooling water discharges into the sea at a rate of 60 $m^3 s^{-1}$. Required regular water monitoring by Research and Development (R&D) experts of the power plant showed that concentrations of chlorine and other constituents in the outfall were very low relative to the large volume of discharge. Their bioassay had shown no acute or chronic toxicity of the outfall water to larvae of some marine larvae (R&D personal communication). To assess the thermal impacts on biofouling assemblages, two stations located in the similar environment were chosen. The impact site (affected by the warm water effluent) was located at 20 m distance from the outfall, while the control site (unaffected by warm water effluent) was close to the intake and approximately 1000 m apart from the impact site (Fig. 1).

2.2. Environmental factors at impact and control sites

Environmental factors, including pH, dissolved oxygen (DO) and salinity were measured monthly using a CTD (Ocean Seven 316 Idronaut, Italy). Water temperature at 1 m depth was continuously monitored over the study period at 30-min intervals using temperature data loggers (HOBO Data Loggers, Onset, USA). Since water was turbulent and well mixed at the outfall (impact site), water temperature at 5 m depth was almost the same as in 1 m depth, as was measured by CTD. At each sampling event, water samples were taken and transferred to the laboratory in a cooling box. Nutrients (nitrate, nitrite, silicate and phosphate), as well as chlorophyll *a* (chl-α) concentrations were measured in the lab using standard protocols (Adams, 1990; Federation and Association, 2005).

2.3. Sampling design

On July 2014, polyvinylchloride (PVC, PMMA Topco) replicated panels (15 × 15 × 0.3 cm), were hung vertically from solid permanent structures at the two sites using ropes, at 1 and 5 m depth, and exposed to biofouling colonization (Supplementary Fig. S1). Three replicate panels were used at different depths and time intervals at the impact and control sites. In order to position the panels vertically in the water column and also to keep a 1.5 m distance between hanging ropes and prevent any physical contact between the panels, a 10 kg iron tube was attached to the end of the ropes. The vertical position of the panels was chosen in order to ensure an equal chance of colonization by photo- and heterotrophic organisms. Two sets of panels (namely 1-month old panels (1MOP) and 3-month old panels (3MOP)) were used in order to assess the impact of the age structure of the community. 1MOP were named by the representative month and 3MOP were named by the representative season. The 1MOP are regarded as recruitment, whereas 3MOP represent the development at each season i.e., restart of the 3 months biofouling process at different seasons of the year. These panels were retrieved and replaced with new panels every month or every three months during the sampling period, respectively. Due to weather instability, replacement of 1MOPs were done every 1 month ± 7 days. Thus, in the end, a total of 11 samplings were achieved over the annual cycle. After each retrieval, settlement panels were transferred to the laboratory and photographed from both sides using a digital camera (Cannon Power Shot G15). Panels were stored in the freezer at −20 °C until further analyses.

2.4. Laboratory analyses

In order to reduce errors associated with visual estimation, the image analysis software CPCe (Kevin E Kohler and Gill, 2006) was used to determine percent coverage of different groups of biofouling assemblages on each plate. In this method, each image was sub-divided into a 3 × 3 grid of 9 cells, with 11 random points per cell producing 99 points analyzed per picture (Kevin E. Kohler and Gill, 2006). Subsequently, total percent coverage was calculated, which can well exceed 100% in instances with more than one layer of biofoulers attached to a panel (Canning-Clode et al., 2013).

The panels were hung vertically and left free to spin, and therefore assumed to be similar at both sides. Therefore, the data of both sides were pooled and variables were calculated as means per square meter. Since a complete list of biofouling species in the Persian Gulf was not available, different identification keys were used (Bosch et al., 1994; Carpenter et al., 1997; Trono, 1997; Chan et al., 2009; Naderloo and Tuerkay, 2012; Shahdadi et al., 2014; Kokabi and Yousefzadi, 2015). Species identities were verified by different taxonomic experts within Iran and abroad. Biofouling assemblages, including macroalgae and sessile macro-invertebrates were identified to the lowest possible taxonomic level. For identification of bryozoans, after bleaching with sodium hypochlorite, SEM images were taken. Bryozoan species were then identified by Dr. Paul Taylor from the Natural History Museum, London. Species richness was calculated as the total number of species present on each panel (Barboza et al., 2012).

In this study, functional groups were ascertained using four different traits according to Canning-Clode et al. (2009) and Wahl (2009). The used traits encompassed body size, growth form, trophic type, and modularity (see details in Supplementary Table S1). Consequently, functional richness for a given panel was defined as the number of functional groups colonizing the respective panel.

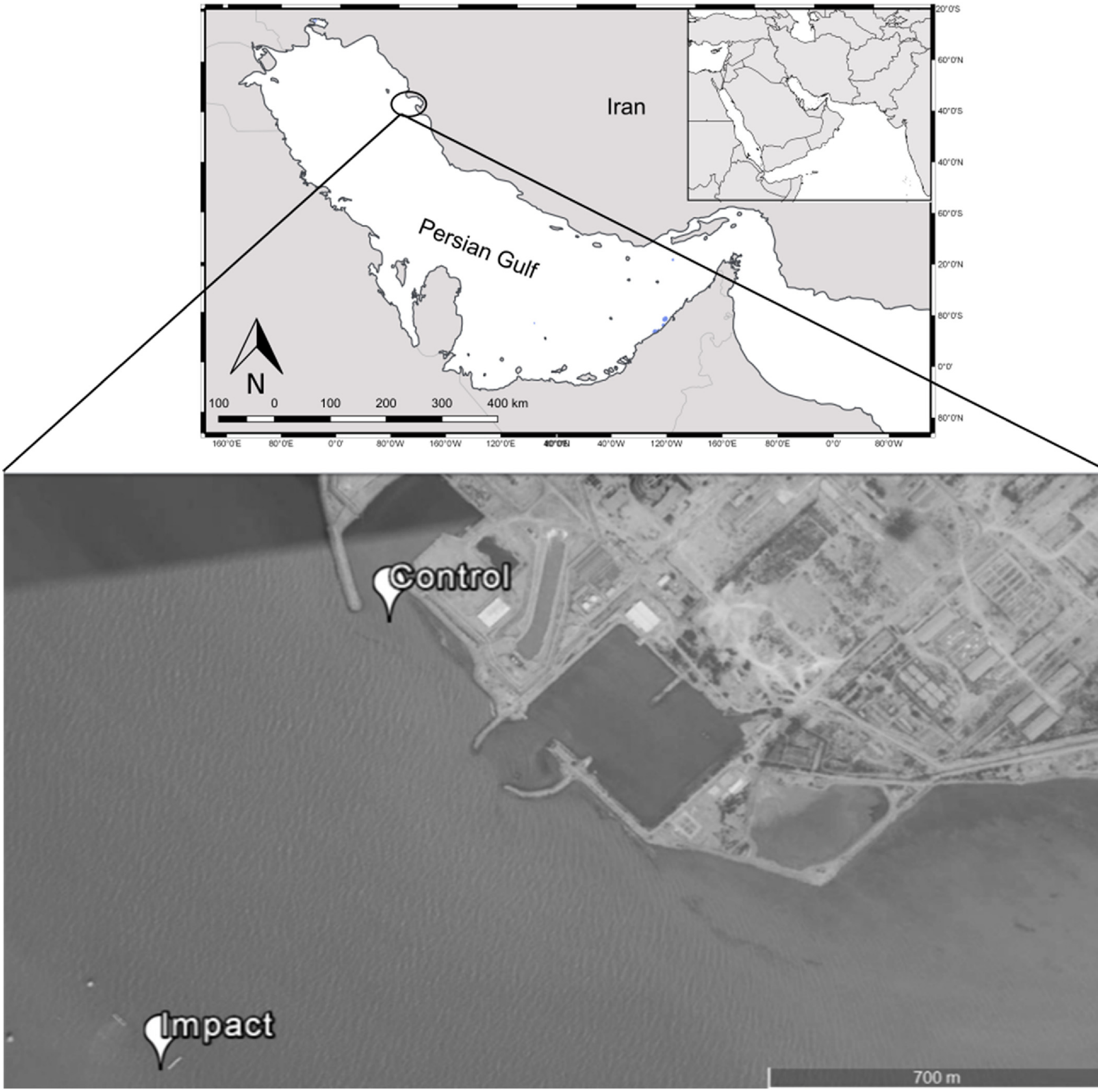

Fig. 1. Location map of the study area in the vicinity of Bushehr city on the Iranian coast of the Persian Gulf. Circle indicates where the current study was conducted (satilite image of the site was taken using Google Maps).

2.5. Statistical analyses

The permutational multivariate analysis of variance (PERMANOVA) was applied using the PERMANOVA + add-on in PRIMER 6.0 (Anderson et al., 2008) to elucidate the effects of sampling site, time (month) and depth on the different response variables measured. The p-values from 4999 permutations were obtained based on binomial deviance dissimilarities, which is appropriate for empirical distributions (Anderson and Millar, 2004). We used square-root transformed data for assemblage structure and present/absent transformed data for species composition. Our PERMANOVA design had three fixed factors: “month” (11 levels), “station” (2 levels), “depth” (2 levels), and the interaction terms between these three factors. Similarity Percentages Analysis (SIMPER) was applied to identify taxa that contributed greatly to the dissimilarity between stations. PERMANOVA based on Bray-Curtis similarity matrix on square-root transformed percent cover data was applied for total coverage, species richness, and functional richness. To elucidate the effects of measured environmental parameters on biofouling community parameters (total coverage, species richness, and functional richness) for 1MOP, we used RDA (Redundancy Analysis) on the log-transformed environmental data matrices using the ordination program CANOCO for Windows V4.0.

3. Results

3.1. Environmental parameters

The analyses of the environmental conditions at sampling sites

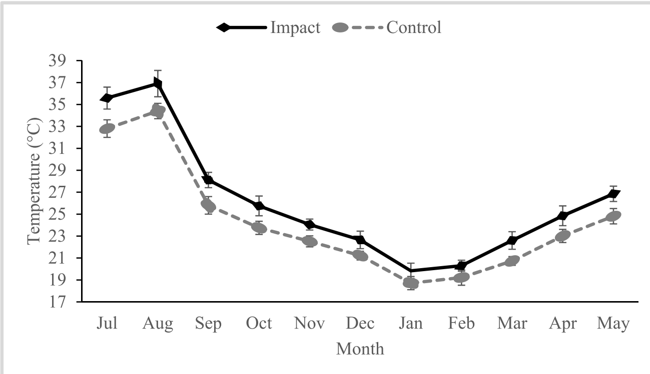

Fig. 2. Mean (± SE) seawater temperature in 1 m depth over the one-year experiment at the impact and at the control site.

(control and impact) revealed that both locations are almost similar in all abiotic factors except for the temperature. The ambient temperature ranged from 18.5 to 34.5 °C at the control site, while at the impact site it ranged between 20 and 37 °C (Fig. 2). Salinity at both sites was constant throughout the year (control: 39.48 ± 0.44 psµ, impact: 39.5 ± 0.43 psµ). pH followed a relatively similar trend in both sites ranging from 7.38 to 8.58. Ammonia (control: 0.024, impact: 0.015), nitrate (control: 0.087, impact: 0.076), phosphate (control: 0.078, impact: 0.085), silicate (control:0.40, impact: 0.33) and TSS (control: 34.2, impact: 32.5) also showed similar fluctuations at both sites. Chl-α varied from 0.29 to 1.93 (control: 1.81, impact: 1.12), showing slightly higher values at the control site (see also Supplementary Fig. S2 for details on all mentioned parameters).

3.2. Mean cover percent and functional grouping

In total, 180 settlement panels were assessed for biofouling assemblages over the period of the experiment (one year) at the two sites, two depths and two time sets (1MOP, n = 132; and 3MOP, n = 48). The results led to the identification of 15 taxa comprised of macroalgae, barnacles, annelids, bryozoans, ascidians, sponges, solitary corals, crabs, gastropods, and bivalves, belonging to 15 families from 8 classes of biofouling assemblages and 6 taxa of motile invertebrates (*Pilumnopeus convexus, Hyastenus hilgendorfi, Alpheus* sp, *Nanosesarma sari, Thais mutabilis*). Furthermore, six functional groups i.e. MMSS, LMSS, LSSA, LFAC, XFAC, and XESC were recognized (Tables 1–3), all of which are described in Table S1.

3.3. 3. Biofouling structure and species composition

PERMANOVA results showed that biofouling structure and species composition were significantly different at different stations, in different months and at different depths, in both 1MOP and 3MOP (interactions in Table 4). This analysis also showed that the total coverage was influenced by station and month in both 1MOP and 3MOP, but not by depth (interactions in Table 5). At the impact site, the highest total coverage occurred on 1MOP and 3MOP, respectively, in July (117.2 ± 7.7) and spring (198.9 ± 7.8), correspondingly (Tables 1–3, Figs. 3 and 4). In 1MOP, total species richness and functional richness were significantly different between stations and months. For 3MOP, species richness was significantly different between month and depth, and functional richness was significantly different between months only (interactions in Table 5). In both 1MOP and 3MOP and at both control and impact sites, species richness and functional richness followed a relatively similar temporal trend through the value of functional richness was usually lower than that of species richness (Fig. 5). At the impact site (1MOP), the highest value of the mean total species (5) and functional (4) richness were observed in July. Both values then

Table 1
Mean cover percent ± SE and functional grouping of biofouling taxa observed for 1-month old panels (1MOP) at the impact site during the study period (July 2014 to May 2015). The information is presented by sampling events. Cover percent was not achieved for motile organisms (see details in the main text). Data for the two different depths (1 and 5 m) were pooled.

Phylum	Species	FG[a]	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Arthropoda	*Amphibalanus amphitrite*	MMSS	25.59 ± 6.64	41.50 ± 9.6	77.44 ± 13.4	34.18 ± 11.6	8.25 ± 2.2	7.24 ± 2.8	2.49 ± 1.8	0.42 ± 0.33	1.60 ± 1.3	25.76 ± 16.37	12.46 ± 4.7
	Chelonibia patula	LMSS	0.76 ± 0.33	0.08 ± 0.08	0	0.42 ± 0.27	0.25 ± 0.17	2.36 ± 1	0.34 ± .33	0	0	0.34 ± 0.16	12.96 ± 3.4
Mollusca	*Saccostrea cucullata*	LSSA	63.55 ± 8.9	19.11 ± 9.5	10.94 ± 6.8	30.64 ± 12.7	8.42 ± 3.6	2.19 ± 0.5	0.08 ± 0.08	0	0	0	5.79 ± 1.8
	Pinctada radiata	LSSA	2.59 ± 0.6	0	0	0	0	0	0	0	0	0	0
Annelida	*Hydroides elegans*	LMSS	1.60 ± 1.3	0	0	0.67 ± 0.57	0.59 ± 0.33	2.27 ± 1.8	1.35 ± 1.34	0	30.30 ± 13.74	1.43 ± 0.92	12.96 ± 8.58
Cnidaria	*Paracyathus stokesii*	MMSS	0	0.42 ± 0.24	0.51 ± 0.4	0.08 ± 0.08	0.08 ± 0.08	0	0	0	0	0	0
Chlorophyta	*Ulva compressa*	LFAC	0	0	0	0	0	0	0	0	6.48 ± 6.8	0	0
	Ulva lactuca	XFAC	0	0	0	0	0	0	0	0	3.45 ± 3.4	0	0
Ochrophyta	*Feldmannia* sp.	LFAC	1.85 ± 0.9	0	0	0	0	0	0	0	5.64 ± 3.5	31.67 ± 20.06	19.70 ± 5.9
Chordata	*Didemnum* sp.	XESC	20.81 ± 10.11	1.85 ± 1.8	0	0.59 ± 0.58	0	0	0	0	0	0	0
Porifera	Sponge	XESC	0	0	0	0	0	0	0.59 ± 0.58	0	0	0	0
Bryozoa	3 species[b]	XESC	0.51 ± 0.5	0.42 ± 0.4	0	1.01 ± 1.01	1.01 ± 1.01	2.36 ± 1.4	0	0	1.60 ± 1.59	5.22 ± 3.09	9.76 ± 3.7
Total coverage			117.24 ± 7.77	63.38 ± 5.15	88.89 ± 9.09	67.60 ± 5.11	18.60 ± 1.3	16.41 ± 0.8	4.85 ± 0.3	0.42 ± 0.21	49.07 ± 3.2	64.41 ± 4.5	73.63 ± 2.9
Total species richness			8	6	3	7	6	5	5	1	6	5	6
Total functional richness			5	5	2	4	4	4	4	1	5	4	5

[a] Body size: M (1–10 mm), L (10–100 mm), XL (100–1000 mm); Growth form: M (Massive), F (Filamentous), E (Encrusting), B (Bushy); Trophic type: S (Suspension feeder), A (Autotroph); Modularity: S (Solitary).
[b] Since the species could not be distinguished in the picture which was used for the calculation of coverage, further SEM clarified these three different species (*Parasmittina egyptica*, *Acanthodesia* sp. and *Celleporaria* sp.).

Table 2
Mean cover percent ± SE and functional grouping of biofouling taxa observed for 1-month old panels (1MOP) at the control site during the study period (July 2014 to May 2015). The information is presented by sampling events. Cover percent was not achieved for motile organisms (see details in the main text). Data for the two different depths (1 and 5 m) were pooled.

Phylum	Species	FG[a]	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Arthropoda	*Amphibalanus amphitrite*	MMSS	1.52 ± 0.22	8.00 ± 4.7	34.26 ± 9.5	4.04 ± 2.7	3.45 ± 1.4	7.83 ± 1.95	9.60 ± 2.2	12.65 ± 2.9	5.39 ± 1.7	0.25 ± 0.25	0
	Chelonibia patula	LMSS	0	0	0	0	0	0	0	0	0	0	0
Mollusca	*Saccostrea cucullata*	L SSA	43.77 ± 1.9	37.68 ± 6.7	18.52 ± 5.1	38.13 ± 8.9	17.59 ± 3.4	7.83 ± 1.6	0	0	0	0	45.54 ± 6.4
	Pinctada radiata	L SSA	0.67 ± 0.33	0.25 ± 0.25	0	0	0	0	0	0	0	0	0
Annelida	*Hydroides elegans*	LMSS	0.67 ± 0.33	0	0	3.96 ± 3.5	1.36 ± 0.86	4.71 ± 0.86	5.39 ± 2.01	4.38 ± 1.8	6.14 ± 3.92	1.18 ± 0.84	12.12 ± 7.6
Cnidaria	*Paracyathus stokesii*	MMSS	0	0.51 ± 0.41	1.35 ± 1.34	0.93 ± 0.92	0	0	0	0	0	0	0
Chlorophyta	*Ulva compressa*	LFAC	0	0	0	0	0	0	0	0	0	0	0
	Ulva lactuca	XFAC	0	0	0	0	0	0	0	0	0	0	0
Ochrophyta	*Feldmannia* sp.	LFAC	6.40 ± 6.3	0	0	0	0	0	0	0	0	23.53 ± 12.49	18.85 ± 9.17
Chordata	*Didemnum* sp.	XESC	0	0	2.19 ± 1.18	0.67 ± 0.67	2.95 ± 0.63	0.93 ± 0.58	0	0	0	9.848 ± 4.65	0
Porifera	Sponge	XESC	0	0	0	0	0	1.26 ± 0.99	0	0	0	0	0
Bryozoa	3 species[b]	XESC	8.25 ± 0.7	0	0	0	1.60 ± 0.8	3.44 ± 0.9	4.55 ± 1.44	3.96 ± 1.2	6.11 ± 1.5	5.72 ± 3.76	12.20 ± 3.64
Total coverage			61.27 ± 5.09	46.42 ± 4.44	56.31 ± 4.36	47.72 ± 4.4	26.94 ± 2.03	26 ± 1.2	19.52 ± 1.2	20.98 ± 1.54	17.64 ± 1.08	40.53 ± 2.88	88.71 ± 5.5
Total species richness			6	4	4	5	5	6	3	3	3	5	4
Total functional richness			5	2	3	4	4	4	3	3	3	4	4

[a] Body size: M (1–10 mm), L (10–100 mm), XL (100–1000 mm); Growth form: M (Massive), F (Filamentous), E (Encrusting), B (Bushy); Trophic type: S (Suspension feeder), A (Autotroph); Modularity: S (Solitary).
[b] Since the species could not be distinguished in the picture which was used for the calculation of coverage, further SEM clarified these three different species (*Parasmittina egyptica, Acanthodesia* sp., *Celleporaria* sp.*)*.

Table 3
Mean cover percent ± SE and functional grouping of biofouling taxa observed for 3-month old panels (3MOP) at the impact and control site during the study period (July 2014 to May 2015). The information is presented by sampling seasons. Cover percent was not achieved for motile organisms (see details in the main text). Data for the two different depths (1 and 5 m) were pooled.

Phylum	Species	FG[a]	Impact site				Control site			
			summer	autumn	winter	spring	summer	autumn	winter	spring
Arthropoda	*Amphibalanus amphitrite*	MMSS	68.52 ± 13.3	67.84 ± 14.45	37.88 ± 15.56	0	30.13 ± 13.74	35.77 ± 6.52	11.78 ± 4.8	0
	Chelonibia patula	LMSS	1.85 ± 1.1	3.70 ± 2.12	0	0	0	8.25 ± 7.47	0	0
	Striatobalanus amaryllis	LMSS	10.10 ± 10.1	13.47 ± 13.46	0	0	0	0	0	0
Mollusca	*Saccostrea cucullata*	LSSA	18.35 ± 4.09	16.24 ± 5.4	0	0	36.87 ± 7.71	32.74 ± 7.82	0	26.26 ± 4.15
	Pinctada radiata	LSSA	2.02 ± 2.2	1.52 ± 1.52	0	0	0	0	0	6.06 ± 1.19
	Barbatia foliata	LSSA	0	0	0	0.84 ± 0.8	0	0	0	0
Annelida	*Hydroides elegans*	LMSS	0	11.53 ± 6.43	40.49 ± 18.44	95.79 ± 2.66	1.35 ± 1.3	3.20 ± 7.82	31.31 ± 12.2	2.53 ± 1.15
Cnidaria	*Paracyathus stokesii*	MMSS	8.25 ± 5.2	3.20 ± 3.19	0	0	2.19 ± 2.18	2.86 ± 2.86	0	0
Ochrophyta	*Feldmannia* sp.	LFAC	0	16.67 ± 16.66	43.00 ± 20.22	39.56 ± 17.70	0	30.13 ± 16.4	19.86 ± 9.13	16.33 ± 7.3
	Colpomenia sinuosa	LBAC	0	0	0	8.42 ± 5.48	0	0	0	0
Porifera	Sponge	XESC	11.11 ± 7.3	0	0	5.89 ± 3.7	0	1.85 ± 1.85	0	0
Chordata	*Didemnum* sp.	XESC	0	5.89 ± 4.3	0	14.31 ± 6.44	3.87 ± 2.47	11.45 ± 8.11	0	26.26 ± 4.01
Bryozoa	3 species[b]	XESC	0	27.36 ± 9.09	54.49 ± 13.81	34.18	0	18.08 ± 9,68	36.87 ± 15.8	12.96 ± 5.81
Total coverage			120 ± 4.5	167.42 ± 4.5	175.86 ± 5.3	198.98 ± 6.7	74.41 ± 10.25	144.34 ± 19.29	99.83 ± 10.29	90.40 ± 3.5
Total species richness			7	10	4	7	5	8	4	6
Total functional richness			4	5	4	5	4	5	4	4

[a] Body size: M (1–10 mm), L (10–100 mm), XL (100–1000 mm); Growth form: M (Massive), F (Filamentous), E (Encrusting), B (Bushy); Trophic type: S (Suspension feeder), A (Autotroph); Modularity: S (Solitary).
[b] Since the species could not be distinguished in the picture which used for the calculation of coverage, further SEM clarified these three different species (*Parasmittina egyptica, Acanthodesia* sp, *Celleporaria* sp.).

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Table 4
PERMANOVA results of biofouling structure and species composition based on binomial deviance measure of (a) square-root transformed data for assemblage structure and (b) present/absence transformation for species composition at different stations (ST), months (M)/season (S) and depths (D) in 1-month old panels (1MOP) and 3-month old panels (3MOP).

	Source	df	(a) Square-root transformed			(b) Present/absence transformed		
			MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
1 MOP	Station	1	22.388	24.811	< **0.001**	20.368	24.437	< **0.001**
	Month	10	16.316	18.082	< **0.001**	15.45	18.536	< **0.001**
	Depth	1	25.3	28.038	< **0.001**	25.275	30.323	< **0.001**
	ST × M	10	4.5661	5.0603	< **0.001**	4.161	4.9921	< **0.001**
	ST × D	1	2.1531	2.3861	0.1388	1.718	2.0611	0.194
	M × D	10	2.2902	2.5381	**0.002**	1.8927	2.2707	**0.0134**
	ST × M × D	10	0.27776	0.30782	0.9416	0.11647	0.13974	0.9692
	Residuals	88	0.90234			0.83351		
	Total	131						
3 MOP	Station	1	5.7068	4.4753	**0.0048**	4.4011	3.6603	**0.0174**
	Season	3	33.801	26.507	< **0.001**	33.332	27.721	< **0.001**
	Depth	1	36.14	28.341	< **0.001**	34.598	28.775	< **0.001**
	ST × S	3	7.2528	5.6877	**0.0006**	6.863	5.7078	**0.0002**
	ST × D	1	1.6817	1.3188	0.3296	1.5134	1.2587	0.3674
	S × D	3	3.3762	2.6477	**0.0192**	3.29E+00	2.73E+00	**0.0208**
	ST × S × D	3	0.11855	9.30E-02	0.9326	4.02E-02	3.35E-02	0.9452
	Residuals	32	1.2752			1.2024		
	Total	47						

P-values were obtained using 4999 permutations of residuals under a reduced model. Significant results ($P < 0.05$) are highlighted in bold.

decreased toward September, increased again in October and reached a plateau during November and September. During January and February, both values declined to the lowest level and then they rose again (Table 1, Fig. 5). In 3MOP, the highest mean species (4.5) and functional (3.5) richness was found in autumn at the impact site while the lowest mean values (2.5) of functional and species richness were observed in winter at the impact site and in summer at the control site (Table 3, Fig. 5).

3.4. Similarity of control and impact sites (SIMPER analysis)

The results of the SIMPER analysis for the similarity of control and impact sites are shown in Table 6. In 1MOP, the oyster, *Saccostrea cucullata,* the barnacle, *Amphibalanus amphitrite,* the polychaete, *Hydroides elegans*, Bryozoa and the brown alga *Feldmannia* sp. accounted for almost 71.2% of the dissimilarities between the two stations, while in 3MOP, *Amphibalanus amphitrite, Hydroides elegans*, Bryozoa, *Feldmannia* sp. and *Saccostrea cucullata* contributed about 65.0% of the dissimilarities between the two stations.

3.5. Coverage trends

In general, fouling coverage on 1MOP was the highest during summer months (i.e., 117.24% in July), but decreased during autumn months (i.e., 18.6% in November) and was almost zero during winter months (i.e., 0.4% in February), but increased again in spring (64.4% in April; Fig. 4(. Although a similar trend of fouling pressure was observed at both sites over time, but in general, the total coverage was higher at the impact site. However, the winter months (January and February) showed a stronger fouling pressure at the control site (Fig. 4). The

Table 5
Results of the three-way PERMANOVA for coverage, species richness and functional richness at different stations (ST), month (M)/season (S) and depths (D) in 1-month old panels (1MOP) and 3-month old panels (3MOP).

	Source	df	Coverage			Species richness			Functional richness		
			MS	Pseudo-F	P (perm)	MS	Pseudo-F	P (perm)	MS	Pseudo-F	P (perm)
1 MOP	Station	1	0.17191	9.2331	**0.0042**	0.17794	9.7409	< **0.001**	0.17814	9.7582	**0.001**
	Month	10	0.1132	6.0799	< **0.001**	8.86E-02	4.8501	< **0.001**	0.088091	4.8255	< **0.001**
	Depth	1	6.04E-03	0.32454	0.6234	4.05E-03	0.22191	0.5848	0.003189	0.17469	0.6392
	ST × M	10	8.99E-02	4.8296	**0.0006**	8.24E-02	4.5097	0.0002	0.082439	4.5159	**0.0002**
	ST × D	1	6.88E-03	0.36932	0.5898	4.07E-03	0.22287	0.6018	0.004367	0.23922	0.5866
	M × D	10	3.74E-02	2.0069	**0.0342**	3.63E-02	1.9856	0.0376	0.035928	1.9681	**0.037**
	ST × M × D	10	2.07E-02	1.1124	0.3564	2.01E-02	1.0978	0.3762	0.019874	1.0887	0.374
	Residuals	88	1.86E-02			1.83E-02			0.018255		
	Total	131									
3 MOP	Station	1	1795.4	42.14	< **0.001**	8.2742	0.17947	0.7088	7.5131	0.28297	0.595
	Season	3	318.88	7.4846	< **0.001**	332.12	7.2036	< **0.001**	200.12	7.5371	< **0.001**
	Depth	1	16.336	0.38343	0.5778	271.29	5.8841	**0.0192**	2.3427	0.088234	0.7876
	ST × S	3	142.54	3.3456	0.0272	107.78	2.3378	0.0842	33.946	1.2785	0.2914
	ST × D	1	6.0552	0.14213	0.7732	55.27	1.1988	0.2844	59.174	2.2287	0.1478
	S × D	3	45.459	1.067	0.3702	86.991	1.8868	0.149	257.93	9.7145	**0.0004**
	ST × S × D	3	33.278	0.78109	0.5348	21.042	0.4564	0.7288	8.8336	0.33271	0.8064
	Residuals	32	42.605			46.105			26.551		
	Total	47									

P-values were obtained using 4999 permutations of residuals under a reduced model. Significant results ($P < 0.05$) are highlighted in bold.

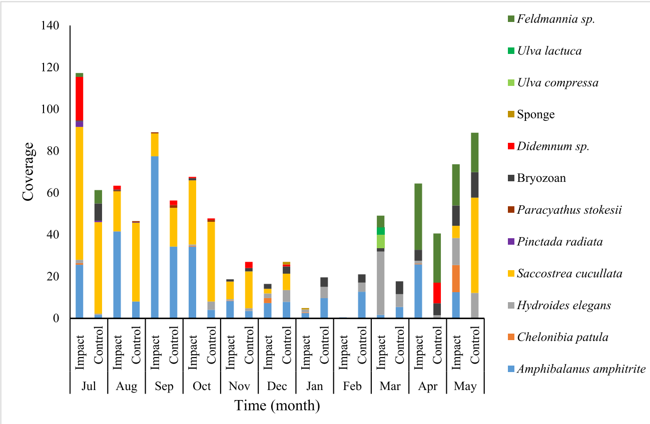

Fig. 3. Cover percent of fouling species on 1 month old panels (1MOP) during July 2014 to May 2015 at the impact and control sites.

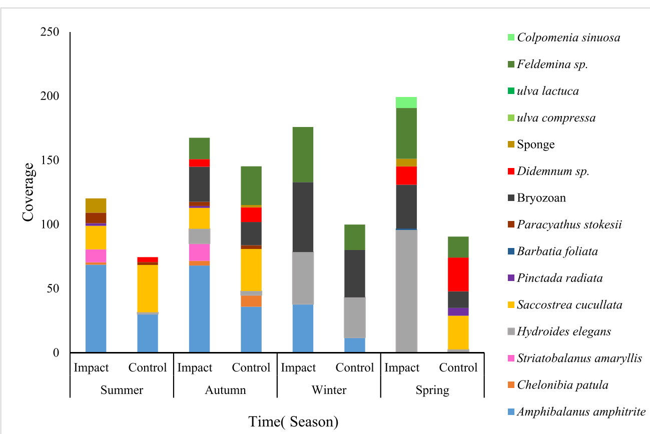

Fig. 4. Cover percent of fouling species on 3 months old panels (3MOP) during July 2014 to May 2015 at the impacted and control sites.

highest cover was observed for the oyster *Saccostrea cucullata* and the barnacle *Amphibalanus amphitrite* in May–July and September, respectively. Interestingly, at the impact site, coverage of oysters had peaked in July, while at the control site oysters were dominant in May-July-August. Common to both sites, a pronounced shift from an autotrophic to a heterotrophic community was observed over the seasonal cycle, with higher algal cover in spring compared to the rest of the year (Fig. 3).

For 3MOP, fouling coverage at the impact site increased from summer (120%) to spring (198.8%; Fig. 4). During summer and autumn, the barnacles (*Amphibalanus amphitrite*) had the highest cover, whereas, during winter and spring, alga (*Feldmannia* sp.), bryozoans and tube-building polychaets (*Hydroides elegans*) had the highest percent of cover (Fig. 4). Coverage in all seasons was lower at the control site than the impacted site, ranging from 74.4% in summer to 144.3% in autumn (Fig. 4).

3.6. Relationship between environmental parameters and biofouling

The relationship between all measured environmental parameters and fouling coverage, species richness and functional groups are shown in Fig. 6. Environmental parameters, such as temperature, salinity, chl-α, silica, phosphate concentrations mainly influenced the coverage of fouling species. The most conspicuous positive relationship was observed between temperature and fouling coverage.

4. Discussion

This is the first investigation into the relationship between the elevated water temperature and macro-fouling communities in the Persian Gulf. The countries bordering the Persian Gulf are widely using its coastal waters for siting desalination and power plants. The marine environment adjacent to power plants is exposed to the negative effects of their chemical effluents and discharge of hot water from cooling systems. Temperature is arguably the most significant physical factor in the environment running the physiological activities of invertebrates (Hochachka and Somero, 2002; Doney et al., 2012). Therefore, we hypothesized that an increase in seawater temperature will influence the cover and composition of biofouling communities. In the present study, the total biofouling coverage was higher on the panels exposed to elevated temperatures near the power plant outflow compared to the control. This suggests that warming of seawater may be one of the main factors leading to increased biofouling coverage.

High temperatures, to some extent, especially in the presence of high food concentrations, such as plankton, increase metabolic rates (a key component of energy budgets) and feeding efficiency in invertebrates (Anderson, 1994). This in turn, leads to more energy accumulation to cover growth and reproductive costs in adults (Todd, 1998; Wolowicz and Sokolowski, 2006) and also increases the larval settlement and recruitment (Whalan and Webster, 2014). As a result, the increase of biofouling coverage observed in the present study can be explained by the higher rate of biological processes due to elevated temperatures. Enhanced rates of biofouling on artificial surfaces due to warming has been previously demonstrated using bare experimental panels (Greene and Grizzle, 2007; Poloczanska and Butler, 2010; Rao, 2010; Sokołowski et al., 2017). Using a “hot-plate” (electrically heated settlement panels) system, Smale et al., 2011 showed that warming by 0.67 °C resulted in doubling of the coverage of a colonial ascidian. Similarly, our results showed that warming by 2 °C can increase the mean biofouling coverage by a factor of 1.5.

Despite the fact that our design of using a cooling system of the power plant as ‘natural treatment’ is rather limited compared to laboratory and mesocosm studies and cannot be replicated, it has strong advantages. First, the impact of temperature was investigated on a large number of organisms in a relatively large area. Second, in such system, elevated temperatures may influence not only adult fouling organisms, but also their adjacent larvae. It is well established by experimental research that increased temperature may affect the larval stages of invertebrates (e.g., Nasrolahi et al., 2012; Pansch et al., 2012; Yuan et al., 2016). For example, in the case of *Amphibalanus improvisus*, Pansch et al. (2012) demonstrated that warming favored survival of nauplii but conversely, decreased survival of cyprids. Warming also affects other non-fouling species, such as planktons (Poornima et al., 2005; Muthulakshmi et al., 2019), grazers, and predators (a factor neglected in many other studies). These organisms can affect biofouling communities directly and/or indirectly (Leclerc and Viard, 2018). Third, our experiment allowed us to investigate possible changes of biofouling communities throughout the year. Thus, our approach provides a more realistic response of biofouling communities to warming, compared to previous and commonly applied laboratory and mesocosm studies. Similar field approaches have been applied to the effect of temperature on benthic communities, such as the study by Suresh et al. (1993). It showed that warming led to a decrease in the abundance and even elimination of macroepifauna, with only barnacles and gastropods surviving. Also, there are some studies investigating the impacts of acidification on benthos (Martin et al., 2008; Crook et al., 2012; Pettit et al., 2013; Inoue et al., 2013; Fabricius et al., 2015), which demonstrate lower abundance of calcifying species at lower pH. However, it should also be noted that although in this study the investigated sites were almost similar in all the measured environmental factors but the seawater temperatures, we cannot rule out the possible effects of other factors, such as different paths of larval supply at each station.

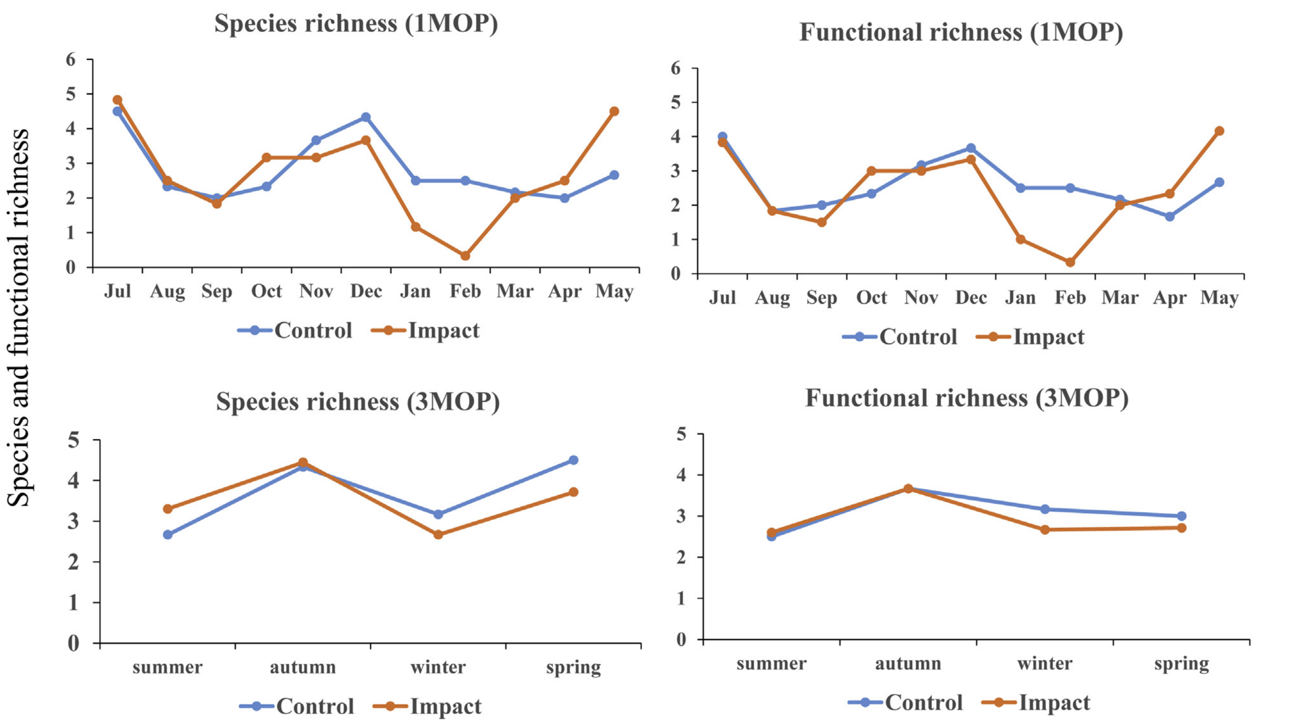

Fig. 5. Mean species and functional richness of biofouling communities on 1 month old panels (1MOP) and 3 months old panels (3MOP) during July 2014 to May 2015 at the impact and control sites.

Table 6
SIMPER analysis of biofouling species contributions (> 5%) at each station for 1-month old panels (1MOP) and 3-month old panels (3MOP) according to taxa coverage during the study period.

Species		Impact	Control	Contribution %
		Average Coverage	Average Coverage	
1 MOP	*Saccostrea cucullata*	2.20	3.23	26.49
	Amphibalanus amphitrite	3.49	2.05	24.67
	Hydroides elegans	0.93	1.09	13.21
	Bryozoan	0.64	1.44	12.62
	Feldmannia sp.	0.86	0.77	9.31
	Didemnum sp.	0.37	0.48	5.11
3 MOP	*Amphibalanus amphitrite*	5.33	3.39	17.27
	Hydroides elegans	4.20	1.87	16.29
	Bryozoan	3.82	2.85	14.81
	Feldmannia sp.	2.68	4.11	14.15
	Saccostrea cucullata	1.98	2.44	12.97
	Didemnum sp.	1.01	2.02	8.44
	Sponge	0.83	0.14	3.22
	Chelonibia patula	0.52	0.36	2.99

Through succession, fouling species composition continuously changes by the variance of biotic and abiotic factors (Greene and Schoener, 1982; Lin and Shao, 2002). In our study, we observed a clear seasonal shift between communities developing in summer and winter. Besides, elevated temperatures in the impact site caused algal species to emerge earlier than in the control site. It should be noted that phenology change in marine alga is strongly correlated with the combination of temperature and nutrient and light availability (Kain, 1989). Moreover, warming favored fouling of barnacles more than oysters. This may be due to strong tolerance of juvenile barnacles to increased temperature, as demonstrated by Pansch et al. (2012). Elevated temperature also caused a slight reduction in species and functional

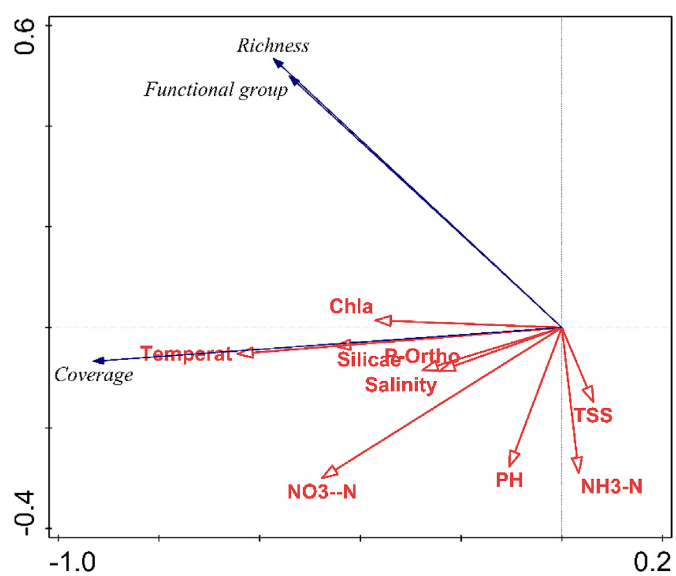

Fig. 6. Redundancy Analysis (RDA) as a relationship between environmental data and the fouling community parameters including coverage, species richness and functional group. TSS (Total Suspended Solids), NH3–N (ammonia nitrogen), NO3–N (Nitrate nitrogen), P-Ortho (orthophosphoric acid), Silicae (silicic acid), Chla (chlorophyll a), Temperat (temperature).

richness of the biofouling communities. Our findings are in line with previous studies (Schiel et al., 2004; Wernberg et al., 2011; Kordas et al., 2015; Ashton et al., 2017). For example, Schiel et al. (2004), using thermal outfall of a power plant, showed that a 3.5 °C increase in seawater temperature caused substantial community-wide changes in 150 species of algae and invertebrates of a rocky shore in California. Also, Kordas et al. (2015) and Ashton et al. (2017) observed a reduction in the diversity of biofouling assemblages on heated settlement panels. Such shifts in the structure and composition of biofouling communities, even if minor, may have important ecological consequences and alter biological interactions, community function, and ecological services in the future (Wood et al., 2008; Yang and Rudolf, 2010; Kroeker et al., 2013). It can also facilitate the dominance of non-native species (Stachowicz et al., 2002; Sorte et al., 2010; Kim and Micheli, 2013). Although the native rage of most identified species in the current study is difficult to determine, the bryozoan *Parasmittina egyptica* and likely the barnacle species (*Amphibalanus amphitrite* and *Chelonibia patula*), the polychaete *Hydroides elegans* and the oyster *Pinctada imbricata radiata* are non-native species in the region. From these species, *Amphibalanus amphitrite* showed the most positive response to warming.

Barnacles, especially *Amphibalanus amphitrite,* were the major fouling species and played a significant role in dissimilarities between community developed at the two locations. It is known that *Amphibalanus amphitrite* is the major fouling species in tropical waters (Shahdadi et al., 2014). After few days of planktonic life, larvae permanently attach to the substrate and become adults within few months. Temperatures around 30 °C led to the lower mortality of this species even at lower salinity (10–20 ppt; Anil et al., 1995). Lower temperatures, on the other hand, resulted in lower recruitment of this species during winter months in Hong Kong waters (Qiu and Qian, 1999). The mean coverage of this species at the warmer site in our study was 2.5 times higher than the control throughout the year. Increasing the coverage of barnacles at higher temperatures can be caused by the higher growth rates, greater larval settlement and shorter larval duration (Smale et al., 2011; Nasrolahi et al., 2013). Additionally, omitting some non-tolerant species by warming can make more space available for opportunistic species, such as barnacles. It seems that during unusual conditions such as warming, some tolerant groups overtake their rivals and become dominant. For instance, barnacles which are more successful rivals than other groups, usually grow faster and defeat other taxa (Richmond and Seed, 1991). The positive effect of warming on the abundance of barnacles indicated that high temperatures in our experiment (maximum 36.3 °C) was still lower than the physiological tolerance of this species.

Our results demonstrated mainly positive effects of warming on biofouling communities, besides weak decreases in functional and species richness. Since the response of some other Persian Gulf communities to warming, especially in the absence of rapid adaptation, could be negative (Feary et al., 2013; Hume et al., 2015), the balance of ecosystems in the future might be altered with warming. Mitigating and management strategies should, therefore, be undertaken to reduce the increasing issues of biofouling driven by global warming (Dobretsov et al., 2019).

In conclusion, our study showed that the structure and composition of biofouling communities in the control and impact sites were significantly different. Elevated water temperatures increased the mean coverage of biofouling communities but decreased the functional and species richness. Our results indicate that warming will likely increase the biofouling pressure by few species adapted to higher temperatures in the future. The outcome of this research should be taken into account in future antifouling studies and monitoring and mitigation efforts.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2019.102403.

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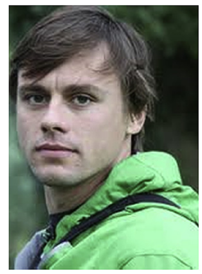
Maral Khosravi is a Ph.D. student at GEOMAR Helmholtz Center for Ocean Research. One of her research interests is the effect of environmental and biological stressors on marine invertebrates. She is currently doing her PhD on the impact of endoparasite (trematode) on snails in the Persian Gulf.

Ali Nasrolahi is an Assistant Professor at the Department of Aquatic Science and Biotechnology, Shahid Beheshti University. His main research interest are stress ecology and climate change, biofouling communities and rocky shore biodiversity.

Mohammad Reza Shokri is a marine biologist with research and teaching interests in coral reef ecology at the Department of Marine Biology, Faculty of Life Sciences and Biotechnology, Shahid Beheshti University. He is interested in coral reef ecology, reef fish ecology, marine conservation, and marine environmental management. His particular research interests include testing the surrogacy value of biotic and abiotic features of marine ecosystems, selecting and designing marine protected areas, coral reef molecular ecology, reef fish ecology, and the management and conservation of marine biodiversity.

Sergey Dobretsov is the President of European Society of Marine Biotechnology, the UNESCO Chair of Marine Biotechnology and the Director of the Center of Excellence in Marine Biotechnology. He is an Associate Professor at the College of Agricultural and Marine Sciences, Sultan Qaboos University. He is a marine biotechnologist and he has been working with marine biofouling and antifouling solutions more than 25 years. In particular, he is interested in interactions between microbes and larvae of invertebrates.



Christian Pansch is an Ecologist/Ecophysiologist. During his career, he investigated climate change impacts on marine benthic systems, applying single-species to community approaches. The field of environmental variability and its significance as amplifier or buffer of climate change impacts is a field of research that he followed through these years. In addition, he has worked on marine fouling, with respect to processes and solutions.