

# A quantitative and statistical biological comparison of three semi-enclosed seas: the Red Sea, the Persian (Arabian) Gulf, and the Gulf of California

William B. Ludt<sup>1</sup> · Link Morgan<sup>1</sup> · James Bishop<sup>2</sup> · Prosanta Chakrabarty<sup>1</sup>

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**Abstract** Similar habitats separated by great distances can provide remarkable examples of convergent evolution in biological diversity, and have been influential in our understanding of community ecology, historical biogeography, and evolution. Here, we compare three semi-enclosed seas in arid regions of the northern hemisphere, the Red Sea, the Persian (Arabian) Gulf, and the Gulf of California, and test whether they show similar biodiversity patterns. Despite large geographic separations between the seas, the similar shapes and latitudinal locations lead to several analogous abiotic conditions. These similarities, however, do not result in equivalent biodiversity patterns, even when correcting for different regional species pools. Comparisons revealed that the Red Sea contains a greater species diversity of vertebrates, but that the Gulf of California contains the greatest species diversity of invertebrates. Notably, vertebrate abundance patterns were statistically similar between the Persian Gulf and the Gulf of California. Divergences are likely due to variable habitats within each sea, several influential abiotic differences, and dissimilar histories among the seas. While these results

support a null hypothesis of biological dissimilarity despite abiotic similarities, they are the first statistical comparisons of the biotas of these three regions. Continued statistical comparisons among marine ecosystems have the potential to reveal ecological and evolutionary patterns that typically go unnoted.

**Keywords** Biodiversity · Biogeography · GBIF · Rarefaction · Species richness · Climate change

## Introduction

Similar habitats in vastly separated locations were a major source of comparison for early natural historians and explorers, leading to foundational research on biogeography and evolution (comte de Buffon 1785; Darwin 1859). Comparing convergent habitats reveals patterns that provide insights into general properties of community ecology (Bellwood et al. 2002; Wills et al. 2006) and biogeography (Hubbell 1997). In terrestrial habitats, global parallels have been drawn between tropical rainforests (Gentry 1993; Corlett and Primack 2006), chaparral shrub land (Cowling et al. 1996), and deserts (Kelt et al. 1996), among others. Similar comparisons between regions have also been made in marine systems, including coral reefs (Bellwood and Hughes 2001), kelp forests (Steneck et al. 2002), and rocky intertidal zones (Blanchette et al. 2009). Here, we present a novel biotic and abiotic comparison of three semi-enclosed seas in arid regions of the northern hemisphere: the Red Sea, the Persian Gulf (also referred to as the Arabian Gulf), and the Gulf of California.

The three seas in question share certain physical characteristics, but do these similar abiotic conditions result in statistically comparable biological species compositions?

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✉ William B. Ludt  
wbludt@gmail.com

<sup>1</sup> Ichthyology Section, 119 Foster Hall, Museum of Natural Science, Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA

<sup>2</sup> Ecosystem-based Management of Marine Resources, Environment and Life Science Research Centre, Kuwait Institute for Scientific Research, P.O. Box 24885, 13109 Safat, Kuwait

Comparisons between various pairs of these seas have been casually made for certain taxa [Red Sea vs. Gulf of California fishes (Thomson et al. 2000); Red Sea vs. Persian Gulf reef taxa (DiBattista et al. 2016b)]. Here, we explore this question among all three seas, including all marine taxa, by using geo-referenced species data to test the biogeographic hypothesis that the analogous abiotic conditions of each sea resulted in similar biodiversity patterns.

### Abiotic environment/region of study

The three seas in question share similar physical characteristics; they are elongate bodies of water on a northwest to southeast axis and have overlapping latitudinal ranges (Fig. 1). Each sea contains a single opening to surrounding oceans in the southeast, with the exception of the man-made Suez Canal connecting the Red Sea to the Mediterranean Sea. For the Red Sea and Persian Gulf, this opening is narrow, through the Bab el-Mandeb Strait and Strait of Hormuz, respectively, while the Gulf of California contains a much larger, and deeper, opening. Arid deserts surround all three seas, and although the Persian Gulf and Gulf of California do have freshwater input from the north, recent diversions have led to all three seas currently having negligible freshwater input (Brusca et al. 2005; Kämpf and Sadrinasab 2006). The result is that evaporation is higher than precipitation for all basins, creating an inflow of water through their openings. The resulting dry atmospheric conditions, along with seasonal wind patterns, influences circulation within each sea (Alvarez-Borrego 2010; Yao et al. 2014a, b; Pous et al. 2015).

In all three seas, circulation is comprised of a series of cyclonic and anti-cyclonic gyres, which vary seasonally (Kämpf and Sadrinasab 2006; Lavín et al. 2014; Yao et al. 2014a, b; Pous et al. 2015). These gyres create areas of retention for larval movement, preventing exchange between neighboring oceans (Sheppard et al. 1992; Marinone 2003). All three seas also have considerable seasonal fluctuations in water properties, such as temperature and salinity, due to the latitudinal extent of each (Table 1). The most dramatic variation occurs in the Persian Gulf due to its shallow average depth of 34 m, with temperature ranges exceeding 15 °C throughout the year (Al-Yamani et al. 2004) and salinity exceeding 45 psu (physical salinity units; Buchanan et al. 2016). Temperatures and salinities vary similarly in the northern Gulf of California, where shallow coastal areas are comparable to the Persian Gulf, but stabilize more towards the southern entrance to the eastern Pacific (Brusca et al. 2005). The Red Sea also contains water in excess of 40 psu (Yao et al. 2014b), but while temperatures vary by approximately 10 °C seasonally and geographically, on average, they are warmer than the Persian Gulf and Gulf of California (DiBattista et al. 2013). As such, the physical conditions of these seas put severe stresses on the organisms that inhabit them, which will likely

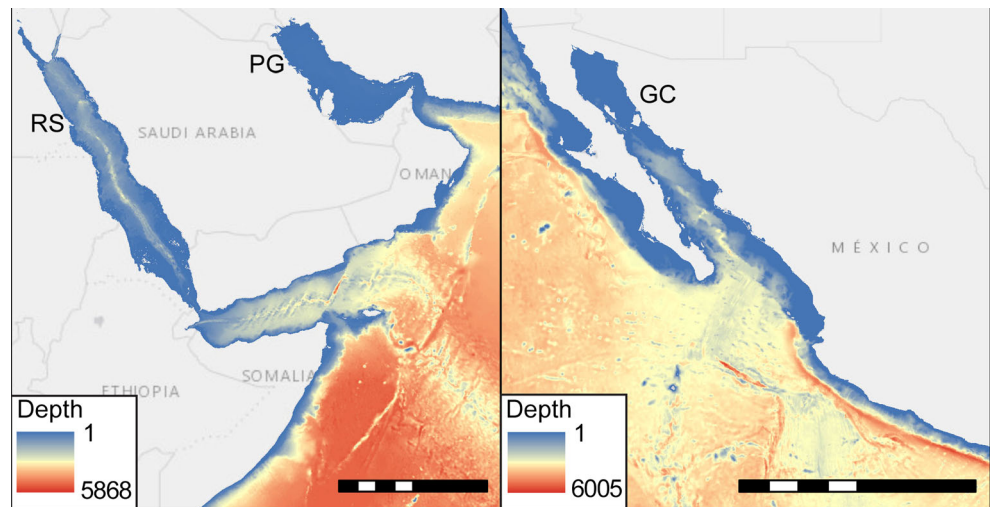
become more severe as global warming increases (Thomson and Lehner 1976; Buchanan et al. 2016; DiBattista et al. 2016a). Understanding how these physical conditions influence community composition will aid in our understanding of how climate change, and other anthropogenic impacts, will likely affect each sea in the future.

### Methods

To determine if abiotic conditions influence biotic comparisons, we examined overall species richness patterns in each sea. Estimating biodiversity is generally based on repeated sampling of a region; as more samples are collected, species richness will increase until, theoretically, an asymptote is reached, where increased sampling will not yield more species (Bunge and Fitzpatrick 1993). Rarefaction curves created by randomly subsampling abundance data can determine the extent of sampling for a region as it approaches the asymptote, or theoretical species richness (Gotelli and Colwell 2001, 2011). Comparing rarefaction curves between regions is difficult due to variations in sampling effort, methods, randomness, and underlying variation in the overall species pool of different regions (Gotelli and Colwell 2011). However, recent advances have allowed for comparisons to be made across distinct regions, even when underlying species assemblages do not share similar species (Cayuela et al. 2015).

Individual-based macro (>0.5 mm) species occurrence data were gathered for major marine phyla (Online Table 1) from geo-referenced specimen data on the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org>, accessed December 2015) using a polygon search area in the R package “*rgbif*” (Chamberlain et al. 2015). All species were verified against the World Register of Marine Species (WoRMS; <http://www.marinespecies.org>). These data were then combined into vertebrate and invertebrate datasets for each sea. Individual-based rarefaction curves were then constructed using the *rarefaction.individual* function of the R package “*rareNMtests*” (Cayuela et al. 2015), with the species richness Hill number,  $q = 0$  (Hill 1973; Chao et al. 2014). Pairwise comparisons of rarefaction curves were then conducted testing against ecological or biogeographic null models using the species richness Hill number,  $q = 0$ , 200 replications, and a log-normal distribution for the biogeographic comparisons in “*rareNMtests*”. These null models predict that two curves are sampling species from the same species pool (ecological null model) or that species richness and accumulation curves follow the same patterns, despite samples coming from distinct species pools (biogeographic null model; Cayuela et al. 2015), and can help determine the similarity of biodiversity among the three seas.

**Fig. 1** A map of the Red Sea (RS), the Persian Gulf (PG), and the Gulf of California (GC). The colors indicate depth in meters. Bathymetry data were gathered from the MARSPEC database (Sbrocco and Barber 2013). The scale bars for both maps represent 1000 km



## Results

In total, 85,445 species occurrence points were used, representing a total of 9,636 unique, verified species. Of these, 44,953 occurrences were of vertebrate taxa and 40,492 were from invertebrate taxa, representing 3,043 and 6,593 unique species, respectively (Fig. 2; Online Resource 1). Sampling differed among the three seas, with the Gulf of California producing the most records, followed by the Red Sea and the Persian Gulf. Rarefaction curves for vertebrate and invertebrate taxa in all seas failed to reach an asymptote (Fig. 3). Species richness and abundance profiles differ significantly in all ecological models for vertebrate and invertebrate taxa ( $p < 0.01$ ). Similarly, all abundance profiles differed significantly for the biogeographic models, except for vertebrate comparisons between the Gulf of California and the Persian Gulf (Table 2).

## Discussion

The Red Sea, Persian Gulf, and Gulf of California share certain abiotic features, yet biotic comparisons among the three seas reveal important differences rather than convergence. While observing similarities between congruent habitats may reveal certain patterns, it can be more beneficial at times to ask why regions are different rather than why they are similar (Corlett

and Primack 2006). For instance, the regional diversity of surrounding oceans of these three seas varies, and, therefore, the sources of biodiversity differ. The ecological null model test assumes that observations are taken from the same species pool, and all the pairwise comparisons for this test were significant, rejecting the notion that observations are coming from the same species pool (Table 2). The majority of species in the Gulf of California are shared with the eastern Pacific, a region that is notably species-poor and has been described as having a “reduced speciation capacity” (Cowman and Bellwood 2013). The Persian Gulf and Red Sea both contain species from the Indian Ocean, yet endemism levels differ dramatically between the two (DiBattista et al. 2016b), likely driving the observed differences recovered in the ecological null tests. While regional species pools could drive the differences observed between our datasets, the biogeographic null test accounts for different underlying species assemblages, and still shows significant differences in most pairwise comparisons. There are several physical properties of these seas that may explain the differences in species accumulation curves.

The overall surface area and water volume of the three seas vary considerably due to average depths (Table 1), and, yet, even if the values obtained here are corrected for either surface area or volume, they are not equivalent. The volumetric differences between the seas are caused by average depth and geological history. The Persian Gulf, at its deepest, is

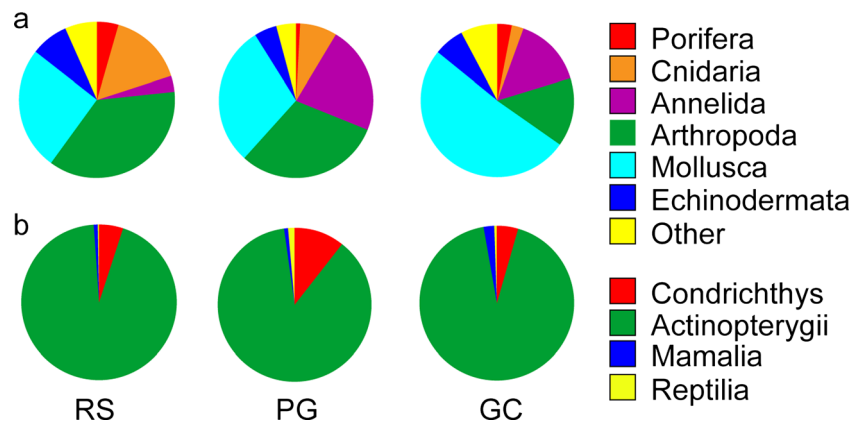
**Table 1** Physical properties of the three seas compared in this study

Sea	Surface area	Volume	Depth <sup>a</sup>	SSS <sup>a</sup>	SST <sup>a</sup>
Red Sea	450,000	251,000	484/2,847	34.1–41.5	12–32.8
Persian Gulf	239,000	8,780	34/194	32.6–41.5	12.6–34.4
Gulf of California	177,000	145,000	965/4,435	33.9–36.2	11.3–31.8

Approximate surface area and volume are reported in km<sup>2</sup> and km<sup>3</sup>, respectively. Depth is reported in meters and as mean/max. Sea surface salinity (SSS) ranges are reported in physical salinity units (psu) and sea surface temperature (SST) ranges are reported in degrees Celsius

<sup>a</sup> Data obtained from the MARSPEC database (Sbrocco and Barber 2013).

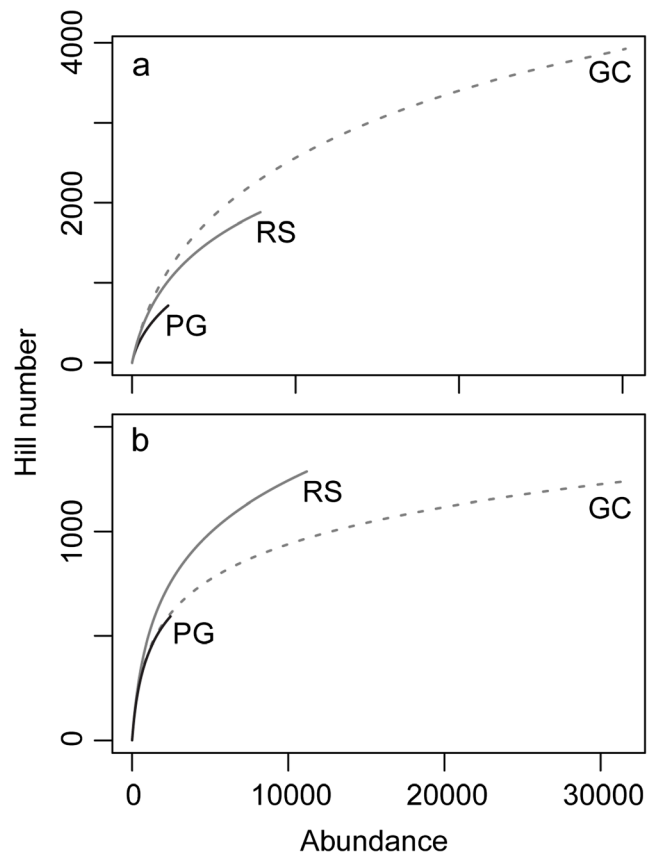
**Fig. 2** Species richness summaries of major marine classes found for invertebrate (a) and vertebrate (b) taxa in the Red Sea (RS), Persian Gulf (PG), and Gulf of California (GC). Raw values for each class can be found in Online Resource 1



shallower than 200 m (Table 1), and, therefore, would not contain any species adapted to deep environments that might be found in the Red Sea or Gulf of California, which reach a maximum depth of 2,847 m and 4,435 m, respectively (Kuronuma and Abe 1986). Both seas, however, were formed by rifting tectonic plates (Kassler 1973; Ledesma-Vázquez and Carreño 2010), which, in addition to creating deeper troughs, have led to variable habitats in each sea, from sandy beaches and mudflats, to rocky reefs and coral reefs (the only example of which in the Gulf of California is Cabo Pulmo). The succession of each basin also varies, despite similar origination times. While the Red Sea began forming in the Eocene, it did not connect with the Indian Ocean until the late Miocene/early Pliocene, approximately 5 Mya (Bailey et al. 2007), around the same time that the Baja Peninsula separated from mainland Mexico, forming the Gulf of California (Ledesma-Vázquez and Carreño 2010). The Gulf of California continued to expand to the north throughout the Pliocene (Nagy and Stock 2000), during the same time that the Zagros folding of eastern Iran completed the current shape of the Persian Gulf (Kassler 1973). Notwithstanding overlapping formation times, Pleistocene sea level fluctuations impacted the seas individually, and are known to have had a large impact on marine systems worldwide (Ludt and Rocha 2015). The Persian Gulf was entirely exposed during the last glacial maximum (LGM), and was only inundated with water approximately 6 kya (Lambeck 1996), resulting in the Persian Gulf being the youngest of the three seas, and possibly resulting in a depauperate Persian Gulf biota (Price et al. 2002). Meanwhile, while some suggest that the Red Sea was hypersaline during the LGM (Klausewitz 1989), recent studies indicate persistent occupation (although in periodic isolation) of its fauna throughout the Pleistocene (DiBattista et al. 2013, 2016a). Contrary to this, the Gulf of California does not seem to have been isolated at all throughout the Pleistocene, with species retaining their full dispersal potential, even during sea level lows (Ludt and Rocha 2015).

Additionally, while all three seas have cyclonic and anti-cyclonic gyres, circulation patterns differ among them.

Surface waters enter the Persian Gulf (Kämpf and Sadrinasab 2006), while surface waters exit the Gulf of California (Alvarez-Borrego 2010). The Red Sea exhibits a combination of these patterns throughout the year; in the winter, it resembles the Persian Gulf, but in the summer, there is a surface water outflow from the basin similar to that of the Gulf of California (Yao et al. 2014a, b). The difference in circulation patterns affects the flow of nutrients and, consequently,



**Fig. 3** Individual-based rarefaction curves comparing invertebrate (a) and vertebrate (b) species richness between the Red Sea (RS; solid gray), Persian Gulf (PG; solid black), and Gulf of California (GC; dotted gray). Curves were constructed using the Hill number  $q = 0$ , with the rareNMtests R package (Cayuela et al. 2015)

**Table 2** Faunal comparisons of ecological and biogeographic species richness/abundance estimates between the three semi-enclosed seas

Comparison	Vertebrate		Invertebrate	
	Eco	Biog	Eco	Biog
Red Sea vs. Persian Gulf	<0.01	<0.01	<0.01	<0.01
Red Sea vs. Gulf of California	<0.01	<0.01	<0.01	<0.01
Gulf of California vs. Persian Gulf	<0.01	0.47	<0.01	<0.01

All entries are *p*-values calculated using the rareNMtests R package (Cayuela et al. 2015) with the species richness Hill number,  $q = 0$ , 200 iterations, and a log-normal distribution for the biogeographic comparison. Significant values ( $p < 0.05$ ) indicate deviation from the null hypothesis that the fauna of each sea are derived from the same species assemblage (*Eco*) or that the seas share a similar species richness or relative abundance distributions, despite dissimilar species assemblages (*Biog*)

primary production, which is lowest in the Red Sea (Raitsos et al. 2013) and higher in the Persian Gulf (Al-Yamani et al. 2006) and Gulf of California (Zeitzschel 1969).

Finally, we cannot reject the possibility that the differences recovered in this study are due to data biases. Species occurrence data from large databases such as GBIF can contain erroneous identifications and are subject to biases associated with sampling effort and taxonomic expertise for various groups (Yesson et al. 2007). Despite the possible errors associated with conglomerate species occurrence datasets, they have proven to be valuable in macroecological studies (García-Roselló et al. 2015). Comparisons between absolute species richness values from the Gulf of California gathered from this study versus a thorough literature review by Brusca et al. (2005) revealed similar values. Furthermore, general patterns in our results match a recent comparison of shallow-water taxa between the Red Sea and Persian Gulf that did not use GBIF occurrence data (DiBattista et al. 2016b), providing support for the robustness of GBIF records used here.

Notably, all rarefaction curves for the three seas failed to reach an asymptote (Fig. 3). Under-sampling is apparent for the Persian Gulf, and may be the underlying reason why vertebrate accumulation curves could not be distinguished from the Gulf of California. This under-sampling reflects a long history of limited research in the Persian Gulf, which has historically been less often studied than the neighboring Red Sea (Vaughan and Burt 2015). However, under-sampling of species richness is typical in empirical datasets (Chao et al. 2009), and while it may influence point estimates between rarefactions curves (Gotelli and Colwell 2001), the randomized rarefactions tests performed here account for differences in sample size (Cayuela et al. 2015). Furthermore, differences in sampling effort did not always result in the highest amount of unique species for the Gulf of California (the sea with the greatest sample size), as the Red Sea contained a greater richness of vertebrates than the Gulf.

## Conclusions

The Red Sea, Persian Gulf, and the Gulf of California share general physical properties. Biotic comparisons among the three seas, however, reveal different biodiversity patterns, even when accounting for different underlying species assemblages. These results were not unexpected, given that each sea is a conglomeration of many different habitat types driven by abiotic differences and dissimilar geological histories, and, yet, they raise specific questions: Why does the Gulf of California have a greater invertebrate diversity, and why, despite extensive sampling in the Gulf of California, does the Red Sea have a greater vertebrate diversity? Our novel statistical comparisons indicate the need for additional studies in these seas that compare biodiversity within specific habitat types to find the underlying causes of the patterns we recover. Furthermore, rarefaction analyses, such as those used in this study, could reveal striking patterns in other global comparisons, and should be used to compare additional widely separated regions. Finally, this study highlights the increased need for sampling in the Middle East. Continued collections in the Red Sea and Persian Gulf will increase the accuracy of comparisons such as those used here, and will ultimately result in a better understanding of the historical biogeography of these seas.

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