Zoogeography of the coral reef fishes of the north-eastern Gulf of Aden, with eight new records of reef fishes from Arabia

Article *in* Fauna of Arabia · November 2000

1 author:

Jeremy Kemp

FAUNA OF ARABIA **18**: 293–321 Date of publication: 30.11.2000

Zoogeography of the coral reef fishes of the north-eastern Gulf of Aden, with eight new records of coral reef fishes from Arabia

Jeremy M. Kemp

Abstract: A survey of the fish assemblages of Hadramaut and Shabwa provinces of the Republic of Yemen, in the north-eastern Gulf of Aden, reveals regionally high levels of diversity in some families of coral reef fishes, and striking local and regional species distribution patterns. The following species of fish are recorded for the first time from the coast of Arabia: *Chaetodon trifasciatus*, *Chaetodon zanzibarensis*, *Halichoeres cosmetus*, *Thalassoma quinquevittatum*, *Ecsenius lineatus*, *Acanthurus leucocheilus* and *Acanthurus triostegus*. A preliminary checklist of shallow coastal fishes of the north-eastern Gulf of Aden is provided, and a discussion of zoogeographic affinities of the species assemblage presented. A 'zoogeographically displaced' component of the northern Gulf of Aden fish community is almost entirely limited to a single small island, and may occur here because of complex oceanographic conditions arising from the seasonal monsoons of the Arabian Sea. This unusual assemblage raises the possibility that settlement strategies of larval reef fishes may in some cases affect species distributions at zoogeographic scales.

الجغرافيا الحيوانية لأسماك الشعب المرجانية في شمال شرق خليج عدن مع ثمان تسجيلات جديدة لأسماك الشعب المرجانية لشبه الجزيرة العربية

جيرمي م. كمب

خلاصة: بينت نتائج مسح للمجاميع السمكية في شمال شرق خليج عدن بالقرب من إقليمي حضرموت وشبوه في الجمهورية اليمنية وجود مستويات إقليمية عالية من التنوع في بعض عائلات اسماك الشعب المرجانية وأنماط ملفتة للنظر في توزع الأنواع محليا وإقليمياً. سجلت ثمانية أنواع جديدة للمرة الأولى من سواحل شبه الجزيرة العربية. ويتضمن البحث قائمة تصنيفية أولية للأسماك الساحلية الضحلة لشمال شرق خليج عدن ومناقشة للصلات الجغرافية الحيوانية لمجاميع الأنواع المدروسة. ينحصر توزيع الأنواع "غير المألوفة" من الناحية الجغرافية الحيوانية كلياً في جزيرة وحيدة صغيرة ويمكن أن يحصل هنا بسبب الأحوال الجغرافية المحيطية المعقدة الناتجة عن الرياح الموسمية الحولية في بحر العرب. يثير هذا التجمع غير الاعتيادي على أن احتمال وجود إستراتيجيات توطن ليرقات أسماك الشعب المرجانية يمكن أن يؤثر أحيانا على توزع الأنواع على مستوى جغرافي حيواني.

INTRODUCTION

Considerable work has been carried out on the coastal fishes of the seas around Arabia over the past twenty years (see RANDALL 1983, 1994, 1996; SMITH et al. 1987; ROBERTS et al. 1992;

SHEPPARD et al. 1992; RANDALL et al. 1994; RANDALL & HOOVER 1995), but the ichthyofauna of large areas of Arabian coast remains poorly known. The most conspicuous geographical gaps, where very little is known of shallow marine habitats and fish species distributions, are the entire Gulf of Aden (with the possible exception of Djibouti), the Arabian Sea coast of the Republic of Yemen between the Gulf of Aden and southern Oman, and both sides of the Red Sea to the south of the Farasan and Dahlak archipelagos (RANDALL 1994, KEMP 1998 b).

Research on shallow marine communities and species in the Gulf of Aden has been extremely sparse, and much of the published work is several decades old. Studies have concentrated on the southern shores of the Gulf of Aden, in the area of Djibouti and western Somalia in the west (PELLEGRIN 1904; GRAVIER 1910 a, 1910 b, 1911; RANDALL & MAUGÉ 1978; BARRATT & MEDLEY 1990; RANDALL 1994; MCCLANAHAN & OBURA 1997; OBURA 1997) and the Socotra Archipelago in the east (SCHEER 1964, 1971; KEMP 1997, 1998 a, 1998 b; KEMP & OBURA in press). Even so, none of these areas is yet very well characterised, either in terms of habitats or of detailed species distributions.

Prior to studies by FRASER-BRUNNER (1950) virtually no work had been carried out on the northern (Republic of Yemen) shore of the Gulf of Aden, and little has been done since. With the exception of a study of seagrasses of Khor Umeirah, to the west of Aden (HIRTH et al. 1973), no information about this coast was published after FRASER-BRUNNER's (1950) work until ORMOND & BANAIMOON (1994) reported on macroalgae of the Hadramaut coast of the eastern Gulf of Aden. Subsequently, in 1995, a rapid survey of shallow coastal habitats of the northern shore of the Gulf of Aden, carried out for a fisheries development programme, revealed the presence of well developed but scattered coral communities (HUNTINGTON & WILSON 1995, SHEPPARD et al. in press), however, no significant studies of fishes were carried out. In 1996 a rapid survey of several sites from the Bab al-Mandab to Shasar, east of al-Mukalla, was carried out (WATT 1996). This survey revisited many of the sites identified in the 1995 survey and added some detail to knowledge of distribution of coral habitats, but again no studies of fishes were carried out. AL-SAKAFF & ESSEEN (1999) provided a checklist of 195 fish species in 75 families from the northern Gulf of Aden, on the basis of commercial trawl catch. A number of families on their checklist, such as emperors (Lethrinidae), snappers (Lutjanidae) and triggerfishes (Balistidae), are frequently found in association with coral communities, but the authors provided no discussion of the checklist.

Recent studies immediately to the east and south of the Gulf of Aden, in Oman (RANDALL & HOOVER 1995; RANDALL 1996) and at the Socotra Archipelago (KEMP 1997, 1998 b), have revealed that the fish fauna of southern Oman and the south-eastern Gulf of Aden is distinctively 'South Arabian' (KEMP 1998 b), and that it includes a minor but important East African element. This assemblage type may serve to define the south Arabian section of the Arabian zoogeographic subprovince proposed by KLAUSEWITZ (1989). The East African influence is more marked at Socotra than in Oman, and at the Socotra Archipelago results in sympatry of sister taxa previously believed to have entirely allopatric distributions (KEMP 1998 b).

An expedition to the Gulf of Aden in early 1998 enabled studies of reef fishes to be carried out along the northern coast, in Hadramaut and Shabwa provinces in the east and at Ras Imran in the west. Prior to the 1998 expedition, the ichthyofauna of the north-eastern Gulf of Aden remained almost entirely undescribed, and the distributions of characteristic fish species from the Red Sea, Oman, northern Arabia, and the Indian Ocean in this area were unknown. The purpose of this paper is to present the new records and species list produced as a result of the 1998 survey in Hadramaut and Shabwa provinces, and to provide a discussion of the zoogeographic affinities of the assemblage.

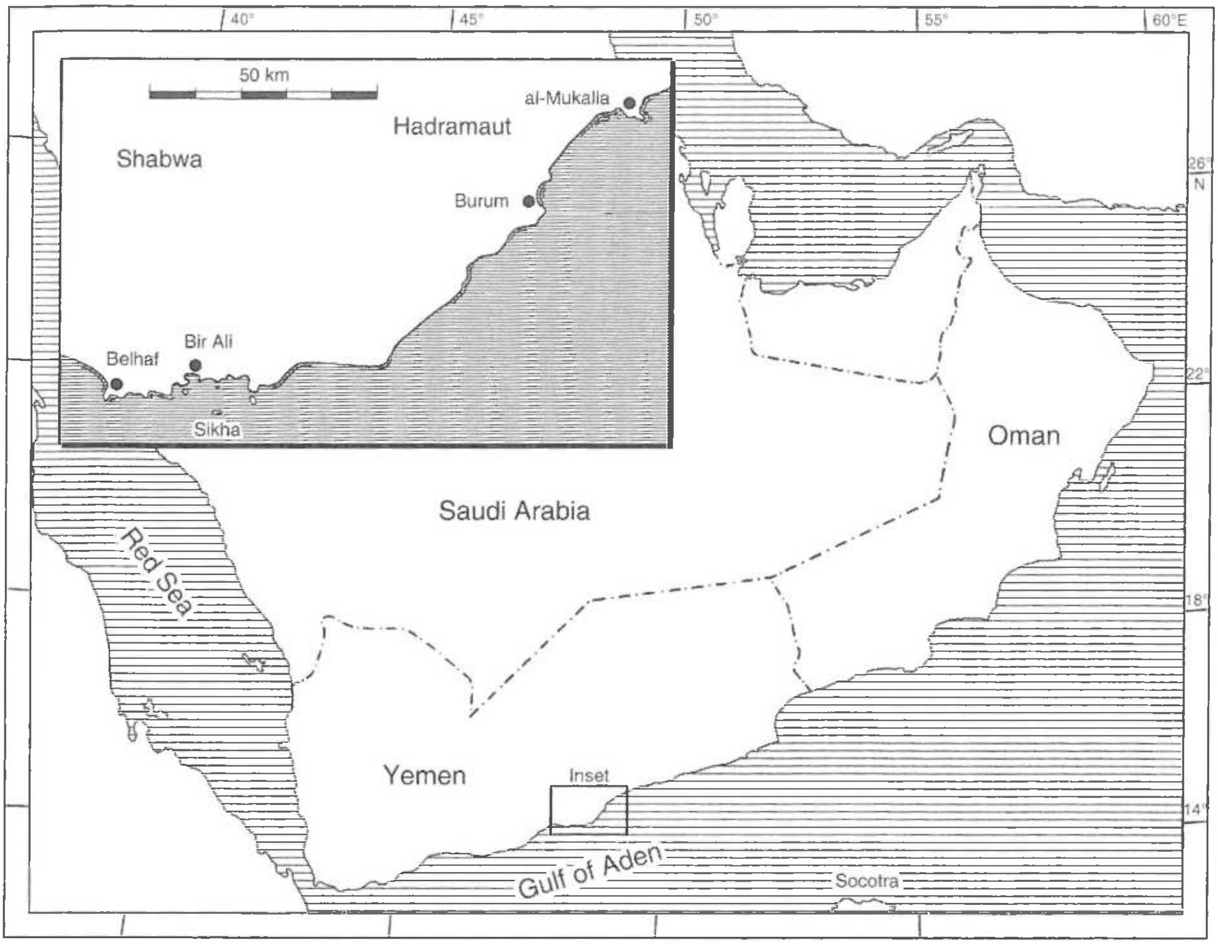


Fig. 1: Locations of the survey areas in eastern Yemen. **Inset:** Hadramaut and Shabwa provinces, Yemen.

METHODS AND STUDY AREA

The author accompanied the Arabian Seas Expedition to the Arabian Sea, Gulf of Aden and southern Red Sea coasts of Arabia, from January to April 1998. Surveys of coastal fish communities and habitats were carried out in four areas of Hadramaut and Shabwa provinces of the Republic of Yemen, in the eastern Gulf of Aden, in February and March of 1998 (Fig. 1). These areas were al-Mukalla in Hadramaut Province (14°31'N 49°9'E) and Bir Ali (14°01'N 48°20'E), Belhaf (13°59'N 48°10'E) and Sikha Island (13°56'N 48°23'E), all in Shabwa Province. Sikha is located in relatively deep water approximately 8 km offshore, and all other survey areas were on the mainland or very near-shore islands. Similar surveys were carried out in southern Oman, the western Gulf of Aden and the southern Red Sea during the expedition, and they enable comparisons to be made between these regions and the north-eastern Gulf of Aden.

The benthic habitats of the northern Gulf of Aden are dominated by unconsolidated sandy and gravel substrates, but rocky habitats and extensive high-cover coral communities occur in a number of locations, including the survey areas of al-Mukalla, Bir Ali, Belhaf and Sikha Island (Huntington & Wilson 1995, Watt 1996, Kemp & Benzoni 2000, Sheppard et al. in press). The coast between Belhaf and al-Mukalla consists of igneous rocky headlands, many of which are several kilometres in length, interspersed with sandy bays. The sublittoral morphology at rocky shore sites was typically a

Table 1: Quantitative survey sites in southern Oman, the northern Gulf of Aden and the southern Red Sea. Site latitudes and longitudes calculated from British Admiralty Charts # 6, 3784 and 141.

Survey area	Site	Location	Transect depth [m]
Southern Oman			
Hallaniyat Islands	Shallow 1	17°30'N 56°20'E	3
	Shallow 2	17°30'N 56°19'E	3
	Shallow 3	17°29'N 56°20'E	3
	Shallow 4	17°30'N 56°20'E	3
	Deep 1	17°29'N 56°20'E	14
	Deep 2	17°30'N 56°19'E	10
	Deep 3	17°29'N 56°20'E	10
	Deep 4	17°30'N 56°20'E	10
Rahah Bay (mainland)	Shallow 1	16°56'N 54°48'E	3
	Shallow 2	16°56'N 54°48'E	3
	Deep 1	16°56'N 54°48'E	12
	Deep 2	16°56'N 54°48'E	12
Gulf of Aden			
Hadramaut Province	al-Mukalla Shallow 1	14°30'N 49°09'E	3
	al-Mukalla Shallow 2	14°30'N 49°09'E	3
	al-Mukalla Shallow 3	14°30'N 49°10'E	2
	al-Mukalla Shallow 4	14°30'N 49°10'E	3
	al-Mukalla Shallow 5	14°30'N 49°10'E	3
	al-Mukalla Deep 1	14°30'N 49°09'E	10
	al-Mukalla Deep 2	14°31'N 49°09'E	13
	al-Mukalla Deep 3	14°31'N 49°09'E	10
	al-Mukalla Deep 4	14°30'N 49°10'E	11
	al-Mukalla Deep 5	14°30'N 49°10'E	11
Shabwa Province	Bir Ali Shallow 1	14°01'N 48°21'E	3
	Bir Ali Shallow 2	14°01'N 48°21'E	3
	Bir Ali Shallow 3	14°01'N 48°21'E	3
	Bir Ali Shallow 4	14°00'N 48°20'E	2
	Bir Ali Shallow 5	14°00'N 48°21'E	3
	Bir Ali Shallow 6	14°00'N 48°20'E	3
	Bir Ali Deep 1	14°00'N 48°20'E	8
	Bir Ali Deep 2	14°00'N 48°20'E	8
	Bir Ali Deep 3 (Belhaf)	13°59'N 48°10'E	8
	Bir Ali Deep 4 (Belhaf)	13°59'N 48°10'E	8
	Sikha Island Shallow 1	13°56'N 48°23'E	2
	Sikha Island Shallow 2	13°56'N 48°23'E	3
	Sikha Island Shallow 3	13°56'N 48°23'E	3
	Sikha Island Shallow 4	13°54'N 48°23'E	3
	Sikha Island Shallow 5	13°54'N 48°23'E	3
	Sikha Island Shallow 6	13°54'N 48°23'E	3
	Sikha Island Deep 1	13°56'N 48°23'E	12
	Sikha Island Deep 2	13°56'N 48°23'E	14
	Sikha Island Deep 3	13°56'N 48°23'E	12
	Sikha Island Deep 4	13°54'N 48°23'E	11
	Sikha Island Deep 5	13°54'N 48°23'E	12
	Sikha Island Deep 6	13°54'N 48°23'E	12
Ras Imran	Shallow 1	12°45'N 44°45'E	3
	Deep 1	12°48'N 44°38'E	8
Southern Red Sea			
Kamaran Islands	Uqban Shallow 1	15°29'N 42°24'E	2
	Uqban Shallow 2	15°28'N 42°25'E	2
	Uqban Shallow 3	15°28'N 42°25'E	3
	Uqban Shallow 4	15°29'N 42°24'E	3
	Uqban Deep 1	15°27'N 42°23'E	14
	Uqban Deep 2	15°28'N 42°25'E	12
	Uqban Deep 3	15°28'N 42°25'E	10
	Uqban Deep 4	15°29'N 42°24'E	10

coral-covered or rocky slope of between 10 and 50°, extending to a depth of between 8 and 14 m where it meets a level or gently sloping sandy sea floor (KEMP & BENZONI 2000). In places, high-cover healthy coral communities also extended several hundred metres offshore, sometimes apparently developed on an unconsolidated sand/gravel substrate. Rocky and coral habitats at depths greater than 14 m were only encountered at Sikha Island where, due to its location offshore in approximately 60 m of water, the sublittoral slopes steeply to between 15 and 60 m. A diverse range of coral community types is present throughout the north-eastern Gulf of Aden (KEMP & BENZONI 2000) and extensive, well-developed and varied shallow coral communities are present at many locations (Plates 1 and 2). The majority of studies throughout Hadramaut/Shabwa were carried out at sites with a hard substrate (rocks and/or coral), although extensive qualitative observations were also made at two sandy bay sites on the mainland coast.

Detailed studies of the fish communities were carried out at 34 sites in the northern Gulf of Aden, 12 sites in southern Oman and 8 sites in the southern Red Sea (Table 1). These studies concentrated on the Chaetodontidae (butterflyfishes), Pomacanthidae (angelfishes), Pomacentridae (damselfishes), Acanthuridae (surgeonfishes) and Balistidae (triggerfishes). At each site underwater visual census (UVC) transects of pomacanthid and chaetodontid fishes were carried out. Transects were 250 m in length, following the depth contour, and all pomacanthid and chaetodontid fishes within 5 m of the central line of the transect were identified to species and recorded on prepared recording sheets printed on waterproof paper. Transects were initially measured using a 50 m tape, to provide a baseline. Subsequently transect lengths were estimated by timing them (at 5 min per 50 m), and were re-measured after every ten or twelve transects in order to ensure that transect lengths were being estimated consistently. Habitat characterisation was carried out along the line of each UVC transect, using five replicate quadrats spaced at 50 m intervals along the first 200 m of each transect. Habitat characterisation consisted of estimated percentage cover of 17 categories of substrate, including life-forms of living hard and soft corals, in 5 × 5 m quadrats (KEMP & BENZONI 2000). In addition to the quantitative transect, all pomacentrid, balistid and acanthurid species occurring at each site were recorded, along with any additional chaetodontid and pomacanthid species observed outside the quantitative transect area. Thus a species list for every survey site was compiled for each of these five families. As a secondary task, a record of all other fish species positively identified in each of the four survey areas was compiled. No collection of fishes was possible, so all identifications presented are photographic or sight records, and uncertain identifications have been omitted.

Cluster analysis (Ward's method of hierarchical agglomerative clustering) was used to assess relationships between species assemblages of the five principal families studied, in all areas visited during the 1998 expedition (Fig. 3). This cluster analysis is based only on presence/absence data for each region, with no weighting for species abundance. Ward's method calculates the squared Euclidean distance to the cluster means for each case, and sums them for all cases. At each step the clusters which, when merged, give the smallest increase in the sum of squared within-cluster distances, are merged. Cluster analysis was carried out on the statistics package SPSS for Windows, Version 6.0.

RESULTS

New records

Chaetodon trifasciatus **Park, 1797** Plate 3

Chaetodon trifasciatus Park, 1797. — Transactions of the Linnean Society 3: 34. Type locality: Sumatra.

Remarks: A single small subadult (6-7 cm total length) was observed on the northern side of Sikha Island, in approximately 1 m of water in a shallow sheltered bay with very high cover of healthy living coral. This individual was closely associated with subadults of the locally very abundant close relative *Chaetodon melapterus* Guichenot, 1862, an Arabian endemic species (RANDALL 1994) which ranges from the Arabian Gulf around the Arabian Peninsula to the southern Red Sea.

Distribution (Fig. 2): *Chaetodon trifasciatus*, one of four members of the obligate corallivorous chaetodontid subgenus *Corallochaetodon* Burgess, 1978, is commonly distributed throughout the coral-rich regions of the Indian Ocean (BURGESS 1978, BLUM 1989), with the exception of Arabia and the Gulf of Aden. It is replaced in the Pacific by *Chaetodon lunulatus* Quoy & Gaimard, 1824 (KUITER 1995). Around Arabia *C. trifasciatus* is replaced by *C. melapterus* in the Arabian Gulf, Gulf of Oman, Arabian Sea coast, Gulf of Aden, Socotra Archipelago, and the extreme southern Red Sea (RANDALL 1994, 1996; KEMP 1998 b). Within the Red Sea *C. melapterus* is replaced by *C. austriacus* Rüppell, 1836, which is common in the northern two thirds of the sea (ROBERTS et al. 1992), and has recently been reported to be common at several locations in the extreme south of the Red Sea (WATT 1996, BRODIE et al. in press), where it is sympatric with *C. melapterus*. Waifs of *C. austriacus* are recorded from as far afield as Oman (RANDALL 1996).

Chaetodon zanzibarensis Playfair, 1866 — Plate 4

Chaetodon zanzibarensis Playfair, 1866. — In: The fishes of Zanzibar: 33. Type locality: Zanzibar.

Remarks: Four adult *Chaetodon zanzibarensis* were observed and photographed over a two-week period at Sikha Island. Three were consistently observed among or near very large *Porites* corals in a sheltered bay on the south coast of the island, and one was observed on one occasion only, among *Porites* corals in the northern bay. This species was not observed anywhere else in the region. All four individuals were fully grown adults.

Distribution: Western and central Indian Ocean. This species has been recorded throughout East Africa as far north as Mombassa, and in the Seychelles, Mascarenes and the Chagos Archipelago (BURGESS 1978, BLUM 1989, WINTERBOTTOM et al. 1989, TMRU 1994). It is not yet recorded from the Maldives (RANDALL & ANDERSON 1993) or the Socotra Archipelago (KEMP 1998 b).

Halichoeres cosmetus Randall & Smith, 1982 — Plate 5

Halichoeres cosmetus Randall & Smith, 1982. — Ichthyological Bulletin 45: 15. Type locality: Maldives.

Remarks: Several individuals of this species were seen amongst hard and soft corals in sheltered sites at Sikha Island, between depths of 3 and 8 m. One was photographed in 3-4 m of water in a sheltered shallow bay on the northern side of Sikha, amongst massive *Porites* and scattered branching hard and soft corals on sand.

Distribution: Western Indian Ocean including the Seychelles, Maldives, Mascarenes, Chagos Archipelago and Comores and East Africa from Natal to northern Kenya (RANDALL & SMITH 1982). RANDALL & SMITH (1982) explicitly exclude the Gulf of Aden, Red Sea and Arabian Gulf from this species' range. Considerable further work since 1982, particularly surveys of the ichthyofauna of the southern Red Sea, south-western Gulf of Aden and Oman (RANDALL 1994; MCCLANAHAN & OBURA 1997; RANDALL 1996) has failed to record it in Arabian waters.

Thalassoma hardwicke (Bennett, 1830) — Plate 6

Sparus hardwicke Bennett, 1830. — A selection of rare and curious fishes found upon the coast of Ceylon 6: 12. Type locality: Sri Lanka.

Remarks: At least four individuals of this species were observed, and two photographed, in 1-3 m of water in the very shallow coral-rich area of the northern bay at Sikha Island. The specimen pictured is one of the two largest, at approximately 17-18 cm total length. Two others were

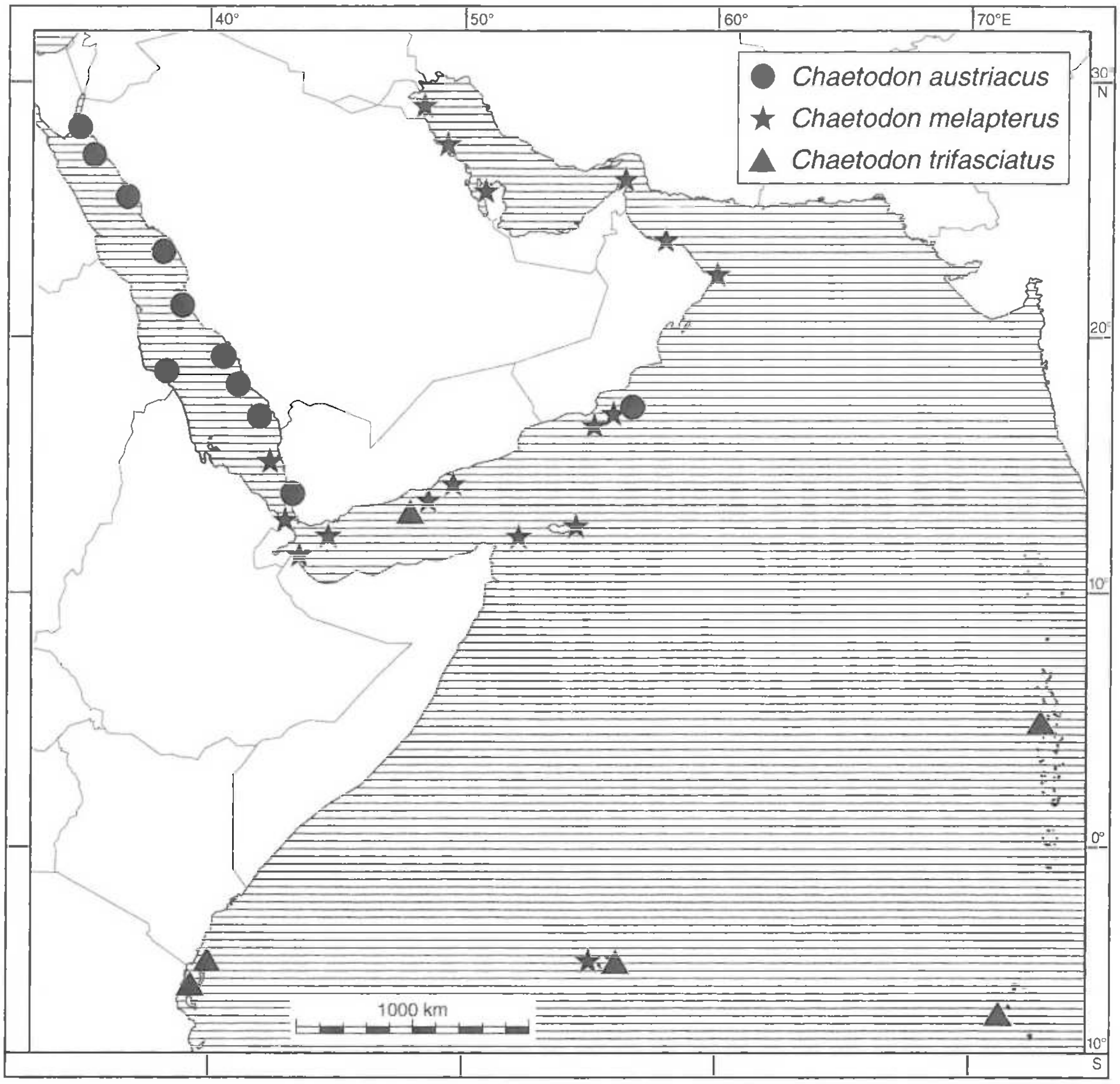


Fig. 2: North-western Indian Ocean distributions of three species of the obligate corallivorous chaetodontid subgenus *Corallochaetodon* Burgess, 1978. Each of the three out-liers (*C. melapterus* in the Seychelles, *C. trifasciatus* in Yemen and *C. austriacus* in Oman) are isolated records of waifs (this paper; RANDALL 1994, 1996). The distribution of *C. austriacus* on the African side of the Red Sea probably follows the distribution on the Arabian side. Both *C. austriacus* and *C. melapterus* are rare in the southern Red Sea, and southern Red Sea rarity may have been severely exacerbated by recent (early 1990's) massive bleaching-related mortality of shallow scleractinian corals throughout the Yemen Red Sea region (J. Kemp, unpublished data). Sources: AL-BAHARNA 1986 (Bahrain); BARRATT & MEDLEY 1990 (Djibouti); T. Burkitt & A. Dawson-Shepherd, pers. comm. (Sudan); BURGESS 1978 (Seychelles); BLUM 1989 (Ras al-Hadd, Oman); CARPENTER et al. 1997 (Kuwait); D. Fabian, pers. comm (Asseb, Eritrea); FRASER-BRUNNER 1950 (Aden); KEMP 1998 b (Socotra Archipelago); F. Krupp, pers. comm. (Jubail, Saudi Arabia); ORMOND et al. 1984 (Red Sea, Saudi Arabia); RANDALL 1994 (Yemen Red Sea); RANDALL 1996 (southern Oman); RANDALL & ANDERSON 1993 (Maldives); SMITH et al. 1987 (Arabian Gulf); WATT 1996 (Bab al-Mandab); WINTERBOTTOM et al. 1993 (Chagos Archipelago); J. Kemp, unpublished data (Gulf of Oman, Musandam, eastern Gulf of Aden, Aden [Ras Imran], southern Red Sea [Kamaran Islands]).

smaller (13-14 cm). All were observed only within a single 50 × 100 m area of corals composed of mixed branching *Acropora* and *Stylophora* and foliose and branching *Montipora*.

Distribution: Throughout the Indo-West Pacific, excluding the Red Sea, Oman, and the Arabian Gulf. Not recorded from the Socotra Archipelago.

Thalassoma quinquevittatum Lay & Bennett, 1839 Plates 7, 8

Thalassoma quinquevittatum Lay & Bennett, 1839. — In: Zoology of Captain Beechey's voyage to the Pacific and Behrings Straits [...]: 66. Type locality: Loo Choo Islands.

Remarks: Observed in large numbers at between 0.5 and 5 m depth, on the south-western side of Sikha Island. The site was a coral-free rocky headland, highly exposed to waves and swell, and densely covered in algal turf, barnacles and small invertebrates. Dor (1984) cites records of this species from inside the Red Sea, but Randall & Edwards (1984) state that it does not extend its range there. Goren & Dor (1994) do not record this species inside the Red Sea. In particular, records of the species from the northern Red Sea, at Tiran and elsewhere in the vicinity of Sinai (see Dor 1984) are likely to be a result of confusion with *Thalassoma klunzingeri* Fowler & Steinitz, 1956, a Red Sea endemic species which is extremely abundant in shallow reef habitats throughout the northern and central Red Sea, and which is a sister species to *T. quinquevittatum* (Randall & Edwards 1984, Ormond & Edwards 1987). This confusion may arise from the fact that some specimens of *T. klunzingeri* have in the past been misidentified as *T. guentheri* (see comments in Randall & Edwards 1984). *Julis guentheri* Bleeker, 1862 is a junior synonym of *T. quinquevittatum*. The record of *T. quinquevittatum* at Sikha Island is thus the first confirmation of the species in Arabian waters. Most individuals observed at Sikha were very closely associated with the rocky substrate, although many were also engaged in spawning in the high energy surge zone at 0.5-3.0 m depth.

Ecsenius lineatus Klausewitz, 1962 Plate 9

Ecsenius lineatus Klausewitz, 1962. — Senckenbergiana biologica 43 (2): 145. Type locality: Madewaru Island, Fadiffulu Atoll, Maldives.

Remarks: One individual of this species was photographed at Sikha Island, in a coral-rich area of the northern bay, in approximately 5 m of water. Another was observed at a depth of 3 m at Belhaf, in an area of very large colonies of *Porites*.

Distribution: Central and eastern Indian Ocean and western Pacific, from the Maldives and Mauritius to Taiwan and the Ryukyu Islands. Not known from East Africa, from the Indo-Malay archipelago anywhere east of Sumatra, or from eastern Australia (Springer 1988).

Acanthurus leucocheilus Herre, 1927 Plate 10

Acanthurus leucocheilus Herre, 1927. — Philippines Journal of Science 34 (4): 419. Type locality: Philippines.

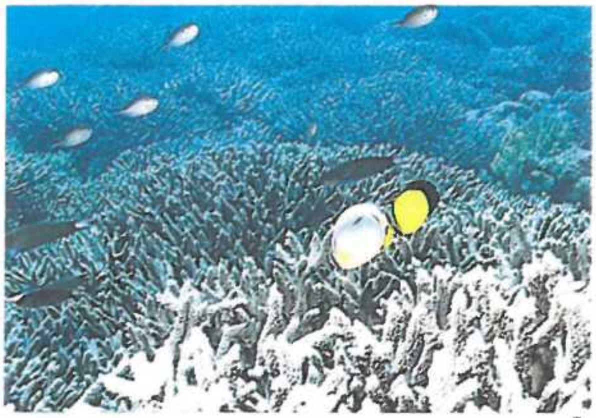
Remarks: Several adults (approximately 30 cm length) were observed on the exposed east and south coasts of Sikha Island. All were in 1-4 m of water, browsing on exposed rocky surfaces with very low coral cover, and a high cover of algal mat or turf, as shown in the photograph. The photograph does not show the fish very clearly, but the species was identified on the basis of: a dark brown overall colour with a white caudal blade and white or pale bar across the caudal peduncle, white mouth, variably pale to white chin-strap, tail paler than the colour of the body, moderately to strongly lunate and with a blue-grey margin.

Distribution: Indo-Pacific. In the north-western Indian Ocean at the Maldives, Chagos Archipelago, Sri Lanka (Debelius 1993, Randall & Anderson 1993, Winterbottom & Anderson 1997).

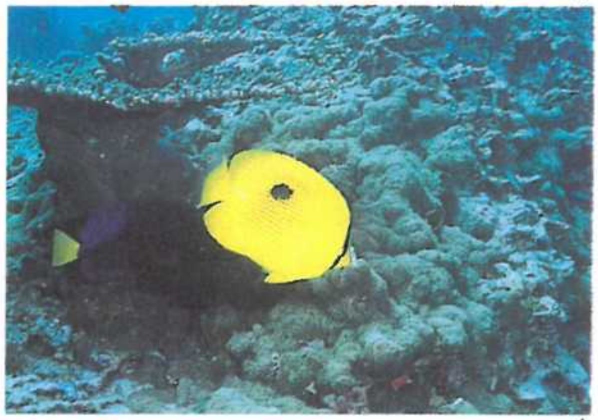
Plates 1-8: 1: Shallow coral community dominated by branching corals at Bir Ali, Shabwa Province. **2:** Coral community dominated by massive *Porites* corals at Bir Ali. **3:** Subadult *Chaetodon trifasciatus* with juvenile and subadult *C. melapterus* at Sikha Island, Shabwa Province. **4:** Adult *Chaetodon zanzibarensis* at Sikha Island. **5:** *Halichoeres cosmetus* at Sikha Island. **6:** *Thalassoma hardwicke* at Sikha Island. 7: Male *Thalassoma quinquevittatum* at Sikha Island. **8:** Female *Thalassoma quinquevittatum* at Sikha Island.

1

2



3



4

5

6

7

8

Acanthurus triostegus (Linnaeus, 1758)

Chaetodon triostegus Linnaeus, 1758. — Systema Naturae 10 (1): 274. Type locality: "Indies".

Remarks: Adults of this species were observed at al-Mukalla in Yemen, and at the Hallaniyat (Kuria Muria) Islands in Oman (17°30'N 56°19'E). In both cases only rare individuals were recorded, at shallow rocky inshore sites. At al-Mukalla two were seen at one site to the east of the town, and at the Hallaniyat Islands single individuals were seen at each of two sites, approximately 1.5 km apart. No photographs were taken of this species, but it is large, conspicuous and unmistakable.

Distribution: Indo-Pacific, from East Africa, the Seychelles, Maldives and Chagos Archipelago to the eastern Pacific. Recently recorded at the Socotra Archipelago (KEMP 1998 b).

Further species records from Hadramaut and Shabwa

A preliminary checklist of all species of shallow coastal fishes recorded throughout the survey in eastern Yemen is presented in Table 2 (Appendix). Because no collection of fishes was possible, there is a bias in the species identified in this study towards larger, diurnal and non-cryptic species. Lists for the five families which were central to zoogeographic studies and which were always identified (Chaetodontidae, Pomacanthidae, Pomacentridae, Acanthuridae and Balistidae) are probably quite comprehensive for the area. The checklists for all other families listed were compiled as a secondary task, and should be regarded as incomplete. Further surveys will certainly extend this checklist considerably.

DISCUSSION

The benthic communities of shallow sublittoral hard substrates in the Hadramaut/Shabwa region are dominated by scleractinian corals (KEMP & BENZONI 2000), with extensive, healthy and diverse coral communities being widespread throughout the region. Although biogenic reef structures are very uncommon in the region, the fish assemblages associated with these coral communities are dominated by characteristically coral reef associated groups such as chaetodontids, pomacanthids, scarids, labrids, acanthurids and balistids (for discussion of definitions of coral reef fishes see CHOAT & BELLWOOD 1991; BELLWOOD 1996, 1998; ROBERTSON 1998).

RANDALL (1996) lists seven different zoogeographic components of the ichthyofauna of the coast of southern Oman, a region contiguous with the coast of Hadramaut and Shabwa but 600 km to the east. These components are: cosmopolitan in warm seas; Indo-Pacific; Indian Ocean; Red Sea and Gulf of Aden; Gulf of Oman; southern Africa; Oman endemics. All but one of the new records presented here (*Chaetodon zanzibarensis*) belong to the broadly distributed Indo-Pacific group, although this is the first record of *Ecsenius lineatus* from the western margin of the Indian Ocean. The cosmopolitan species group, for instance *Aetobatus narinari* (Euphrasen, 1790) and *Aluterus scriptus* (Osbeck, 1765), is present in Hadramaut/Shabwa, but does not provide any significant zoogeographic information, and will not be discussed further here. All of the other components of the Oman assemblage identified by RANDALL (1996) are represented in the Hadramaut/Shabwa assemblages, but each takes a slightly different form from the equivalent group in Oman.

The Indo-Pacific, Indian Ocean and Red Sea / Gulf of Aden groups are more speciose as well as more generally abundant in Hadramaut/Shabwa than in Oman. Conversely, although the Oman endemic and Gulf of Oman assemblages are present – e.g. *Cirrhitichthys calliurus* Regan, 1905, *Chaetodon dialeucos* Salm & Mee, 1989 and *Ecsenius pulcher* (Murray, 1887) – they are greatly reduced in diversity. RANDALL's (1996) southern African group is represented in Hadramaut/Shabwa by just one taxon (*Diplodus sargus capensis* Smith, 1844). The almost complete absence of the southern African assemblage from Hadramaut/Shabwa may be significant. RANDALL (1996) remarks that the link between southern Oman and southern Africa may be environmental, being related to the presence of cold monsoon upwelling in Oman (CURRIE et al. 1973; BARRATT et al. 1984, 1986; SAVIDGE et al. 1990), and RANDALL & HOOVER (1995) note the existence of a centre of endemism on the Arabian Sea coast of Oman which may be related to the same seasonal upwelling event. The Hadramaut/Shabwa area lies at the western edge of the effects of the upwelling, and if RANDALL's hypothesis is correct the effects may not be pronounced enough in Hadramaut/Shabwa to allow many of the southern African species to establish successfully.

There are three principal distributional features of the fish species assemblages of the Hadramaut and Shabwa area, at varying geographic scales, which become apparent from this study. Firstly, there is a pronounced overlap of ichthyofaunas with different zoogeographic affinities. Secondly, and closely related to the first point, there is a clear difference between fish assemblages of al-Mukalla and Bir Ali, just 100 km apart. Thirdly, the fish assemblage of Sikha Island, the only location of six of the eight new records, is highly unusual both locally and regionally.

The pronounced overlap of zoogeographically distinct species assemblages in Hadramaut/Shabwa gives rise to previously unrecorded sympatry between sister species, particularly in the Chaetodontidae, a family with high levels of endemism around Arabia (ORMOND & EDWARDS 1987, BLUM 1989, KLAUSEWITZ 1989). Two Red Sea and Gulf of Aden endemic butterflyfishes, *Chaetodon fasciatus* Forsskål, 1775 and *Heniochus intermedius* Steindachner, 1893, are sympatric here with their Indo-West Pacific sister taxa *C. lunula* (Lacepède, 1802) and *H. acuminatus* (Linnaeus, 1758), respectively. The *C. fasciatus* and *C. lunula* pair were only sympatric at Sikha, where an apparently stable heterospecific pair was observed repeatedly and photographed over a two-week period (Plate 11), while the *Heniochus* were sympatric throughout the region. In the Balistidae the Indo-West Pacific species *Sufflamen chrysopterus* (Bloch & Schneider, 1801) and its Red Sea and Gulf of Aden endemic sister species *S. albicaudatus* (Rüppell, 1829) are sympatric at Sikha. The blenniid genus *Ecsenius* provides a further example of overlap of zoogeographic ranges, although not between sister taxa. In this genus the Arabian Gulf and northern Arabian Sea species *Ecsenius pulcher* (Murray, 1887) and the Red Sea species *Ecsenius frontalis* (Ehrenberg, 1836) are both common in Shabwa. Both of these records are considerable range extensions, with *E. frontalis* previously only known from the Red Sea and Djibouti (SPRINGER 1988) and *E. pulcher* from the Arabian Gulf, Pakistan and Oman (SPRINGER 1988, RANDALL 1996), although KEMP (1998 b) records it from Socotra.

Zoogeographic trends between Shabwa Province and al-Mukalla

Over the relatively short 100 km distance between the Bir Ali area and al-Mukalla, zoogeographic trends consistent with the larger scale east-west divergence between Oman and Hadramaut/Shabwa are apparent. A significant part of the divergence between Oman and Yemen described above is due to the species assemblage at Bir Ali (including Sikha Island), with the assemblage of al-Mukalla being intermediate between those of Oman and Bir Ali.

The influences of the Red Sea and Indian Ocean species assemblages are more apparent throughout the Bir Ali area, both mainland and islands, than at al-Mukalla. The chaetodontid assemblage of Bir Ali is more heavily dominated by Red Sea species (22.2 % at Shabwa, 13.3 % at al-Mukalla) with the Red Sea species *Chaetodon semilarvatus* Cuvier, 1831 and *C. larvatus* Cuvier, 1831 both common at Bir Ali but absent or very rare at al-Mukalla. Similarly, four Indian Ocean or Indo-West Pacific chaetodontid species recorded at Bir Ali were not present at al-Mukalla and are not recorded from Oman (*Chaetodon lineolatus* Cuvier, 1831, *C. melannotus* Bloch & Schneider, 1801, *C. trifasciatus* and *C. zanzibarensis*). In other families the Red Sea species *Larabicus quadrilineatus* (Rüppell, 1835) (Labridae), *Neopomacentrus xanthurus* Allen & Randall, 1981 (Pomacentridae) and *Sufflamen albicaudatus* (Balistidae) are all common throughout the Bir Ali area, but were not recorded at al-Mukalla. The Red Sea scarid *Chlorurus genazonatus* (Randall & Bruce, 1983) (Plate 12) was common at Sikha, but was not recorded at al-Mukalla. Four Indo-West Pacific balistids and two acanthurids which extend their ranges from the Indian Ocean around the Horn of Africa into the Red Sea, but not eastwards to Oman (a distribution common to many families, Kemp 1998 b) were present at Bir Ali, but not at al-Mukalla. The reverse of this is also true, although to a less marked degree, with some species, such as *Pomacanthus semicirculatus* (Cuvier, 1831), which are common in southern Oman being present at al-Mukalla but not at Bir Ali. The damselfish *Amphiprion* sp. (Plate 13), present at al-Mukalla, may represent a Yemen sister taxon to *Amphiprion omanensis* Allen & Mee, 1991. Although the status of the al-Mukalla *Amphiprion* remains to be ascertained, it very closely resembles *Amphiprion omanensis* in all respects of size, general shape and coloration, except for the width of the two white bars, which are wider than those found in Oman populations of *A. omanensis*.

The divergence between the fish assemblages of al-Mukalla and the Bir Ali area may be due to the occurrence of a significant faunal break between the two areas. This is illustrated by the results of a hierarchical cluster analysis (Ward's method), illustrated in Fig. 3. This shows the relationship between the species assemblages of five families of fishes (Chaetodontidae, Pomacanthidae, Pomacentridae, Acanthuridae and Balistidae), totalling 80 species, in all regions of southern and eastern Arabia visited during the 1998 expedition. The al-Mukalla species assemblage for these five families more closely resembles that of southern Oman 600 km to the east than it does that at Shabwa less than 100 km to the west. The dendrogram reveals that the Bir Ali assemblage is a Gulf of Aden fauna, clustering with the assemblage from Ras Imran to the west. The species assemblage of Sikha Island is deeply separated from the Bir Ali / Ras Imran cluster.

The occurrence of this zoogeographic change, from a Gulf of Aden fish species assemblage to one more closely resembling that of southern Oman, along only 100 km of coastline is at first sight surprising. However, Roberts (1986) and Roberts et al. (1992) described a similarly pronounced change in coral reef fish assemblages at approximately 20°N in the southern Red Sea, attributing the difference to oceanographic and habitat changes. An examination of the oceanography of the eastern Gulf of Aden reveals a possible explanation for the Bir Ali – al-Mukalla discontinuity. This region lies at the extreme western edge of the Arabian Sea upwelling, with raised nutrient levels, high primary productivity and low water temperatures in the Arabian Sea to the east during summer, and warmer and more oligotrophic waters in the Gulf of Aden to the

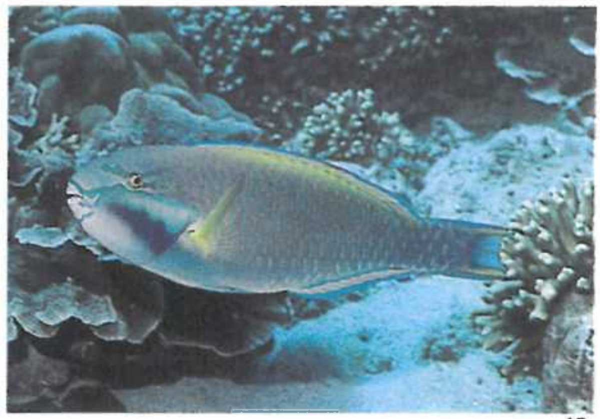
---

Plates 9-16: 9: *Ecsenius lineatus* at Sikha Island, Shabwa Province. This species was also present at the nearby mainland. **10:** *Acanthurus leucocheilus* at Sikha Island. See text for description. **11:** Heterospecific pair of *Chaetodon lunula* and *C. fasciatus* at Sikha Island. This pair was observed on several occasions over a two-week period. **12:** The 'Red Sea endemic' scarid *Chlorurus genazonatus* at Sikha Island. **13:** Unidentified *Amphiprion* sp., bearing a close resemblance to *Amphiprion omanensis* in all respects except for the width of the two white bars (see text) at al-Mukalla. **14:** *Pseudanthias marcia*. This species is extremely abundant on *Porites*-dominated slopes at Sikha Island. **15:** *Pseudanthias townsendi* at Sikha Island. **16:** The Oman butterflyfish *Chaetodon dialeucos* at Sikha Island.


9


10


11


12


13


14


15


16

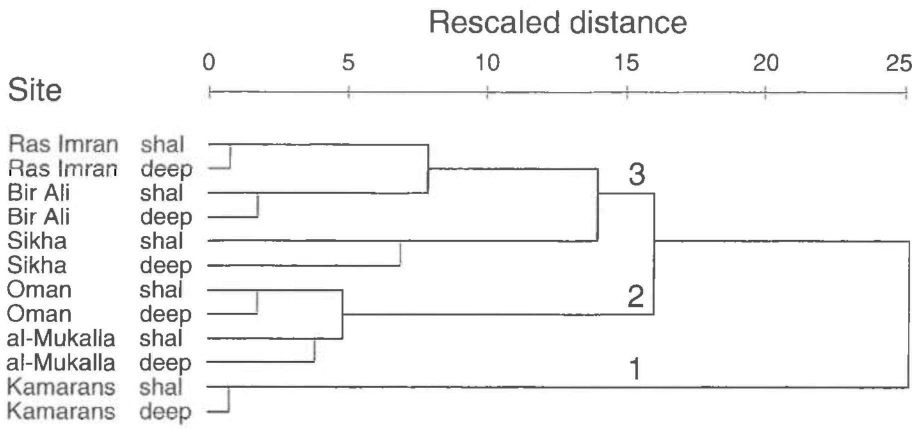


Fig. 3: Dendrogram (Ward's method) of species assemblages for five families of coral-associated fishes (Chaetodontidae, Pomacanthidae, Pomacentridae, Acanthuridae and Balistidae), totalling 80 species, in six areas on the coast of southern and eastern Arabia. Shallow assemblages (shal) were at 1-3 m depth, and deep assemblages (deep) were at 8-12 m depth. The dendrogram reveals three major clusters of species assemblages (labelled 1, 2 and 3), and illustrates the divergence between the al-Mukalla assemblage and those of the Bir Ali mainland shore and Sikha Island. The assemblage of al-Mukalla is more closely related to that of southern Oman, 700 km to the east, than it is to that of Bir Ali, 100 km to the west. The three clusters are: (1) the Kamaran Islands, southern Red Sea, (2) the Gulf of Aden and Arabian Sea coast of Yemen and Oman, from al-Mukalla to the Hallaniyat (Kuria Muria) Islands, and (3) the Gulf of Aden from Aden (Ras Imran) to Bir Ali.

west. Upwelling systems are unstable environments in which physical, chemical and biological characteristics are subject to continuous change, a feature which creates a relatively stressful environment for marine organisms (SAKKO 1998). In Oman and eastern Yemen the Arabian upwelling causes reduced water temperatures and raised productivity from June to September, during the summer monsoon (SHEPPARD et al. 1992). Steep clines in temperature and primary productivity occur between al-Mukalla and Bir Ali during the upwelling, with al-Mukalla generally exposed to more pronounced upwelling effects than Bir Ali. Sea surface temperatures (SST) at Bir Ali are commonly between 1 and 2 °C higher during the summer monsoon upwelling than at al-Mukalla (NOAA data provided by the Climate Diagnostics Center at www.cdc.noaa.gov, SLUTZ et al. 1985, WOODRUFF et al. 1993). Shallow sub-surface (4 m depth) temperatures follow similar patterns, with temperatures of 19-20 °C at al-Mukalla from August to September 1984, and 25-27 °C in the Bir Ali area at the same time (STIRN 1985, cited in WATT 1996). Over the same period primary productivity, as measured by sea surface colour, typically demonstrates a similarly pronounced cline (Plate 17), with phytoplankton pigment concentration falling from as high as 10 mg/m^3 in the al-Mukalla area to as low as 2 mg/m^3 in the Bir Ali area. The areas of lower temperature and higher primary productivity correspond to the areas of more intense monsoon upwelling (CURRIE et al. 1973, SAVIDGE et al. 1990). These areas in turn correspond closely to the centre of endemism identified in Oman by RANDALL & HOOVER (1995) and to disjunct Arabian fish distributions described below. If the effects of monsoon upwelling are significant direct or indirect factors determining the distributions of fish species and the composition of fish communities in southern and eastern Arabia, then the distributions of these environmental variables may explain the clustering pattern of species assemblages in Fig. 3.

The closer relationship of the al-Mukalla species assemblage to that of southern Oman is not completely consistent across all families. In the Pseudochromidae, *Pseudochromis aldabraensis* Bauchot-Boutin, 1958 is abundant in Oman, from Musandam in the north to Salalah in the south (RANDALL 1996, Kemp personal observation), but is absent from Hadramaut and Shabwa. Here it

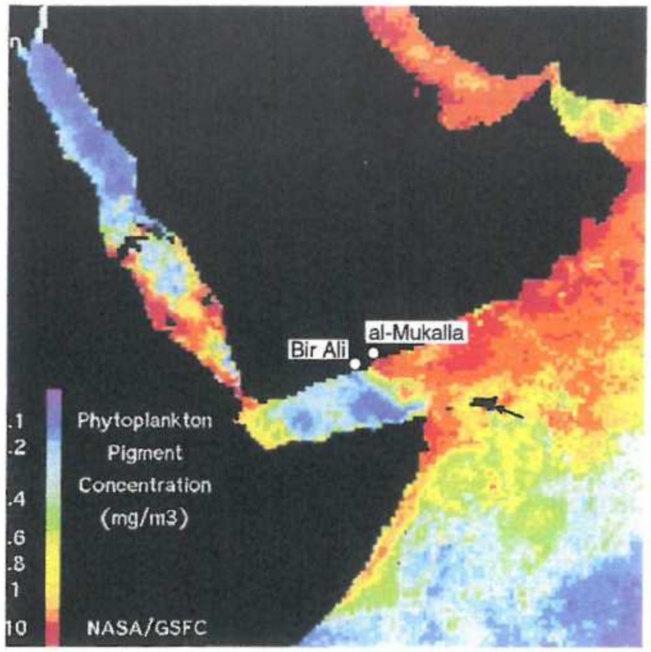


Plate 17: Coastal Zone Colour Scanner image of phytoplankton pigment concentration in the north-western Indian Ocean region in summer 1979 (July–August–September), showing the areas of upwelling (yellow, orange and red) along the Indian Ocean coast of Somalia and the Arabian Sea coasts of Yemen and Oman. The relatively low productivity in the Gulf of Aden is conspicuous. Bir Ali and al-Mukalla lie either side of the most pronounced cline in upwelling along the mainland of Arabia, where the intensity of upwelling in the Arabian Sea rapidly declines moving westwards into the Gulf of Aden.
(Data from http://seawifs.gsfc.nasa.gov/SEAWIFS/IMAGES/CZCS_DATA.html).

is replaced by the locally abundant Red Sea / Gulf of Aden species *P. sankeyi* Lubbock, 1975. These two species occupy similar habitats, both being most commonly found in small groups closely associated with vertical rocky faces and overhangs. In the Serranidae, the Oman species *Pseudanthias marcia* Randall & Hoover, 1993 (Plate 14) is extremely abundant on steeper coral-rich slopes at Sikha, but was not recorded at al-Mukalla. The Arabian Gulf and Oman species *Pseudanthias townsendi* (Boulenger, 1897) was also present at Sikha Island, but in very low numbers, with only one male and less than half a dozen females recorded at one site (Plate 15). Rare individuals of the Oman butterflyfish *Chaetodon dialeucos* were also present at Sikha Island (Plate 16), but were recorded nowhere else in Yemen.

Disjunct Arabian distributions and the Oman area of endemism

The southern Oman centre of endemism noted by Randall & Hoover (1995) is a significant feature of fish species distributions in eastern Arabia. In addition to high levels of endemism in this region, Randall & Hoover (1995) and Randall (1996) noted the occurrence of Indian Ocean or Indo-West Pacific species here which are otherwise absent from Arabia. The opposite is also the case: a number of species have markedly disjunct distributions in eastern Arabia, being common either side of the Oman area of endemism, but rare or absent within it.

This distributional feature is well illustrated by two species of *Pomacanthus* in Oman and Yemen, *P. semicirculatus* and *P. maculosus* (Forsskål, 1775). *Pomacanthus semicirculatus*, a widespread Indo-West Pacific species, appears to replace *P. maculosus* in the area of most pronounced upwelling, approximately from Masirah Island in Oman to the eastern Gulf of Aden in Yemen. *Pomacanthus maculosus* is very common in the Gulf of Aden and the Gulf of Oman to either side, where *P. semicirculatus* is absent or very rare (KEMP 2000). *Pomacanthus semicirculatus* was absent at Bir Ali, but was sympatric with *P. maculosus* at al-Mukalla (KEMP 2000). Other species which appear to have similar Arabian distributions include the pomacentrid *Pomacentrus trichourus* Playfair & Günther, 1867, the balistid *Rhinecanthus assasi* (Forsskål, 1775), and the acanthurid *Acanthurus sohal* (Forsskål, 1775), amongst others. Such species are rare in southern Oman but common in the Gulf of Oman or Arabian Gulf to the north, and the Red Sea and Gulf of Aden to the west.

The unusual ichthyofauna of Sikha Island

A significant feature of the eight new records presented here is that seven come from the very small island of Sikha. In spite of extensive surveys of nearby coral communities fringing the mainland shore, and at nearshore islands, six of these species were not recorded anywhere else (*Ecsenius lineatus* was recorded at both Sikha Island and the Bir Ali mainland). The fish community of Sikha is highly unusual in the entire Hadramaut/Shabwa area, and studies of charts of the area (Admiralty Chart # 6, Gulf of Aden, 1993) reveals that there are no further sites in the northern Gulf of Aden which resemble Sikha (islands more than 1 km offshore, in more than 40 m of water). Of a total of 267 species of fish listed in Table 2 (Appendix), five are included as photographic records for the region (from DEBELIUS 1998). Of the remaining 262 species identified in Hadramaut and Shabwa during the 1998 expedition, 50 (= 19 %) were only recorded at Sikha. This contrasts with 12 species (= 4.5 %) only recorded at al-Mukalla, and 21 species (= 8.0 %) only recorded at coastal and nearshore sites (including al-Mukalla), and not recorded at Sikha Island.

Diversity of the five target families in Hadramaut and Shabwa is high in comparison to many other regions of Arabia, and most of this diversity comes from Sikha Island. The most striking example of this is in the Chaetodontidae. Eighteen species of chaetodontids were recorded at Sikha, a total unprecedented for any other region of Arabia (Fig. 4). With less than 4 km of coastline Sikha Island has a higher species richness of butterflyfishes than southern Oman, the Gulf of Oman, the Arabian Gulf, or any section of the Red Sea (the entire Red Sea has 15 confirmed species). At a more local scale, eight of these butterflyfish species (44 %) were not recorded anywhere else in Hadramaut or Shabwa. Only one butterflyfish species present in Hadramaut/Shabwa was not recorded at Sikha Island (*Chaetodon leucopleura* Playfair & Günther, 1867, recorded at al-Mukalla). In the Acanthuridae, five of 15 species (= 33 %) were only present at Sikha. In the Balistidae and Pomacentridae the figures are 40 % and 15 %, respectively. The new records are thus just one feature of a generally unusual ichthyofauna at this island. The higher diversity at Sikha, and lower diversity elsewhere, is not a result of sampling bias. Twenty hours were spent SCUBA diving at Sikha Island, approximately half of the total time spent SCUBA diving at all other areas of Hadramaut and Shabwa (41 hours). Approximately equal amounts of time (6-8 hours) were spent snorkelling in each area.

The new records are of species with broad distributions in the Indian Ocean. Most are known from all of the areas surrounding Arabian seas to both south and east, including East Africa, the Seychelles, the Chagos Archipelago and the Maldives. With the exception of *Acanthurus triostegus* none of the new records have yet been recorded from the Socotra Archipelago (*A. triostegus* was also the only species among the new records which was present at al-Mukalla and in southern Oman, but not in Shabwa). Although both Hadramaut/Shabwa and Socotra are dominated by

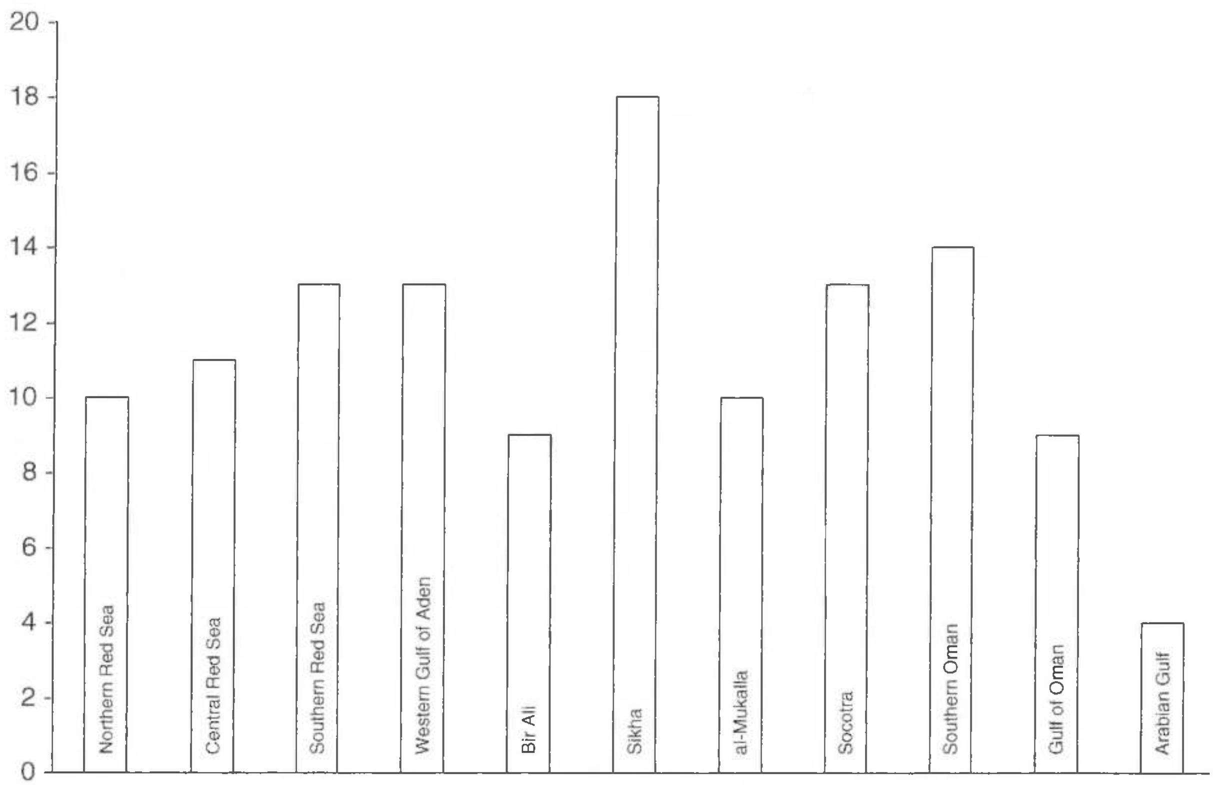


Fig. 4: Species richness of butterflyfishes (Chaetodontidae) in different regions of Arabian seas. With approximately 4 km of coastline Sikha Island is more speciose than any other single large region.

similar characteristically South Arabian species (for instance, in the Chaetodontidae the Arabian endemic taxa *Chaetodon vagabundus pictus* Fraser-Brunner, 1950 and *C. melapterus* are very dominant in both areas), in some respects the ichthyofaunas of the two areas differ considerably from each other. The assemblage of distinctively Indian Ocean or Indo-West Pacific species present at Socotra but absent from Arabia (Kemp 1998 b) is completely different from the analogous assemblage at Sikha. A number of Indo-West Pacific and Indian Ocean species present or even common at Socotra (Kemp 1998 b) were not recorded anywhere in Hadramaut/Shabwa, e.g. *Chaetodon kleinii* Bloch, 1790, *Dascyllus carneus* Fischer, 1885, *Acanthurus lineatus* Linnaeus, 1758, *Balistoides conspicillum* (Bloch & Schneider, 1801) and *Ostracion meleagris* Shaw, 1796. Conversely, none of the Shabwa new records have yet been recorded from Socotra. The Red Sea influence, in the form of Red Sea / Gulf of Aden endemic species, is minimal at Socotra in comparison to both Bir Ali (Shabwa Province) and al-Mukalla (Hadramaut Province).

A similarity between Socotra and Hadramaut/Shabwa, and one both areas share with Oman, is the apparent absence of several widespread Indo-West Pacific fish species which are also found in the Red Sea. These include species such as the pomacentrids *Dascyllus aruanus* (Linnaeus, 1758) and *Pomacentrus sulphureus* Klunzinger, 1871, and the pomacanthid *Pygoplites diacanthus* (Boddaert, 1772). This supports the observation of Kemp (1998 b) that such species may have disjunct distributions, being present in the Red Sea and extreme west of the Gulf of Aden and in most of the Indian Ocean, but absent from the intervening central and eastern Gulf of Aden, Oman, Socotra and the northern Horn of Africa. This is likely to have significant implications for gene flow, evolution and conservation of these species.

Long-distance planktonic dispersal of fishes to and from Arabia

The nature of the fish assemblage of Sikha has implications for understanding of the relationship between larval dispersal and the distribution of fishes at a zoogeographic scale throughout the north-western Indian Ocean region. The only species of the new records which, on the basis of the 1998 survey, can be unequivocally said to have an established Arabian breeding population (sensu Williamson 1996) is *Thalassoma quinquevittatum*, observed spawning in large numbers at Sikha Island. Most of the other species are very rare in the Bir Ali area and may successfully spawn here rarely or not at all. Pyle & Randall (1994) suggest that locally rare species (such as species at or near the edges of their ranges) may have very low levels of reproductive success. For most of the new records presented here, and other locally rare species, the Gulf of Aden is likely to be a sink rather than a source of larvae. It is thus possible that at least some of these species are only represented in Shabwa by widely dispersed products of spawning events outside Arabian seas, where established populations are known to occur.

Adults of the majority of tropical reef fishes are territorial or site-attached (Sale 1980), but most species go through a pelagic planktonic phase as eggs and/or larvae (Leis 1991). It is during this phase that long-distance dispersal is believed to occur, principally by passive advection by currents. The duration of the larval phase varies between and within families, ranging from as little as nine to over 100 days, and dispersing larvae over distances ranging from a few meters to thousands of kilometres (Leis 1991). At the end of this time the larvae settle onto a benthic habitat, and before, during or after settlement metamorphose into the adult form (Victor 1991).

The Arabian Sea coast of Arabia is swept by two major currents through the course of the year (Fig. 5). These currents are driven by the Indian Ocean monsoon winds, and may disperse fish larvae of many species to and from the Arabian Peninsula. From November to March the north-east monsoon current flows westwards across the Arabian Sea, past Arabia and southwards along the African coast. This pattern is reversed between April and October during the South-west monsoon, when the Somali current flows north along the African and Arabian coasts before turning eastwards in the Arabian Sea towards India and the Maldives.

Several instances of long-distance dispersal of Arabian endemic species via these currents, to areas outside their normal ranges, have been recorded. Ahl (1923) recorded a single juvenile of *Chaetodon melapterus* at the Seychelles, and Randall & Anderson (1993) reported the occurrence of a single adult *Zebrasoma xanthurum* (Blyth, 1852) in the Maldives. Randall (1996) remarks that juveniles of this latter species appear in the Gulf of Oman in the summer. This is at the time when the prevailing currents in the Arabian Sea are moving in an easterly direction. Thus, the observed occurrence of juveniles in the Gulf of Oman coincides with the only time of year when larvae could be transported from Arabia to the Maldives, the only non-Arabian location where the species has been recorded, and a distance of at least 2200 km. The dispersal of the juvenile *C. melapterus* from Arabia to the Seychelles must have occurred between November and March, when the monsoon currents are reversed, flowing from Arabia southwards past East Africa, and then eastwards towards the Seychelles, a minimum straight-line distance of 1900 km. The indirect route the winter currents actually follow from Arabia to the Seychelles means that the true distance travelled by this individual is likely to have been close to 3000 km. Isolated records such as these provide significant information about the dispersal abilities of reef fishes, and confirm the proposition of Leis (1991) that the larval range of many reef fish is likely to be significantly greater than that of established adult populations. This raises the question of where the original source of the very isolated populations of non-Arabian species recorded at Sikha Island is likely to have been, and why these fish settled and survived at Sikha but not elsewhere.

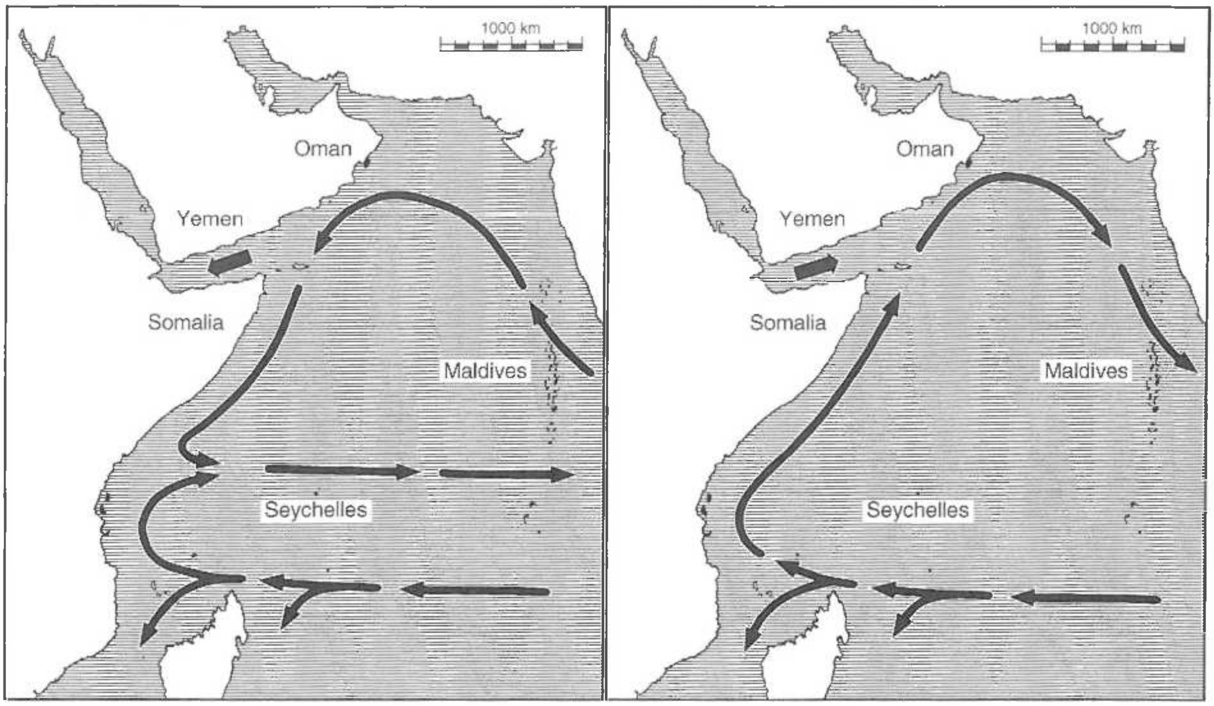


Fig. 5: Prevailing currents in the Arabian Sea and north-western Indian Ocean during the north-east (winter) monsoon (left) and the south-west (summer) monsoon (right). The bold arrows indicate the direction of prevailing winds and surface currents in the Gulf of Aden.

The possibility of dispersal of larvae over long distances in the northern Indian Ocean is already demonstrated by the two non-Arabian records of Arabian endemics described above. Of the Shabwa records, *Chaetodon zanzibarensis* is not known from the Maldives and Laccadives, and so the Sikha population is most likely to have originated in east Africa or the Seychelles, requiring transport via the Somali current during the period of the upwelling. In contrast, *Ecsenius lineatus* is unknown from elsewhere on the western Indian Ocean margin, and the closest record to Arabia prior to that presented here is from the Maldives (SPRINGER 1988). Thus the fish community of the Bir Ali area provides evidence that dispersal of fishes to the eastern Gulf of Aden from the Indian Ocean occurs via both the summer and the winter monsoon currents. Evidence from southern Oman indicates that the same is true of the Arabian Sea coast of Arabia, where isolated records of *Centropyge acanthops* (Norman, 1922) from East Africa, and of *Chaetodon decussatus* Cuvier, 1831 from the Sri Lanka / Maldives region, have been made (RANDALL 1996, DEBELIUS 1998).

The nutrient-rich water of the summer monsoon upwelling produces an area of high productivity along the Indian Ocean coast of Somalia and the Arabian Sea coast of the Arabian Peninsula (CURRIE et al. 1973, SAVIDGE et al. 1990). Under these conditions survival of coral reef fish larvae may be greatly reduced (ROBERTS 1991), and oceanographic conditions prevailing throughout the duration of the summer monsoon may act as a severe limitation on dispersal of fishes from East African coral reef areas to Arabia (KEMP 1998 b). It is thus possible that dispersal to Arabia via this route is a relatively rare event, and the records of East African species, such as *Chaetodon zanzibarensis* and *Centropyge acanthops*, are exceptions to the rule. Hence, Arabian populations of many Indian Ocean or Indo-West Pacific species, such as *Chaetodon lunula*, *C. auriga setifer* Ahl, 1923, *Acanthurus triostegus* and *Acanthurus leucosternon* Bennett, 1832, whose Arabian distributions are restricted to Oman and the Gulf of Aden, may recruit principally during the winter monsoon, originating from the Maldives/Laccadives region. A consequence of this may be unidirectional gene flow, in the Arabian Sea region, for some species of fish.

Two other factors related to the pronounced seasonality of the monsoon currents may also result in unidirectional dispersal and gene flow for many marine taxa in the Arabian Sea and the Gulf of Aden. Firstly, seasonality of spawning in reef fishes is widespread, although with wide geographic and taxonomic variation (Robertson 1991). Seasonality of spawning of any reef fish species in the north-western Indian Ocean region will have a profound effect upon direction of dispersal of those species. Species spawning during the summer monsoon will disperse from Africa towards Arabia, and from the Maldives away from Arabia. Spawning during the winter monsoon will result in the opposite situation.

Secondly, within the Gulf of Aden during the summer monsoon, when the Somali current flows northwards past the Gulf of Aden (Fig. 5), wind-driven surface currents within the Gulf of Aden flow from west to east (Edwards 1987), making it unlikely that fish larvae arriving from East Africa via the Somali current will be able to disperse westwards into the Gulf of Aden (further emphasising the low probability of frequent arrival of East African and Seychelles species, such as *Chaetodon zanzibarensis*, inside the Gulf of Aden). Dispersal of Indian Ocean species into the Gulf of Aden, and thus to Bir Ali and Sikha Island, is likely to occur more frequently during the winter monsoon, when westward-flowing surface currents in the Gulf of Aden (Edwards 1987, Sheppard et al. 1992) would tend to carry larvae, arriving at Arabia from the Maldives/Laccadives region via the north-east monsoon current, into the Gulf of Aden, and consequently towards the Red Sea. This is the only route by which *Ecsenius lineatus* can have arrived at the Bir Ali area, and it is a hypothesis which suggests that populations of many non-endemic Gulf of Aden and Red Sea fish species may be more closely related to those of the Maldives and Sri Lanka region than they are to East African populations. Strong seasonality of Arabian Sea currents, combined with the unusual oceanographic feature of the Somali and Arabian upwelling, may impose strong directionality on dispersal to and from Arabia, and consequently on gene flow in marine taxa of the north-western Indian Ocean region. Identification and confirmation of such source/sink patterns of population and gene flow is of increasing significance for development of regional conservation plans and networks of protected areas (Roberts 1997), and underlines the interdependence of apparently far-flung locations, at a time when complacency about the resilience of widespread and widely-dispersing marine taxa to local or global extinction is rapidly coming to an end (Roberts & Hawkins 1999, Roberts et al. in press).

The coast of Oman is exposed to both the summer and winter monsoon currents, and larvae of the Sikha Island and Bir Ali species, although unknown in Oman, must pass through Omani waters as larvae en route from the Maldives. The lack of records of these species from Oman may be due to a lack of settlement by larvae, or post-settlement mortality, or a combination of the two (although a paucity of sampling and survey effort in the south of Oman means that at least some Indian Ocean species not yet known from Arabia will almost certainly be recorded there in future). Recruits of many non-Arabian species may occur in Oman during the winter monsoons, only for the majority to be killed off by conditions during the subsequent summer monsoon upwelling. The reduced intensity of the upwelling in Shabwa Province will allow many of these species, when settling from the plankton in the Bir Ali area, to survive the summer. This hypothesis is testable by detailed studies of juvenile settlement and mortality on the Arabian Sea coast of Oman, at the Socotra Archipelago, and within the Gulf of Aden.

A number of factors may contribute to the observed differences between assemblages of Indian Ocean origin at Socotra, and at Sikha. The Sikha species may be present at Socotra, but not yet recorded due to limited survey and sampling. Only one study of the fishes of Socotra has been completed to date (KEMP 1998 b), on the basis of studies at a total of 21 sites. However, sites surveyed throughout the Socotra Archipelago included habitats very similar to those of Sikha Island. The Sikha new records are all of large and conspicuous fish, and if any are present at Socotra they are likely to be rare. Alternatively, KEMP (1998 b) argues that the 'pseudo-high latitude' effect arising from the monsoon upwelling of the Somali coast and the Arabian Sea coast of Oman may produce conditions which preclude settlement or survival of many Indian Ocean reef fish species at Socotra. The markedly lower intensity of the upwelling conditions at Bir Ali in comparison to al-Mukalla has already been suggested in this paper as an explanation for the differences between the Bir Ali and al-Mukalla fish assemblages. It follows from this that the Socotra Archipelago, which experiences greater exposure to the effects of upwelling than Bir Ali, would be unlikely to support fish species which are present at Bir Ali and Sikha but do not settle successfully or survive at al-Mukalla.

Implications of the new records for understanding the role of planktonic dispersal and settlement site selection in Arabian reef fish zoogeography

The closest high-cover coral communities to Sikha Island are along the mainland coast at Bir Ali, less than 10 km distant. The absence of six of the seven Sikha new records from these closely neighbouring coral areas in spite of extensive surveys clearly does not indicate that larvae of these species do not arrive at the mainland areas, but rather that the majority of them probably do not settle or successfully colonise anywhere other than Sikha. The fact that the fish observed were of different ages (subadult *Chaetodon trifasciatus*, adult *C. zanzibarensis*, co-occurrence of different size classes of *Thalassoma hardwicke*) further indicates that arrival of these travellers is not infrequent. Differences in intensity of upwelling may explain the observed differences between Bir Ali and al-Mukalla, but they are unlikely to explain the differences between the Bir Ali mainland and Sikha Island.

In addition to six of the new records, a total of 44 other species in 17 families were restricted to Sikha Island. Twenty-three of these species are at or near the geographical limit of their ranges, including Red Sea species (*Chaetodon fasciatus*, *Chlorurus genazonatus*, etc.), and a greater number of Indian Ocean or Indo-Pacific species which do not appear to extend their ranges any further north-east into Oman [*Caesio xanthonota* Carpenter, 1987, *Chaetodon lineolatus*, *C. melannotus*, *Naso brevirostris* (Valenciennes, 1835), *N. fageni* Morrow, 1954, *Balistapus undulatus* (Park, 1797), *Pseudobalistes fuscus* (Bloch & Schneider, 1801)].

This unusual fish community is likely to be a result of differential settlement from the plankton rather than post-settlement migration, because, with the exception of pelagic and epi-pelagic species, post-settlement movement of shallow reef fish between the mainland and Sikha is unlikely. Some studies have shown post-settlement migration to be significant at smaller scales (e.g. LEWIS 1997), but migration of the shallow water species of Sikha, many of which are closely associated with coral-rich habitats, across the several kilometres of deep water between Sikha and the mainland, or vice versa, is unlikely. This suggests that there may be a feature, or features, of the Sikha environment which differs from nearby coastal habitats, and which enables successful settlement and survival of species at the extremes of their ranges. Certainty about the environmental characteristics which give rise to this is not possible at this stage, but some obvious possibilities exist.

Diversity of habitats: Sikha is the only relatively deep water island in the northern Gulf of Aden. Species associated with steep, current-swept coral slopes at Sikha (e.g. *Pseudanthias marcia*) are unlikely to find this kind of habitat anywhere else in the Hadramaut/Shabwa area. Similarly, the only very shallow, very high cover areas of healthy branching corals located during the recent survey were those at Sikha. In close proximity at Sikha are exposed low coral cover, high algal cover rocky slopes, extensive areas of high cover branching and massive corals, large expanses of soft corals, and very diverse mixtures of all of these, and all at a wide range of depths – a feature locally unique to this island.

An offshore location with considerably lower turbidity than the mainland coral communities: The gross level habitat differences described above cannot account for the presence of all the Sikha species. For instance, *Chaetodon zanzibarensis*, *Halichoeres cosmetus* and *Acanthurus leucocheilus* at Sikha Island were all associated with habitat types which were also present at nearby mainland sites (respectively: extensive areas of massive *Porites* corals; mixed hard and soft coral areas; exposed rocky shores with low coral cover). A conspicuous difference between Sikha Island and the inshore areas was turbidity. Turbid conditions inshore at Bir Ali were noticeably more frequent and severe than at Sikha during the 1998 survey period.

Studies inside the Red Sea have revealed marked differences, often of a nature resembling zoogeographic differences, between the fish communities of closely adjacent turbid and clear-water sites. Roberts et al. (1992) found significant differences between fish assemblages of turbid inshore and clear-water offshore reefs in the southern Red Sea. In the central Red Sea at Rabigh (Saudi Arabia), the pomacanthid *Pomacanthus asfur* (Forsskål, 1775) is common in turbid lagoon environments reminiscent of the southern Red Sea (where it is abundant), but is absent from the clear-water seaward reef slopes and offshore patch reefs (J. Kemp, personal observation). The characteristically central and southern Red Sea butterflyfish *Chaetodon larvatus* is uncommon in the northern Red Sea except for localised abundance at inshore areas of high turbidity (C. Roberts, pers. comm.). In Shabwa Province this species is almost six times more abundant at mainland hard coral sites than it is at similar sites at Sikha. It is thus possible that differences in turbidity of the mainland and of Sikha Island impose different selective pressures on the fish assemblages at the two sites.

Differential settlement of fish larvae, due to environmental and habitat differences between Sikha and the adjacent mainland, may explain some of the observed differences between fish assemblages of the two areas. Booth & Wellington (1998) suggest that strong habitat preferences in reef fishes at the time of settlement from the planktonic phase may decouple the relationship between larval supply and recruitment. From the time of settlement fish exhibit strong preferences for particular habitats (Sale 1980). Habitat selection by larval or juvenile coral reef fish at the time of settlement is increasingly recognised as a significant factor structuring fish communities at a range of scales, from preferences between individual coral colonies, to selection between distinct zones in large reef systems (e.g. Milicich & Doherty 1994, Doherty et al. 1996, Light & Jones 1997, Booth & Wellington 1998). This has been documented up to large scales in a range of different circumstances, such as a failure of juveniles of some families of fish to settle in areas of corals destroyed by storm damage, coral bleaching, or crown-of-thorns starfish (see review by Jones & Sims 1998). In the light of the proposition by Leis (1991) that larval fish ranges may be considerably greater than the ranges of adult populations this is a possibility which may have profound implications for studies of reef fish zoogeography and ecology.

Whether the patterns of fish distribution at Sikha and Bir Ali are the result of settlement preferences or differential post-settlement survival, or some combination of the two, is not clear, but whichever is the case the results of this study give a clear indication that pre-settlement mortality is probably not as significant in this case, at least for some species, as processes occurring at or soon after the time of settlement. RANDALL & HOOVER (1995) suggest that the occurrence of the unusual ichthyofauna of the Arabian Sea coast of Oman may be due to physical or biological parameters related to the presence of seasonal monsoon-driven upwelling of cold nutrient-rich water along this coast, which may isolate southern Oman fish populations. The findings of this study support part of this hypothesis, namely that the upwelling directly or indirectly affects the distributions of coastal fishes in southern and eastern Arabia. However, there is reason to doubt whether the effect is entirely due to creation of barriers to dispersal of fish larvae. The evidence from the fish assemblage of the Bir Ali area, and particularly Sikha Island, suggests that habitat effects, either at settlement or immediately post-settlement, may be as significant as larval dispersal in determining the distribution of fish species and the composition of fish communities at both zoogeographic and local scales along the Arabian Sea and Gulf of Aden coast of Arabia. Settlement preferences and post-settlement processes may at least partly determine the very large-scale distribution of tropical reef fish species.

Unusual environmental conditions and habitats at a range of scales, both local and regional, appear to give rise to a 'zoogeographically displaced' Indian Ocean component of the fish fauna at Bir Ali, and particularly at Sikha Island. This component probably originates largely from the Maldives/Laccadives region, although part of it is probably of East African origin. Identification of such locations is likely to provide an unusual opportunity to examine the effects of settlement preferences of larval reef fishes, and the effects of pre- and post-settlement processes, at very large zoogeographic scales.

ACKNOWLEDGEMENTS

Fieldwork throughout Oman and Yemen in early 1998 could not have been successfully carried out without the logistical support and help of Jonathan Ali Khan and other members of the Arabian Seas Expedition. Dr. V.G. Springer of the National Museum of Natural History, Smithsonian Institution, Washington D.C., and Dr. J.E. Randall of the Bernice P. Bishop Museum, Hawaii, provided assistance with identification of photographed fishes, and Dr. A.C. Gill of the Natural History Museum, London, provided advice and assistance with research on collections held there. P.J. Hogarth, C. Dytham and A.V. Morris, all of the University of York, provided constructive criticism of the manuscript.

REFERENCES

British Admiralty Chart Number 6. *Gulf of Aden*. 1993. Taunton, U.K.; Admiralty Charts & Publications.

AHL, E. 1923. Zur Kenntnis der Knochenfischfamilie Chaetodontidae, insbesondere der Unterfamilie Chaetodontinae. *Archiv für Naturgeschichte* **89A** (5): 1-205.

AL-BAHARNA, W.S. 1986. *Fishes of Bahrain*. 294 pp. Bahrain; Directorate of Fisheries.

AL-SAKAFF, H. & ESSEEN, M. 1999. Occurrence and distribution of fish species off Yemen (Gulf of Aden and Arabian Sea). *Naga, the ICLARM Quarterly* **22** (1): 43-47.

BARRATT, L. & MEDLEY, P. 1990. Managing multi-species ornamental reef fisheries. *Progress in Underwater Science* **15**: 55-72.

BARRATT, L., ORMOND, R.F.G. & WRATHALL, T.J. 1986. *Ecological studies of southern Oman kelp communities. Part I.* 22 pp. University of York. Report for the Council for the Conservation of the Environment and Water Resources, Muscat, Sultanate of Oman.

Barratt, L., Ormond, R.F.G., Campbell, A.C., Hiscock, S., Hogarth, P.J. & Taylor, J.D. 1984. *An Ecological Study of Rocky Shores on the South Coast of Oman.* 104 pp. Report of IUCN to UNEP's Regional Seas Programme.

Bellwood, D.R. 1996. The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage. *Coral Reefs* 15 (1): 11-19.

Bellwood, D.R. 1998. What are reef fishes? – Comment on the report by D.R. Robertson: Do coral-reef fish faunas have a distinctive taxonomic structure? (Coral Reefs 17: 179-186). *Coral Reefs* 17 (2): 187-191.

Bennett, J.W. 1830. *A selection of rare and curious fishes found upon the coast of Ceylon.* Part 6. London.

Blum, S.D. 1989. Biogeography of the Chaetodontidae: an analysis of allopatry among closely related species. *Environmental Biology of Fishes* 25: 9-31.

Booth, D.J. & Wellington, G. 1998. Settlement preferences in coral-reef fishes: Effects on patterns of adult and juvenile distributions, individual fitness and population structure. *Australian Journal of Ecology* 23: 274-279.

Brodie, J., Al-Sorimi, M. & Turak, E. [in press]. Fish and fisheries of Yemen's Red Sea. In: *The biology of the Red Sea coasts and islands of the Republic of Yemen.* Brodie, J. & Turak, E. (eds). United Nations Development Programme reports.

Burgess, W.E. 1978. *Butterflyfishes of the world: a monograph of the family Chaetodontidae.* 832 pp. Neptune City; TFH publications.

Carpenter, K.E., Harrison, P.L., Hodgson, G., Alsaffar, A.H. & Alhazeem, S.H. 1997. *Corals and coral reef fishes of Kuwait.* 166 pp. Kuwait; Kuwait Institute for Scientific Research/Environmental Public Authority.

Choat, J.H. & Bellwood, D.R. 1991. Reef fishes: their history and evolution. In: *The ecology of fishes on coral reefs.* Sale, P.F. (ed.): 39-66. San Diego; Academic Press.

Currie, R.J., Fisher, A.E. & Hargreaves, P.M. 1973. Arabian Sea upwelling. In: *The Biology of the Indian Ocean.* Zeitzschel, B. & Gerlach, S.A. (eds): *Ecological Studies* 3 (1.4): 37-52.

Debelius, H. 1993. *Indian Ocean tropical fish guide.* 321 pp. Neu Isenburg, Germany; Aquaprint Verlags GmbH.

Debelius, H. 1998. *Red Sea reef guide.* 321 pp. Frankfurt; IKAN – Unterwasserarchiv.

Doherty, P., Kingsford, M., Booth, D. & Carleton, J. 1996. Habitat selection before settlement by *Pomacentrus coelestis. Marine and Freshwater Research* 47: 391-399.

Dor, M. 1984. *CLOFRES. Checklist of the fishes of the Red Sea.* XXII + 427 pp. Jerusalem; Israel Academy of Sciences and Humanities.

Edwards, F.J. 1987. Red Sea climate and oceanography. In: *Red Sea.* Edwards, A.J. & Head, S.M. (eds): 45-68. Oxford; Pergamon Press.

Fraser-Brunner, A. 1950. *Holacanthus xanthotis*, sp. n. and other chaetodont fishes from the Gulf of Aden. *Proceedings of the Zoological Society of London* 120: 43-48.

Goren, M. & Dor, M. 1994. *An updated checklist of the fishes of the Red Sea CLOFRES II.* 120 pp. Jerusalem; Israel Academy of Sciences and Humanities.

Gravier, C. 1910 a. Sur les récifs coralliens de la Baie de Tadjourah et leurs madréporaires: Gulf of Aden. *Compte Rendu Hebdomadaire des Séances de l'Academie des Sciences, Paris* 51: 650-652.

Gravier, C. 1910 b. Sur quelques particularités biologique des récifs madréporiques de la Baie de Tadjourah: Gulf of Aden. *Compte-Rendu de l'Association Français pour l'Avancement des Sciences, Paris* 39: 167-169.

Gravier, C. 1911. Les récifs de coraux et les madréporaires de la Baie de Tadjourah: Gulf of Aden. *Annales de l'Institute Océanographique, Paris* 2: 99.

Herre, A.W.L.T. 1927. Philippines surgeonfishes and moorish idols. *Phillipines Journal of Science* 34 (4): 403-476.

Hirth, H.F., Kilhoff, L.G. & Harper, K.T. 1973. Seagrasses of Khor Umeirah, People's Democratic Republic of Yemen, and their role in the diet of the Green Turtle *Chelonia mydas. Fishery Bulletin* 71: 1093-1097.

Huntington, T.C. & Wilson, S.C. 1995. *Coastal Marine Habitats Survey. Gulf of Aden Fisheries IV Project, Yemen. Phase I: Preliminary habitat classification and an assessment of the coasts resources, users and impacts.* 125 pp. Report to the European Commission, and to the Ministry of Fish Wealth, Government of the Republic of Yemen. MacAlister Elliott & Partners Ltd., UK / Marine Sciences Resource Research Centre, Aden.

Jones, G.P. & Sims, C. 1998. Disturbance, habitat structure and the ecology of fishes in coral reefs. *Australian Journal of Ecology* 23: 287-297.

Kemp, J.M. 1997. Extensive coral communities of the Socotra Archipelago, Gulf of Aden. *Coral Reefs* 16: 214.

Kemp, J.M. 1998 a. The occurrence of *Nizamuddinia zanardinii* (Schiffner) P.C. Silva (Phaeophyta: Fucales) at the Socotra Archipelago. *Botanica Marina* 41: 345-348.

Kemp, J.M. 1998 b. The zoogeography of the coral reef fishes of the Socotra Archipelago. *Journal of Biogeography* 25: 919-933.

Kemp, J.M. 2000. Hybridisation of the marine angelfishes *Pomacanthus maculosus* and *P. semicirculatus* in the Gulf of Aden. *Fauna of Arabia* 18: 357-367.

Kemp, J.M. & Benzoni, F. 2000. A preliminary study of coral communities in the northern Gulf of Aden. *Fauna of Arabia* 18: 67-86.

Kemp, J.M. & Obura, D. [in press]. Coral reefs of Somalia and Socotra. In: *Coral reefs of the western Indian Ocean: their ecology and conservation.* McClanahan, T., Sheppard, C.R.C. & Obura, D. (eds).

KLAUSEWITZ, W. 1962. *Ecsenius lineatus* n. sp. von den Malediven (Pisces, Blenniidae). *Senckenbergiana biologica* 43 (2): 145-147.

KLAUSEWITZ, W. 1989. Evolutionary history and zoogeography of the Red Sea ichthyofauna. *Fauna of Saudi Arabia* **10**: 310-337.

KUITER, R.H. 1995. *Chaetodon lunulatus*, a sibling species of *C. trifasciatus*, with observations on other sibling species of butterflyfish (Chaetodontidae). *Revue française d'Aquariologie* **21**: 3-4.

LAY, G.T & BENNETT, E.T. 1839. Fishes. In: *Zoology of Captain Beechey's voyage; compiled from the collections and notes made by Captain Beechey, the officers and naturalist of the expedition during a voyage to the Pacific and Behrings Straits performed in His Majestys ship "Blossom"*. Richardson, J., Vigors, N.A., Lay, G.T., Bennett, E.T., Owen, R., Gray, J.E., Buckland, W. & Sowerby, G.B. (eds): 41-75. London; Henry G. Bohn.

LEIS, J.M. 1991. The pelagic stage of reef fishes: The larval biology of coral reef fishes. In: *The ecology of fishes on coral reefs*. Sale, P.F. (ed.): 183-230. San Diego; Academic Press.

LEWIS, A.R. 1997. Recruitment and post-settlement immigration affect the local population size of coral reef fishes. *Coral Reefs* **16** (3): 139-149.

LIGHT, P.R. & JONES, G.P. 1997. Habitat preference in newly settled coral trout (*Plectropomus leopardus*, Serranidae). *Coral Reefs* **16** (2): 117-126.

LINNAEUS, C. 1758. *Systema Naturae*. 10th edition. Tomus 1. 824 pp. Holmiae; Laurentii Salvi.

MCCLANAHAN, T.R. & OBURA, D. 1997. *Preliminary ecological assessment of the Saad ed Din, Awdal Region. Somali Natural Resources Management Programme*. 47 pp. Nairobi; IUCN Eastern Africa Programme.

MILICICH, M.J. & DOHERTY, P.J. 1994. Larval supply of coral reef fish populations: magnitude and synchrony of replenishment to Lizard Island, Great Barrier Reef. *Marine Ecology Progress Series* **110**: 121-134.

OBURA, D. 1997. Coral reefs in the Gulf of Aden. *Reef Encounter* **21**: 17-18.

ORMOND, R.F.G. & BANAIMOON, S.A. 1994. Ecology of intertidal macroalgal assemblages on the Hadramout coast of southern Yemen, an area of seasonal upwelling. *Marine Ecology Progress Series* **105**: 105-120.

ORMOND, R.F.G. & EDWARDS, A.J. 1987. Red Sea Fishes. In: *Red Sea*. Edwards, A.J. & Head, S.M. (eds): 251-287. Oxford; Pergamon Press.

ORMOND, R.F.G., DAWSON-SHEPHERD, A.R. PRICE, A.R.G. & PITTS, R.J. 1984. *Report on the distribution of habitats and species in the Saudi Arabian Red Sea. Parts I and II*. 123 and 151 pp. Reports to the Meteorology and Environmental Protection Administration. Jeddah, Kingdom of Saudi Arabia.

PARK, M. 1797. Description of eight new fishes from Sumatra. *Transactions of the Linnean Society* **3**: 33-38.

PELLEGRIN, J. 1904. Poissons recueillis par M. Cu. Gravier à Djibouti et à Obock. *Bulletin du Muséum d'Histoire naturelle* **8**: 453-455.

PLAYFAIR, R.L. 1866. Acanthopterygii. In: *The fishes of Zanzibar, with a list of the fishes of the whole east coast of Africa*. Playfair, R.L. & Günther, A. 153 pp. London; John van Voorst, Paternoster Row.

PYLE, R.L. & RANDALL, J.E. 1994. A review of hybridisation in marine angelfishes (Perciformes: Pomacanthidae). *Environmental Biology of Fishes* **41**: 127-145.

QUOY, J.R.C. & GAIMARD, P. 1824. Poissons. In: *Voyage autour du monde [...] exécuté sur les corvettes de S.M. "l'Uranie" et "La Physicienne" pendant les années 1817-1820*. 192-401. Paris.

RANDALL, J.E. 1983. *Red Sea Reef Fishes*. 192 pp. London; Immel.

RANDALL, J.E. 1994. Twenty-two new records of fishes from the Red Sea. *Fauna of Saudi Arabia* **14**: 259-275.

RANDALL, J.E. 1996. *Coastal Fishes of Oman*. 439 pp. Bathurst, Australia; Crawford House Publishing.

RANDALL, J.E. & ANDERSON, R.C. 1993 An annotated checklist of the epipelagic and shore fishes of the Maldive Islands. *Ichthyological Bulletin* **59**: 1-47.

RANDALL, J.E. & EDWARDS, A.J. 1984. A new labrid fish of the genus *Thalassoma* from the Pitcairn Group, with a review of related Indo-Pacific species. *Journal of Aquariology and Aquatic Sciences* 4 (2): 13-36.

RANDALL, J.E. & HOOVER, J.P. 1995. *Scarus zhufar*, a new species of parrotfish from southern Oman, with comments on endemism in the area. *Copeia* **1995** (3): 683-688.

RANDALL, J.E. & MAUGÉ, A. 1978. A visit to Djibouti. *The Marine Aquarist* 8 (6): 39-48.

RANDALL, J.E. & SMITH, M.M. 1982. A review of the labrid fishes of the genus *Halichoeres* of the western Indian Ocean, with descriptions of six new species. *Ichthyological Bulletin* **45**: 1-26.

RANDALL, J.E., DOWNING, N., MCCARTHY, L.J., STANALAND, B.E. & TARR, A.B. 1994. Fifty-one new records of fishes from the Arabian Gulf. *Fauna of Saudi Arabia* 14: 220-258.

ROBERTS, C.M. 1986. *Aspects of coral reef fish community structure in the Saudi Arabian Red Sea and on the Great Barrier Reef*. Ph.D. thesis. University of York, UK.

ROBERTS, C.M. 1991. Larval mortality and the composition of coral reef fish communities. *Trends in Ecology and Evolution* **6** (3): 83-87.

ROBERTS, C.M. 1997. Connectivity and management of Caribbean coral reefs. *Science* 278: 1454-1457.

ROBERTS, C.M. & HAWKINS, J.P. 1999. Extinction risk in the sea. *Trends in Ecology and Evolution* **14** (6): 241-246.

ROBERTS, C.M., DAWSON-SHEPHERD, A.R. & ORMOND, R.F.G. 1992. Large-scale variation in assemblage structure of Red Sea butterflyfishes and angelfishes. *Journal of Biogeography* **19**: 239-250.

ROBERTS, C.M., HAWKINS, J.P., CHAPMAN, N., CLARKE, V., MORRIS, A.V., MILLER, R. & RICHARDS, A. [in press]. *The threatened status of marine species.* A report to the World Conservation Union (IUCN) Species Survival Commission, and Centre for Marine Conservation, Washington, DC.

ROBERTSON, D.R. 1991. The role of adult biology in the timing of spawning of tropical reef fishes. In: *The ecology of fishes on coral reefs.* Sale, P.F. (ed.): 356-386. San Diego; Academic Press.

ROBERTSON, D.R. 1998. Do coral-reef fish faunas have a distinctive taxonomic structure? *Coral Reefs* **17**: 179-186.

SALE, P.F. 1980. The ecology of fishes on coral reefs. *Oceanographic Marine Biology Annual Review* **18**: 367-421.

SAKKO, A.L. 1998. The Influence of the Benguela upwelling system on Namibia's marine biodiversity. *Biodiversity and Conservation* 7: 419-433.

SAVIDGE, G., LENNON, J. & PAPASTOVROU, V.A. 1990. A shore-based survey of the upwelling along the coast of the Dhofar region, southern Oman. *Continental Shelf Research* **10**: 259-275.

SCHEER, G. 1964. Korallen von Abd-el-Kuri. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* **91**: 451-456.

SCHEER, G. 1971. Coral reefs and coral genera in the Red Sea and Indian Ocean. *Symposia of the Zoological Society of London* **28**: 329-367.

SHEPPARD, C.R.C., PRICE, A.R.G. & ROBERTS, C.M. 1992. *Marine ecology of the Arabian region: Patterns and processes in extreme tropical environments.* 359 pp. London and San Diego; Academic Press.

SHEPPARD, C.R.C., WILSON, S.C., SALM, R.V. & DIXON, D. [in press]. Reefs and coral communities of the Arabian Gulf and Arabian Sea. In: *Coral reefs of the western Indian Ocean: their ecology and conservation.* McClanahan, T., Sheppard, C.R.C. & Obura, D. (eds).

SLUTZ, R.J., LUBKER, S.J., HISCOX, J.D., WOODRUFF, S.D., JENNE, R.L., JOSEPH, D.H., STEUER, P.M. & ELMS, J.D. 1985: *Comprehensive Ocean-Atmosphere Data Set: Release 1.* 268 pp. Boulder, Colorado; NOAA Environmental Research Laboratory.

SMITH, G.B., SALEH, M. & SANGOOR, K. 1987. The reef ichthyofauna of Bahrain (Arabian Gulf) with comments on its zoogeographic affinities. *Arabian Gulf Journal of Scientific Research* **B5**: 127-146.

SPRINGER, V.G. 1988. The Indo-Pacific blenniid fish genus *Ecsenius*. *Smithsonian Contributions to Zoology* **465**: 134 pp.

STIRN, J. 1985. Oceanographic conditions, pelagic productivity and living resources in the Gulf of Aden. In: *IOC/UNESCO Workshop on Regional Co-operation in Marine Science in the Central Indian Ocean and Adjacent Seas and Gulfs, Colombo 8-13 July 1985*: 255-297.

TMRU 1994. *Habitats and Species of the Diani Coast, Kenya.* TMRU Reports # 94/4. Tropical Marine Research Unit, University of York, UK.

VICTOR, B.C. 1991. Settlement strategies and the biogeography of reef fishes. In: *The ecology of fishes on coral reefs.* Sale, P.F. (ed.): 231-260. San Diego; Academic Press.

WATT, I. 1996. *Coastal habitat survey of the Gulf of Aden. Gulf of Aden Fisheries IV Project, Yemen. Final Report, Phase II: South coast of Yemen.* MacAlister Elliott & Partners Ltd., UK / Marine Sciences Resource Research Centre, Aden.

WILLIAMSON, M. 1996. *Biological Invasions.* 244 pp. Population and Community Ecology Series **15**. London; Chapman & Hall.

WINTERBOTTOM, R. & ANDERSON, R.C. 1997. A revised checklist of the epipelagic and shorefishes of the Chagos Archipelago, central Indian Ocean. *Ichthyological Bulletin* **66**: 1-28.

WINTERBOTTOM, R., EMERY, A.R. & HOLM, E. 1989. An annotated checklist of the fishes of the Chagos Archipelago, central Indian Ocean. *Royal Ontario Museum, Life Science Contributions* **145**: 1-226.

WOODRUFF, S.D., LUBKER, S.J., WOLTER, K., WORLEY, S.J. & ELMS, J.D. 1993. Comprehensive Ocean-Atmosphere Data Set (COADS) Release 1 a: 1980-1992. *Earth System Monitor* **4**: (1) September 1993, NOAA.

Manuscript submitted: 7 December 1998
Manuscript accepted: 22 August 1999

Author's address:
Dr. Jeremy M. Kemp, University of York, Department of Biology, York YO1 5DD, U.K.; e-mail: jmk100@york.ac.uk

APPENDIX

Table 2: A preliminary checklist of reef fish species, Hadramaut and Shabwa provinces. Locations: BA = Bir Ali (Shabwa mainland) only; M = al-Mukalla only; S = Sikha Island only; SH = Shabwa (mainland and Sikha) only. Abundances: 1 = one only; a = abundant; c = common; r = rare. Other: • = photographed; ** = from DEBELIUS (1998). All others widespread in the region.

Torpedinidae — Torpedo rays	
Torpedo panthera Olfers, 1831	• S, 1
Dasyatidae — Stingrays	
Dasyatis sp. [ref Randall 1996: 44]	BA, c
Taeniura lymma (Forsskål, 1775)	• c
Himantura uarnak (Forsskål, 1775)	M, 1
Hypolophis sephen (Forsskål, 1775)	BA, 1
Myliobatidae — Eagle Rays	
Aetobatus narinari (Euphrasen, 1790)	c
Mobulidae — Devil rays	
Mobula thurstoni (Lloyd, 1908)	• S, r
Muraenidae — Moray eels	
Enchelycore pardalis (Temminck & Schlegel, 1846)	• M, r
Gymnothorax favagineus (Bloch & Schneider, 1801)	• c
Gymnothorax flavimarginatus (Rüppell, 1830)	c
Gymnothorax nudivomer (Playfair & Günther, 1867)	BA, 1
Scuticaria tigrina (Lesson, 1829) **	
Siderea grisea (Lacepède, 1803)	• r
Ophichthidae — Snake eels	
Myrichthys maculosus Cuvier, 1816	• M, 1
Chanidae — Milkfishes	
Chanos chanos Forsskål, 1775	c
Synodontidae — Lizardfishes	
Synodus dermatogenys Fowler, 1912	• c
Holocentridae — Squirrelfishes	
Myripritis murdjan (Forsskål, 1775)	• c
Neoniphon sammara (Forsskål, 1775)	c
Sargocentron caudimaculatum (Rüppell, 1838)	c
Sargocentron rubrum (Forsskål, 1775)	M, r
Sargocentron seychellense (Smith & Smith, 1963)	BA, 1
Sargocentron spiniferum (Forsskål, 1775)	• r
Fistulariidae — Cornetfishes	
Fistularia commersonii Rüppell, 1838	r
Scorpaenidae — Scorpionfishes	
Pterois antennata (Bloch, 1787)	• r
Pterois miles (Bennett, 1828)	r
Scorpaenopsis barbatus (Rüppell, 1838)	• c
Scorpaenopsis diabolus (Cuvier, 1829)	• c
Serranidae — Groupers	
Pseudanthias marcia Randall & Hoover, 1993	• S, a
Pseudanthias townsendi (Boulenger, 1897)	• S, r
Pseudanthias sp. 3 (small ♀♀ only, *P. squamipinnis*•)	r
Aethaloperca rogaa (Forsskål, 1775)	c
Cephalopholis argus Bloch & Schneider, 1801	• c
Cephalopholis hemistiktos (Rüppell, 1830)	r
Cephalopholis miniata (Forsskål, 1775)	• c
Epinephelus chlorostigma (Valenciennes, 1828)	• c
Epinephelus fasciatus (Forsskål, 1775)	• c
Epinephelus malabaricus (Bloch & Schneider, 1801)	r
Epinephelus stoliczkae (Day, 1875)	• a
Epinephelus summana (Forsskål, 1775)	r
Epinephelus tukula Morgans, 1959	r
Pseudochromidae — Dottybacks	
Pseudochromis linda Randall & Stanaland, 1989	• c
Pseudochromis nigrovittatus Boulenger, 1897	• r
Pseudochromis sankeyi Lubbock, 1975	• a
Priacanthidae — Bigeyes	
Priacanthus blochii Bleeker, 1853	c
Priacanthus hamrur (Forsskål, 1775)	c
Cirrhitidae — Hawkfishes	
Cirrhitichthys calliurus Regan, 1905	• c
Cirrhitichthys oxycephalus (Bleeker, 1855)	S, r
Cirrhitus pinnulatus (Bloch & Schneider, 1801)	r
Teraponidae — Terapons	
Kuhlia mugil (Forster & Schneider, 1801)	c
Apogonidae — Cardinalfishes	
Apogon aureus (Lacepède, 1802)	• c
Apogon cyanosoma Bleeker, 1853	• c
Apogon exostigma (Jordan & Seale, 1906)	• r
Apogon fraenatus Valenciennes, 1832	• c
Archamia fucata (Cantor, 1850)	• c
Cheilodipterus macrodon (Lacepède, 1802)	• c
Cheilodipterus quinquelineatus Cuvier, 1828	• c
Malacanthidae — Tilefishes	
Malacanthus latovittatus (Lacepède, 1802)	• S, r
Echeneidae — Remoras	
Echeneis naucrates Linnaeus, 1758	S, 1
Carangidae — Jacks	
Carangoides bajad (Forsskål, 1775)	• c
Carangoides ferdau (Forsskål, 1775)	c
Caranx heberi (Bennett, 1828)	• BA, r
Caranx ignobilis (Forsskål, 1775)	c
Caranx sexfasciatus Quoy & Gaimard, 1824	c
Elegatis bipinnulata (Quoy & Gaimard, 1824)	S, r
Gnathodon speciosus (Forsskål, 1775)	• c
Trachinotus baillonii (Lacepède, 1801)	• M, c
Trachinotus blochii (Lacepède, 1801)	S, r
Gerreidae — Mojarras	
Gerres oyena (Forsskål, 1775)	c
Lutjanidae — Snappers	
Lutjanus argentimaculatus (Forsskål, 1775)	S, r
Lutjanus bengalensis (Bloch, 1790)	• a
Lutjanus bohar (Forsskål, 1775)	c
Lutjanus coeruleolineatus (Rüppell, 1838)	• r
Lutjanus ehrenbergi (Peters, 1879)	c
Lutjanus fulviflamma (Forsskål, 1775)	c
Lutjanus fulvus (Forster & Schneider, 1801)	r
Lutjanus gibbus (Forsskål, 1775)	r
Lutjanus rivulatus (Cuvier, 1828)	• c
Caesionidae — Fusiliers	
Caesio lunaris Cuvier, 1830	• c
Caesio varilineata Carpenter, 1987	• c

Caesio xanthonota Carpenter, 1987	• S, r
Haemulidae — Grunts	
Diagramma pictum (Thunberg, 1792)	c
Plectorhinchus flavomaculatus (Cuvier 1830)	c
Plectorhinchus gaterinus (Forsskål, 1775)	• c
Plectorhinchus gibbosus (Lacepède, 1802)	r
Plectorhinchus playfairi (Pellegrin, 1914)	• c
Plectorhinchus pictus (Tortonese, 1835)	c
Plectorhinchus schotaf (Forsskål, 1775)	c
Pomadasys aheneus McKay & Randall 1995 **	
Nemipteridae — Breams	
Scolopsis ghanam (Forsskål, 1775)	c
Scolopsis taeniatus Cuvier, 1830	c
Scolopsis vosmeri (Bloch, 1792)	BA, r
Lethrinidae — Emperorfishes	
Lethrinus mahsena (Forsskål, 1775)	S, r
Lethrinus nebulosus (Forsskål, 1775)	c
Lethrinus obsoletus (Forsskål, 1775)	c
Sparidae — Seabreams	
Acanthopagrus bifasciatus (Forsskål, 1775)	c
Diplodus sargus capensis (Smith, 1844)	c
Rhabdosargus sarba (Forsskål, 1775)	c
Mugilidae — Mullets	
Crenimugil crenilabis (Forsskål, 1775)	c
Mullidae — Goatfishes	
Mulloidichthys flavolineatus (Lacepède, 1801)	c
Mulloidichthys vanicolensis (Valenciennes, 1831)	• a
Parupeneus barberinus (Lacepède, 1801)	• c
Parupeneus bifasciatus (Lacepède, 1801)	r
Parupeneus cyclostomus (Lacepède, 1801)	r
Parupeneus forsskali (Fourmanoir & Gueze, 1976)	r
Parupeneus indicus (Shaw, 1803)	r
Parupeneus macronemus (Lacepède, 1801)	r
Upeneus tragula Richardson 1846	M, r
Pempheridae — Sweepers	
Pempheris vanicolensis Cuvier, 1831	c
Monodactylidae — Monos	
Monodactylus argenteus (Linnaeus, 1758)	c
Kyphosidae — Sea chubs	
Kyphosus cinerascens (Forsskål, 1775)	S, c
Chaetodontidae — Butterflyfishes	
Chaetodon collare Bloch, 1787	• c
Chaetodon dialeucos Salm & Mee, 1989	S, r
Chaetodon fasciatus Forsskål, 1775	• S, r
Chaetodon gardineri Norman, 1939	• c
Chaetodon larvatus Cuvier, 1831	• c (rare at M)
Chaetodon leucopleura Playfair & Günther, 1867	M, 1
Chaetodon lineolatus Cuvier, 1831	• S, r
Chaetodon lunula Lacepède, 1802	• c
Chaetodon melapterus Guichenot, 1862	• a
Chaetodon melannotus Bloch & Schneider, 1801	• S, 1
Chaetodon auriga setifer Ahl, 1923	• S, r
Chaetodon semilarvatus Cuvier, 1831	• SH, c
Chaetodon trifascialis Quoy & Gaimard, 1823	• c
Chaetodon trifasciatus Park, 1797	• S, 1
Chaetodon vagabundus pictus Fraser-Brunner, 1950	• a
Chaetodon zanzibarensis Playfair, 1866	• S, r
Heniochus acuminatus (Linnaeus, 1758)	• c
Heniochus diphreutes Jordan, 1903	S, r
Heniochus intermedius Steindachner, 1893	• c
Pomacanthidae — Angelfishes	
Apolemichthys xanthotis Fraser-Brunner, 1950	• a
Pomacanthus imperator (Bloch, 1787)	• r
Pomacanthus maculosus (Forsskål, 1775)	• c
Pomacanthus semicirculatus (Cuvier, 1831)	• M, c
Pomacentridae — Damselfishes	
Abudefduf notatus (Day, 1969)	• S, r
Abudefduf sexfasciatus (Lacepède, 1801)	S, c
Abudefduf sordidus (Forsskål, 1775)	r
Abudefduf vaigiensis (Quoy & Gaimard, 1825)	• a
Amphiprion sp.	• M, r
Chromis dimidiata (Klunzinger, 1871)	S, 1
Chromis flavaxilla Randall, 1994	• a
Chromis pembae (Smith, 1960)	• c
Chromis weberi Fowler & Bean, 1928	• c
Chrysiptera unimaculata (Cuvier, 1830)	• c
Dascyllus marginatus (Rüppell, 1829)	• c
Dascyllus trimaculatus (Rüppell, 1829)	c
Neopomacentrus cyanomos (Bleeker, 1856)	• c
Neopomacentrus miryae Dor & Allen, 1977	• SH, c
Neopomacentrus xanthurus Allen & Randall, 1981	• SH, c
Pomacentrus aquilus Allen & Randall, 1980	r
Pomacentrus caeruleus Quoy & Gaimard, 1825	• c
Pomacentrus leptus Allen & Randall, 1980	• a
Pomacentrus trichourus Playfair & Günther, 1867	• S, r
Pomacentrus trilineatus Cuvier, 1830	r
Labridae — Wrasses	
Anampses lineatus Randall, 1972	r
Anampses meleagrides Valenciennes, 1840	r
Bodianus axillaris (Bennett, 1831)	S, 1
Bodianus diana (Lacepède, 1801)	S, c
Bodianus macrognathos (Morris, 1974)	c
Cheilinus abudjubbe (Rüppell, 1835)	r
Cheilinus lunulatus (Forsskål, 1775)	r
Coris aygula Lacepède, 1801	S, r
Coris caudimacula (Quoy & Gaimard 1834)	• c
Coris frerei Playfair & Günther, 1867	• c
Gomphosus caeruleus Lacepède, 1801	c
Halichoeres cosmetus Randall & Smith, 1982	• S, r
Halichoeres hortulanus (Lacepède, 1801)	c
Halichoeres iridis Randall & Smith, 1982	c
Halichoeres marginatus (Rüppell, 1835)	c
Halichoeres nebulosus (Valenciennes, 1839)	c
Halichoeres scapularis (Bennett, 1831)	r
Halichoeres zeylonicus (Bennett, 1832)	S, r
Hemigymnus melapterus (Bloch, 1792)	r
Hemigymnus fasciatus (Bloch, 1792)	• r
Hologymnosus annulatus (Lacepède, 1801)	S, r
Hologymnosus doliatus (Lacepède, 1801)	S, r
Labroides bicolor Fowler & Bean, 1928	c
Labroides dimidiatus (Valenciennes, 1839)	• c
Larabicus quadrilineatus (Rüppell, 1835)	• SH, c
Macropharyngodon bipartitus Smith, 1957	c
Novaculichthys taeniourus (Lacepède, 1801)	c
Pseudocheilinus hexataenia (Bleeker, 1857)	c
Stethojulis albovittata (Bonnaterre 1788)	• S, c
Thalassoma hardwicke (Bennett, 1828)	• S, r
Thalassoma lunare (Linnaeus 1758)	c

Thalassoma lutescens (Lay & Bennett, 1839)	• c
Thalassoma quinquevittatum (Lay & Bennett, 1839)	• S, c
Scaridae — Parrotfishes	
Chlorurus sordidus (Forsskål, 1775)	c
Chlorurus genazonatus (Randall & Bruce, 1983)	• S, r
Chlorurus strongylocephalus (Bleeker 1854)	• S, c
Scarus ferrugineus Forsskål, 1775	• a
Scarus frenatus Lacepède, 1802	• c
Scarus ghobban Forsskål, 1775	• c
Scarus niger Forsskål, 1775	c
Scarus rubroviolaceus Bleeker, 1847	• c
Pinguipedidae — Sandperches	
Parapercis hexophthalma (Cuvier, 1829)	c
Parapercis robinsoni Fowler, 1932	S, l
Trypterygiidae — Triplefins	
Helcogramma steinitzi Clark 1979 **	
Blenniidae — Blennies	
Alloblennius pictus (Lotan, 1969)	• SH, c
Cirripectes filamentosus (Alleyne & Macleay, 1877)	• c
Ecsenius frontalis (Ehrenberg, 1836)	• SH, r
Ecsenius lineatus Klausewitz, 1962	• SH, r
Ecsenius nalolo Smith, 1959	• c
Ecsenius pulcher (Murray, 1887)	SH, c
Plagiotremus rhinorynchos (Bleeker, 1852)	c
Plagiotremus townsendi (Regan, 1905)	c
Gobiidae — Gobies	
Asterropteryx semipunctatus Rüppell, 1835	• c
Ctenogobiops maculosus (Fourmanoir, 1955)	c
Cryptocentrus fasciatus (Playfair & Günther, 1867)	c
Cryptocentrus lutheri (Klausewitz, 1960)	c
Eviota guttata Lachner & Karnella, 1978	• c
Eviota sebreei Jordan & Seale, 1906	• c
Lotilia graciliosa Klausewitz, 1960	r
Gnatholepis anjerensis (Bleeker, 1850)	• c
Gobiodon citrinus (Rüppell, 1838)	r
Istigobius decoratus (Herre, 1927)	• c
Valenciennia helsdingenii (Bleeker, 1858)	• r
Valenciennia puellaris (Tomiyama, 1956)	• c
Valenciennia sexguttata (Valenciennes, 1837)	• c
Microdesmidae — Dartfishes	
Ptereleotris arabica Randall & Hoese, 1985	S, r
Ptereleotris evides (Jordan & Hubbs, 1925)	S, r
Callionymidae — Dragonets	
Synchiropus sechellensis Regan 1908 **	
Soleidae — Soles	
Pardachirus marmoratus (Lacepède, 1802)	• c
Sphyraenidae — Barracudas	
Sphyraena barracuda (Walbaum, 1792)	c
Scombridae — Tunas and mackerels	
Rastrelliger kanagurta (Cuvier, 1817)	• c
Ephippidae — Spadefishes	
Platax orbicularis (Forsskål, 1775)	c
Platax teira (Forsskål, 1775)	• c
Siganidae — Rabbitfishes	
Siganus argenteus (Quoy & Gaimard, 1825)	c
Zanclidae — Moorish idols	
Zanclus cornutus Linnaeus, 1758	• c
Acanthuridae — Surgeonfishes	
Acanthurus dussumieri Valenciennes, 1835	S, r
Acanthurus gahhm (Forsskål, 1775)	r
Acanthurus leucocheilus Herre, 1927	• S, r
Acanthurus leucosternon Bennett, 1832	• M, r
Acanthurus mata (Cuvier, 1829)	• c
Acanthurus sohal (Forsskål, 1775)	c
Acanthurus tennentii Günther, 1861	• S, r
Acanthurus triostegus (Linnaeus 1758)	M, r
Ctenochaetus striatus Quoy & Gaimard, 1825)	c
Zebrasoma desjardinii (Bennett, 1835)	SH, a
Zebrasoma xanthurum (Blyth, 1852)	• c
Naso brevirostris (Valenciennes, 1835)	• S, r
Naso lituratus (Schneider, 1801)	c
Naso fageni Morrow, 1954	S, r
Naso unicornis (Forsskål, 1775)	c
Balistidae — Triggerfishes	
Balistapus undulatus (Park, 1797)	S, c
Balistoides viridescens (Bloch & Schneider, 1801)	r
Melichthys indicus Randall & Klausewitz, 1973	c
Odonus niger (Rüppell, 1836)	• a
Pseudobalistes flavimarginatus (Rüppell, 1829)	S, r
Pseudobalistes fuscus (Bloch & Schneider, 1801)	S, c
Rhinecanthus assasi (Forsskål, 1775)	SH, r
Sufflamen albicaudatus (Rüppell, 1829)	• SH, c
Sufflamen chrysopterus (Bloch & Schneider, 1801)	• S, l
Sufflamen fraenatus (Latreille, 1804)	a
Monacanthidae — Filefishes	
Aluterus scriptus (Osbeck, 1765)	c
Cantherines pardalis (Rüppell, 1837)	c
Ostraciidae — Trunkfishes	
Lactoria cornuta (Linnaeus 1758) **	
Ostracion cubicus Linnaeus, 1758	c
Ostracion cyanurus Rüppell, 1828	c
Tetrasoma gibbosus (Linnaeus, 1758)	BA, l
Tetraodontidae — Pufferfishes	
Arothron meleagris (Bloch & Schneider, 1801)	r
Arothron nigropunctatus (Bloch & Schneider, 1801)	• c
Arothron stellatus (Bloch & Schneider, 1801)	r
Canthigaster solandri (Richardson, 1844)	• c
Canthigaster valentini (Bleeker, 1853)	• c
Diodontidae — Porcupinefishes	
Diodon holocanthus (Linnaeus, 1758)	r
Diodon histrix (Linnaeus, 1758)	c
Diodon liturosus Shaw, 1804	r