ORIGINAL ARTICLE

The determinants of species richness of a relatively young coral-reef ichthyofauna

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ABSTRACT

Aim Unique topographic features left the Red Sea and its north-eastern extension into the Gulf of Aqaba practically devoid of coral-reef-based organisms during the last glacial maximum. The current ichthyofauna in these two 'regions' thus represents the product of relatively recent colonization by species found in the Arabian Sea, which adjoins the Red Sea at its southern tip. We used this system to test why some marine species seemingly fail to extend their geographic range, thereby generating spatial heterogeneity in biodiversity.

Location The Arabian Sea, Red Sea, and the Gulf of Aqaba.

Methods A list of coral-reef-associated fish species, belonging to the 10 most speciose families, was compiled for each region using published sources. The data were analysed (major axis regression, randomization tests) for taxonomic and body-size-dependent biases in colonization probabilities. A simple probabilistic model was used to examine the potential contribution of local (within-region) extinctions to determining species composition in the Red Sea.

Results Of the 462 reef-associated species that inhabit the Arabian Sea, 69% have crossed successfully into the Red Sea; of these, 55% have crossed into the Gulf of Aqaba. A species' probability of being found in either 'target' was independent of presumed innate differences, i.e. ecological correlates of taxonomic affiliation and body size. Similarly, local extinctions were found unlikely to have been of consequence over the past several thousand years.

Main conclusions Present-day differences in the species richness of reef-associated fish species among the Arabian Sea, Red Sea and Gulf of Aqaba appear to be the product of external, non-selective constraints on colonization. The random nature of the colonization process is suggestive of ecological redundancy among coral-reef fish species. Importantly, the study places a time frame on the processes that determine spatial patterns of biodiversity in reef fish.

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INTRODUCTION

Spatial heterogeneity in the distribution of species richness is a staple of ecological research. Explanations of large-scale patterns in biodiversity often invoke factors such as area, energy/productivity, environmental stability, and historical events (review in Gaston, 2000). Concomitantly, it is becoming increasingly clear that large-scale patterns themselves can have a significant effect on the structure of local communities (Cornell & Lawton, 1992; Caley & Schluter, 1997). Generalizations, however, remain highly contentious.

Coral reefs are among the most diverse of marine ecosystems, and have been the focus of several recent studies aimed at inferring the causes of large-scale patterns in marine biodiversity (Bellwood & Hughes, 2001; Connolly *et al.*, 2003; Mora *et al.*, 2003). Here too, however, the available data appear to point in somewhat opposing directions. In trying to explain longitudinal gradients in the richness of coral-reef fish

across the Indo-Pacific, Bellwood & Hughes (2001) emphasized the primary role of habitat area. They went further to demonstrate that species composition in local communities represents random samples from the total Indo-Pacific species pool, at least in terms of the relative representation of families. Addressing the same question, Mora *et al.* (2003), on the other hand, emphasized the role of dispersal capacity, including innate inter-specific differences in larval pelagic duration.

These patterns presumably reflect the combined action of evolutionary and ecological processes over extensive temporal and spatial scales. In the present study we ask what insight may be gained from analysing a unique system that is considerably smaller and, more importantly, younger. The Red Sea, with its extension into the Gulf of Aqaba (Fig. 1), constitutes the north-western-most extension of the Indo-Pacific ichthyofauna. Its sole connection with the open ocean is the narrow (18 km at Perim Island) and shallow (137 m by Hannish Island) Straits of Bab el Mandab, which open to the Arabian Sea [i.e. that part of the Indian Ocean situated between the western coast of India, Arabia and the eastern coast of Somalia up from its border with Kenya, including the Gulf of Aden but excluding the Persian Gulf (Manilo & Bogorodsky, 2003)]. The Gulf of Aqaba in turn connects to the Red Sea through the Straits of Tiran (width: *c.* 0.6 km, depth: 250 m).

During the last glacial maximum, *c.* 18 kyr BP, water depth at Bab el Mandab was reduced to *c.* 15 m, greatly limiting water exchange with the Indian Ocean (Siddall *et al.*, 2003). Consequently, salinity within the Red Sea and Gulf of Aqaba surpassed 50‰, decimating most plankton and reef-based organisms (Sheppard *et al.*, 1992; Siddall *et al.*, 2003). Sea level returned to within 20 m of the present level around 8 kyr BP (Siddall *et al.*, 2003), with contemporary reefs becoming re-established around 6–7 kyr BP (Braithwaite, 1987).

It seems, therefore, that the current ichthyofauna of the Red Sea and Gulf of Aqaba represents the outcome of recent colonization, free of evolutionary and deep-historical signatures. At present, the number of reef-associated species, belonging to the 10 most speciose families, drops significantly as one moves from the Arabian Sea to the Red Sea and the Gulf of Aqaba (see below). In the following, we present results from several analyses aimed at inferring whether the observed drop in richness can be related to non-random colonization and/or extinction.

METHODS

In the following we use the abbreviations AS, RS and GA to correspond to the Arabian Sea, Red Sea and Gulf of Aqaba, each of which we treat as an individual 'region'. As a first approximation, we ignore spatial structure in species distribution within regions (Kemp, 1998). Since surface currents through Bab el Mandab and Tiran consistently feed into the Red Sea and the Gulf of Aqaba (Sheppard *et al.*, 1992), we assume that re-colonization of RS by AS species, and of GA by RS species is predominantly unidirectional. Hence, we proceed to refer to the paired regions as separate systems, each consisting of a 'source' and a 'target'.

Fish species richness and body sizes

We compiled separate species lists for GA, RS and AS, using the primary literature and our own (E. Brokovich) unpublished data (Ben-Tuvia *et al.*, 1983; Baranes & Golani, 1993;
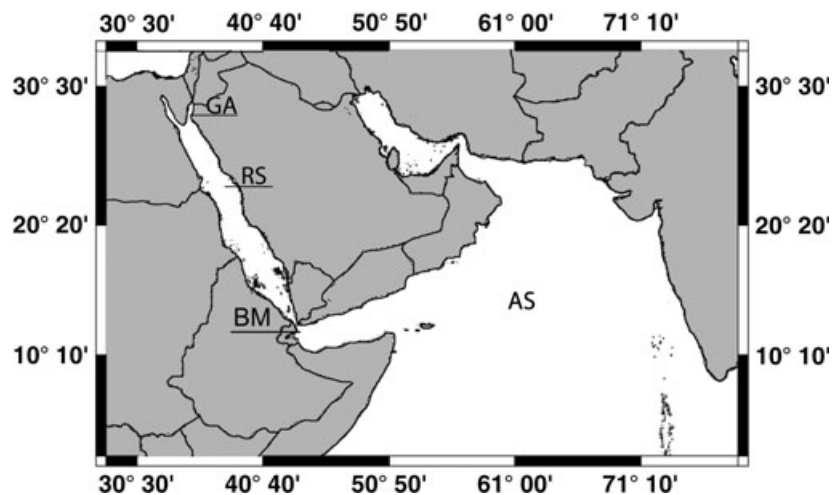

Figure 1 Outline of the three regions considered in this study and the potential barriers to dispersal: the straits of Bab el Mandab (BM), which connect the Arabian and Red seas (AS and RS), and the straits of Tiran, which connect the Red Sea and Gulf of Aqaba (GA). The potentially relevant dimensions of AS, RS and GA are shoreline length: *c.* 703, 7180, and 28,180 km, respectively; and total reefal area: *c.* 407, 16,980, and 993 km^2, respectively (data compiled from Spalding *et al.*, 2001). Consistent, monotonic gradients in salinity and sea-surface temperature (SST) extend from BM to northern GA – salinity: *c.* 36‰ to *c.* 41‰; SST: 32–26 °C in summer, and 26–21 °C in winter (Edwards, 1987); for a more complete view of SST across all three regions see http://www7320.nrlssc.navy.mil/global_ncom/anims/ara/sst12m.gif.

Goren & Dor, 1994; Khalaf & Disi, 1997; Golani & Diamant, 1999; Brokovich, 2001; Khalaf & Kochzius, 2002; Manilo & Bogorodsky, 2003; M. Goren, pers. comm.). The lists included species from the 10 most speciose families in GA, with the intention of maximizing the statistical strength of our analyses (Apogonidae, Blenniidae, Chaetodontidae, Gobiidae, Labridae, Pomacentridae, Scaridae, Scorpaenidae, Serranidae and Tetraodontidae). Species names were verified using FishBase (http://www.fishbase.org).

We excluded reverse-Lessepsian migrants (i.e. species that migrated from the Mediterranean to the Red Sea), Red Sea endemics (in order to exclude the effect of possible local adaptation), and species not defined as reef-associated, for example those inhabiting estuaries and sandy/rocky habitats, pelagic species, etc. Seventy-one species reported from RS and the Indo-Pacific, but not from AS were added to the latter's species list (Appendix S1); that is, we assume that 'missing' species are omissions arising from misidentification and low sampling effort in AS, or that they have only recently gone locally extinct there. The proportion of total family richness contributed by the added species ranged from 0.02 (Chaetodontidae) to 0.45 (Scorpaenidae), with an average of 0.16.

Maximum total lengths reported in FishBase were used to estimate adult body sizes. In cases where total length was not reported (c. 20% of the species), we used species-specific conversion factors to estimate it from the reported standard lengths.

Data analyses

Species richness estimates are likely to be measured with error, regardless of locality. Major axis (MA) regression is the appropriate model for evaluating the association between variables that have been measured with error, and where error variances are expected to be equal (McArdle, 2003). We used MA regression to evaluate the relationship in family-specific richness between each target and its source. For each source–target system, bootstrap standard errors of the MA slope (β_1) and intercept (β_0) were estimated using the standard deviation of the corresponding parameter, calculated for 1000 randomly drawn (with replacement) samples of the 10 families. Similarly, we calculated the bootstrap probability that the observed difference between the two slopes is different from that expected by chance. Regression r-squared (r^2) values were calculated using the sum of squared deviations measured from the observed and MA-predicted values to the bivariate mean.

We used two approaches to test for among-family differences in proportional representation at the target. First, we asked whether per-family richness at the target deviates significantly from that expected by chance, based upon its richness in the source. We addressed this question by examining 95% binomial confidence intervals (Agresti & Coull, 1998; see Appendix S2), with β_1 as the probability of being present in the source. Secondly, we examined whether families deviated consistently from their expected richness at the target by evaluating the concordance among the y-

components of MA residuals (which are measured perpendicularly to the regression line).

For reasons detailed below, we also tested whether regional differences in species richness are associated with: (1) a significant change in the regional frequency distribution of body size; and (2) a loss of generic richness that is different from that expected by chance. We used the G-test to address the first question (four species for which total-length data were unavailable were excluded from the analysis). For the second question we used a simple randomization procedure: for each family, at each of the two targets, we generated expected values by randomly choosing (without replacement, $n = 1000$ iterations) the observed number of species from the species list of the corresponding source, and then counting the number of represented genera. We then examined whether the observed number of genera fell within the expected 95% confidence intervals. As the analysis may be confounded by a high prevalence of genera that, at the source, are represented by a single species, we repeated the analysis using an abridged species list of only those genera represented by ≥ 2 species. Data analyses were carried out using MATLAB (version 6.5; MathWorks, Natick, MA, USA) and SPSS (version 10.0; SPSS Inc., Chicago, IL, USA).

Modelling extinction

We seek to evaluate the most likely rate of local extinction in the Red Sea by examining the observed number of GA species not found in RS (r), assuming that: (1) the probabilities of local extinction in GA and RS are independent, and (2) colonization is unidirectional (see above). Under these assumptions, the probability that a species is absent from RS while being present in AG is $\phi = 1 - P + P(1 - S)$. P is the probability that a species has colonized RS, given its current presence in GA; S is the survival probability of the species in RS. ϕ, therefore, sums the probability of species colonizing (and surviving in) GA without ever having colonized RS, and the probability of their having colonized both RS and GA but having gone extinct in the former. If we further assume that species colonize GA only after having colonized RS (i.e. $P = 1$) then the expected value of ϕ is $(1 - S)$. Thus, the likelihood of any hypothetical value of S given the observed number of AG species that are absent from RS is simply

$$\binom{r}{R}(1 - S)^r S^{R-r},$$

where R is species richness in GA. Note that for $P < 1$, $\partial\phi/\partial P < 0$, which would require higher values of S to generate the same ϕ.

RESULTS

Species richness at the targets does not differ significantly from that expected under random (i.e. probabilistic) sampling, falling consistently within the 95% confidence intervals predicted by the MA estimate of the *family-independent* sampling/
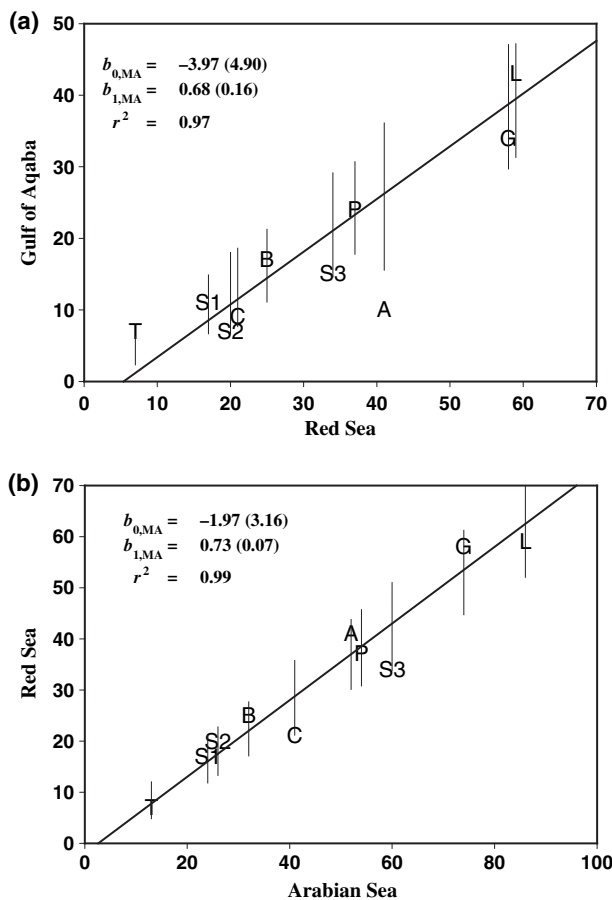
(a)

$b_{0,MA} = -3.97 (4.90)$
$b_{1,MA} = 0.68 (0.16)$
$r^2 = 0.97$

(b)

$b_{0,MA} = -1.97 (3.16)$
$b_{1,MA} = 0.73 (0.07)$
$r^2 = 0.99$

Figure 2 Species richness at the source and target of (a) the Red Sea–Gulf of Aqaba system, and (b) the Arabian Sea–Red Sea system, for 10 fish families. Major axis regression intercepts and slopes are provided with bootstrap standard errors in parentheses (β_0 and β_1, respectively). Vertical lines depict binomial 95% confidence intervals, calculated separately for each family at the target using β_1 as the probability for 'success'. Observed values are depicted by abbreviated family names: A, Apogonidae; B, Blenniidae; C, Chaetodontidae; G, Gobiidae; L, Labridae; P, Pomacentridae; S1, Scaridae; S2, Scorpaenidae; S3, Serranidae; T, Tetraodontidae.

colonization probability (β_1; Fig. 2a,b). The two source–target systems do not differ significantly in their regression slopes [bootstrap probability of $\Delta\beta_1 > (0.73–0.68)$: $P = 0.53$; $n = 1000$], nor does their residual richness covary significantly (Spearman rank correlation: $r_S = -0.21$, $P_{1-tail} = 0.28$). The observed number of genera lost when moving from source to target fell well within the null 95% confidence intervals, for both systems (Fig. 3); similar results were obtained when considering only genera represented by > 1 species (not shown). The three regions did not differ significantly in their body-size frequency distributions ($G \leq 2.86$, d.f. = 15, $P \geq 0.9$; Fig. 4).

DISCUSSION

It would appear that the richness of coral-reef fish species in RS and GA can be regarded as the product of random
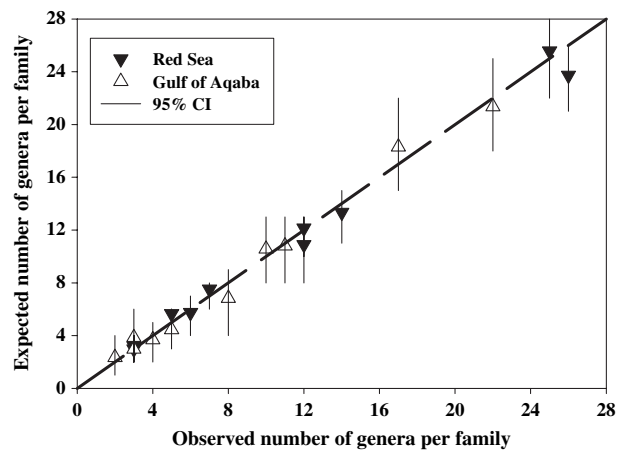

Figure 3 The observed and expected number of genera belonging to the 10 most speciose families of coral-reef fish in the Red Sea and the Gulf of Aqaba. 95% confidence intervals are based on 1000 iterations. Similar results are obtained when considering only genera represented by > 1 species (not shown).
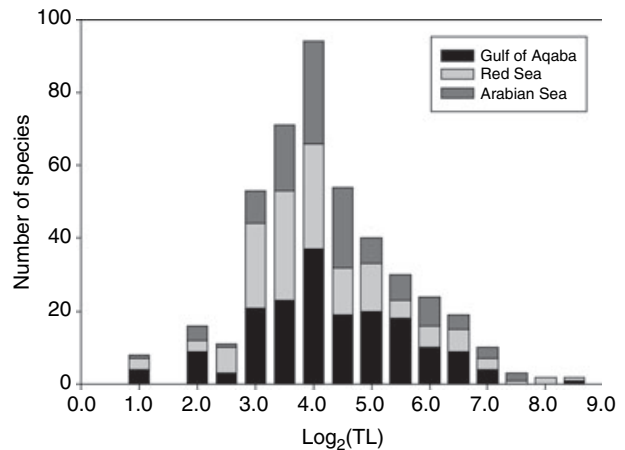

Figure 4 Frequency distribution of the maximum total length (TL, cm) of the reef-associated species belonging to the 10 families of coral-reef fish considered in this study, for each of the three regions. The three distributions do not differ significantly from each other.

sampling from their respective source regions (Fig. 2a,b). Moreover, as the sampling probabilities (β_1) for both source–target systems are indistinguishable, the colonization of both RS and GA would appear subject to similar constraints. Interestingly, these constraints seem independent of among-family differences in factors such as spawning mode or pelagic larval durations, as evidenced by the lack of a positive correlation in residual richness.

Successful colonization requires that species both arrive at the target (i.e. disperse), and establish/maintain a viable population there. Proportional sampling does not necessarily imply that, within families, species do not differ predictably in a manner that affects their colonization potential. Non-random loss of species would be consistent with proportional

sampling if, for example, families varied similarly in physiological tolerances, or if colonization success depended on population size and families shared similar rank-abundance distributions. Differential loss of rare and/or less tolerant species at the targets, in response to extrinsic factors such as habitat size [e.g. total reefal area, shoreline length; (cf. McArthur & Wilson, 1967; Rosenzweig, 1995)] and/or abiotic gradients [e.g. salinity, temperature (Macpherson, 2002; Currie *et al.*, 2004)], could thus affect all 10 families in a similar manner. Unfortunately, no data are available to test directly for such non-random loss of species in RS and GA. We can, however, test for it indirectly if we accept several assumptions.

We begin by considering two premises. First, that species are more (dis)similar to congeners than they are to other confamilials (e.g. Enquist *et al.*, 2002). Secondly, that body size is a good proxy for ecological and life-historical factors that affect abundance (e.g. for reef fish, Ackerman *et al.*, 2004). Under these premises, we tested the predictions that the observed drop in species richness should be accompanied by: first, a loss of generic richness that is either greater or smaller than that expected by chance (i.e. depending on whether congeners are dissimilar or similar, respectively); and secondly, among-region differences in body-size frequency distributions. In neither case did we find evidence in support of non-random loss of species richness (Figs 3 & 4, respectively).

We proceed to examine the potential contribution of local extinctions, under the assumptions listed in 'modelling extinction'. Given that none of the species found in GA were absent from RS, the likelihood of any hypothetical rate of survival in RS (S) equals S^R, where R is the species richness in GA. As the most likely value of S is 1, we find no indication of post-glacial local extinctions in RS as a whole. This would imply that the lower richness in RS, as compared with AS, is likely to be the result of failed colonization. This conclusion would not change if some species were to colonize GA without first colonizing RS (i.e. $P < 1$; see 'Modelling extinction'). While we are unable to extend the same rationale to GA, the similarity in MA slopes of the two source–target systems (Fig. 2) is suggestive of a similar stochastic 'barrier' to dispersal.

The random allocation of species to the RS and GA ichthyofaunas is suggestive of high functional equivalence among reef-associated fish species, and a consequent high degree of redundancy within the communities that they form (see also Bellwood & Hughes, 2001). For the reef-associated fish of RS and GA it appears that species presence/absence can be regarded as a matter of chance, primarily in the presumably ongoing process of colonization. Local extinctions, on the other hand, seem to have been of little consequence over the past several thousand years. It would seem, therefore, that present-day species richness in RS and GA is neither extrinsically limited nor regulated by colonization–extinction dynamics. In looking at relatively young ichthyofaunas [presumably < 8 kyr, given the estimated age of contemporary Red Sea reefs (Braithwaite, 1987)] the present study offers a

timeframe within which the key processes that structure these communities operate.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Appendix S1. Indo-Pacific species of coral-reef fish present in the Red Sea but absent from the Arabian Sea.
Appendix S2. Binomial confidence intervals.

This material is available as part of the online article from http://www.blackwell-synergy.com

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