



**HAL**  
open science

# Estuarine fish biodiversity of Socotra Island (N.W. Indian Ocean): from the fish community to the functioning of *Terapon jarbua* populations

Edouard Lavergne

► **To cite this version:**

Edouard Lavergne. Estuarine fish biodiversity of Socotra Island (N.W. Indian Ocean): from the fish community to the functioning of *Terapon jarbua* populations. Biodiversity and Ecology. Université de Bretagne occidentale - Brest, 2012. English. NNT: . tel-00806383v1

**HAL Id: tel-00806383**

**<https://theses.hal.science/tel-00806383v1>**

Submitted on 30 Mar 2013 (v1), last revised 13 Jan 2017 (v2)

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# UBO

université de bretagne  
occidentale



**UNIVERSITÉ DE BRETAGNE OCCIDENTALE**

*sous le sceau de l'Université européenne de Bretagne*

pour obtenir le titre de  
**DOCTEUR DE L'UNIVERSITÉ DE BRETAGNE OCCIDENTALE**  
*Mention : Biologie Marine*  
Ecole Doctorale des Sciences de la Mer

Thèse réalisée et présentée par

## Edouard Lavergne

préparée à

l'UMR 6539 CNRS/UBO/IRD/IFREMER  
Laboratoire des Sciences de l'Environnement Marin  
Institut Universitaire Européen de la Mer  
Plouzané, France

et

la section Ichtyologie  
Institut de Recherche Senckenberg  
Centre de Recherche de la Biodiversité et du Climat  
Francfort sur le Main, Allemagne

**BIODIVERSITE DES POISSONS  
ESTUARIENS DE L'ILE DE SOCOTRA  
(NORD-OUEST DE L'OCEAN INDIEN):  
du peuplement ichthyologique au fonctionnement  
des populations de *Terapon jarbua***

**ESTUARINE FISH BIODIVERSITY OF  
SOCOTRA ISLAND (NORTH-WESTERN  
INDIAN OCEAN):  
from the fish community to the functioning of  
*Terapon jarbua* populations**

**Thèse soutenue le 25 Mai 2012**

devant le jury composé de:

**Rachid AMARA**

Professeur, ULCO Wimereux / *Rapporteur*

**Jacques CLAVIER**

Professeur, UBO Brest / *Examineur – Président du Jury*

**Jean-Dominique DURAND**

Chargé de Recherche, IRD Montpellier / *Examineur*

**Eric FEUNTEUN**

Professeur, MNHN Dinard / *Rapporteur*

**Jean LAROCHE**

Professeur, UBO Brest / *Directeur de thèse*



**SENCKENBERG**  
world of biodiversity







---

The present study was funded by the Total Foundation, Paris. The Total Foundation is committed to philanthropic endeavours in three areas of activity: 1) community support, 2) culture and 3) environment, especially the protection of marine biodiversity, through research and programmes to safeguard threatened species and ecosystems.

---



To my beloved grandparents,

A mes grands-parents bien-aimés,



## Acknowledgments

*The completion of this thesis in Marine Biology brings together an enjoyable academic path made of atypical milestones. This path started “long time ago” during my childhood in Bordeaux (France), carried on in Swansea (Wales), Villefranche sur Mer (France) and Frankfurt am Main (Germany) and comes to a new start with this manuscript in Brest (France).*

*I wish to thank Friedhelm Krupp for giving me the opportunity to work as technical coordinator of the zoological survey of Arabia at the Senckenberg Research Institute and to develop my own research project. This first expedition in Yemen was the hardest but most intense experience I have ever made, an opportunity of a lifetime, for which I am forever grateful. Thank you for trusting me and the present project and for your help in implementing it. You have been a source of knowledge, motivation and advice throughout those years. I have always valued your honest and constructive criticisms. I would also like to thank Michael Türkay for accepting to be my official co-supervisor in Germany.*

*I would like to express my gratitude to Jean Laroche who accepted to co-supervise my work in France. Your invaluable guidance, patience, continuous support and most helpful and constructive comments on the manuscript made this work possible. You allow me to work independently, yet you were always available whenever I needed advice. I am grateful to Eric Morize for supervising my work on otoliths, sharing his office and for our long fruitful discussions, to Maylis Labonne for her useful tips and help with otolith microchemistry and to Vianney Pichereau for his support. Louis Quiniou is also acknowledged for his pragmatic advice, his help with some statistical issues and our long discussion about fishes and expeditions. Many thanks to Yves-Marie Paulet and H el ene de Pontual for their kind support since the beginning of this Ph.D. adventure and for giving me the opportunity to meet J. Laroche and E. Morize.*

*I would like to thank Uwe Zajonz for his mentorship during this work. His role to the overall success of the present Ph.D. project is undeniable. The combination of our different personalities and sometimes antagonist characters like fire and water created a productive synergetic cooperation and a nice friendship. How many birthdays have we spent together in the field, celebrating on top of a no man land rock in the middle of the ocean? I look forward to more collaboration in the future.*

*This work would not have been the same without the generous assistance from my lab mate Isabelle Calves. Firstly because she never complained about having me squatting her desk during all those years, but also for all the funny and adventurous hours we spent looking for some mysterious blue picks. Your care and friendship always made the lab work more cheerful.*

*We have been through a lot of ups and downs and shared many moments together. I look also forward to more collaboration in the future. Leila Meistertzheim and Gregory Charrier are also acknowledged for their precious help and guidance with genetic issues.*

*Very special thanks to the staff of the doctoral school, Christophe Hémond, Denis Bailly, Elisabeth Bondu and Eric Cornil for their kindness and their efficient administrative assistance. I also thank Gene Cohat, Anne-Sophie Podeur, Agnès Petiot, Marie-Line Tanguy and Michèle Bouchez for their kindness and joyfulness.*

*I am greatly indebted to Fouad, Motea, Saeed, Saleh, Tabet and the fisherman community of Al Mukalla and Socotra for their hospitality and their help in the field. I am also grateful to all my coworkers and friends who influence this work in a way or another: Anne-Cécile, Audrey, Aurélie J., Aurélie L., Camille, Carola, Carole C., Carole L., Cécile, Cédric, Célie, Cindy, Chiara, Claire G., Claire S., Clémentine, Cyril, Daniela, Dédé, Delphine, Eric A., Eric D., Florian, François, Hannes, Horst, Ilka, Jean-Marie, J.P., John, Joonas, Julie, Kay, Laure, Laurent, Lucie, Maggie, Manu, Maren, Maria, Marion, Matthias, Mathilde, Mathieu, Morgana, Maud, Nadia, Nathalie, Nicolas B., Nicolas P., Nisreen, Romain, Rossana, Sabine, Seb, Simon, Sleiman, Stéphane, Tilman, Tiffany, Tonny, Vaitea, Vinsou, and the members of MerSciDoc.*

*Although there is no direct link to this work, but rather to the scientist and the man I become, I wish to thank the ERASMUS exchange programme which gave me the opportunity during my studies to discover another culture and the love of working in an international atmosphere. Thanks to this programme, I also met some of my best mates in particular Vinsou and Maggie who gave me the best present and responsibility friends could ever offer, as I became last year the Godfather of their beautiful son Aël. Thank you!*

*The completion of this work would not have been possible without the immeasurable support of all my family. All the thanks of the World to Mino and Bob my parents for their incommensurable support. Maman, Papa merci pour tout le soutien que vous m'avez apporté, pour votre confiance et la liberté de choix que vous m'avez donnée, pour le goût du travail et de l'effort que vous m'avez transmis, mais surtout pour les merveilleux moments que je passe à chaque fois que je rentre à la maison.*

*I have saved the best for the last. To my beautiful and lovely wife Bunei Nishimura, I can only say "I love you". It is the soft and quiet strength you have shown during your own hard times and your continuing support especially during the last few months before the end of the Ph.D. process that allowed me to finally complete this work.*

## Summary

Understanding connectivity between estuarine nurseries and marine habitats is fundamental to explore fish population dynamics and to the design of effective conservation and fisheries management strategies. The aim of this work was to provide the first faunistic and ecological baseline of Socotra Island (North-Western Indian Ocean) estuaries and lagoon fishes for governmental coastal managers and decision makers, with a particular focus on the population functioning of a sentinel species: *Terapon jarbua*. In this study, a multidisciplinary approach was developed to understand the functioning and importance of Socotra estuaries (TOCE's: Temporarily Open / Close Estuaries) and lagoons for marine fishes. Several biological and chemical tools (taxonomy, ecology, phylogenetics, population genetics, otolith microstructure, otolith microchemistry) were used and the main findings of this work are as follows:

1) Socotra estuaries are composed of 64 species in 30 families, a high figure by regional standards. The comparison with faunistic records from South Africa and Yemen mainland provides further support to Socotra's function as a biogeographic "stepping stone" for certain species. Moreover 33 out of the 64 recorded species were considered as relevant species for the local economy. This underscores the paramount importance of these coastal water bodies as spawning and nursery sites and for the sustainability of vital provisioning ecosystem services.

2) The phylogeography and the genetic structure of *T. jarbua* populations were analyzed considering Cytochrome *c* Oxidase subunit I and microsatellites and underlined two patterns of genetic structure. A high and significant genetic differentiation was observed at the scale of the Indo-West Pacific. Three population clusters could be drawn, the North-Western Indian Ocean cluster (Socotra, Yemen and Iran), the West Indian Shelf cluster and the Chinese Sea cluster. However, the large number of nucleotide differences raised some issues concerning the species identification as *T. jarbua* might be a species complex, despite the fact that it shows a characteristic color pattern easily identifiable. At the restricted scale of the North-Western Indian Ocean, recent population expansion after local extinctions during the Pleistocene glaciations might explain small but significant genetic differentiation. Considering microsatellites, genotyping highlighted a relatively high and significant genetic differentiation between estuaries, over the Socotra-Yemen region. Geographical distance is not a major structuring factor for *T. jarbua* populations in the wider Gulf of Aden region. The strict link between juvenile *T. jarbua* and TOCE's, and the opening/closing associated with possible demographic bottlenecks, could increase the local differentiation among estuaries. Although the dynamic environment of the region driven by the monsoon system could reduce the genetic differentiation between populations, the short larval stage duration (25 days estimated by otolith microstructure

readings) and potential larval retention in particular sectors might reduce homogenization over larger geographical scale.

3) The analysis of otolith nucleus elemental composition suggested the existence of several marine spawning grounds, thus confirming the population genetics approach suggesting a regional model of metapopulation composed of open subpopulations (i.e. multiple sources and more or less pronounced mixtures of larval flows displaying a spatio-temporal variability). In addition, transect Sr:Ba ratio analysis along the otolith growth axis showed clear pattern of post larval migrations into estuarine nurseries where individuals remain for two years. Finally, otolith edges elemental fingerprint assignation tests to nurseries were highly accurate and could conduct in the future to the assessment of the contribution level of a particular nursery to the adult population of *T. jarbua* as well as others ecologically or economically important species.

## Zusammenfassung

Das Verständnis der Verbindung zwischen ästuaren Kinderstuben mariner Fischarten und den offenmarinen Habitaten, welche sie als Adulti bewohnen, ist entscheidend für die Untersuchung ihrer Populationsbiologie sowie für die Entwicklung angemessener Naturschutz- und Fischereimanagementstrategien. Das Ziel der hier vorgelegten Arbeit ist eine faunistische und ökologische Bestandsaufnahme der Fischartengemeinschaften der Ästuare und Lagunen der vor dem Horn von Afrika gelegenen Insel Sokotra, unter besonderer Berücksichtigung der Populationsökologie und -biologie einer Schlüsselart: *Terapon jarbua*. Die Studie soll dabei einen wichtigen Beitrag für die Arbeit von Entscheidungsträgern im Naturschutz- und Küstenzonenmanagement der Insel leisten. Im Rahmen der Arbeit wurde ein multidisziplinärer Ansatz verfolgt, um die Funktion und Bedeutung der temporär offen/gechlossenen Küstenästuar (TOCE's: Temporarily Open / Close Estuaries) und Lagunen Sokotras für marine Fischarten zu verstehen. Hierzu wurde eine Reihe von Methoden aus unterschiedlichen Fachdisziplinen miteinander kombiniert (Taxonomie, Ökologie, Phylogenetik, Populationsgenetik, Otolithen-Mikrostrukturanalyse, Otolithen-Mikrochemie). Die wichtigsten Ergebnisse der Studie stellen sich wie folgt dar:

1) Die Fischartengemeinschaften der Ästuare und Lagunen Sokotras weisen mindestens 64 Arten in 30 Familien auf, ein hoher Wert im regionalen Vergleich. Der faunistische Vergleich mit Ästuaren Südafrikas und der jemenitischen Festlandsküste bestätigt Sokotras Position als "biogeografisches Sprungbrett" zwischen angrenzenden biogeografischen Regionen. Darüber hinaus besitzen 33 der 64 registrierten Arten eine zum Teil große Bedeutung in der lokalen Fischereiwirtschaft. Dies unterstreicht die Wichtigkeit dieser Küstenökosysteme als Laich- und Brutstätten und damit für die nachhaltige Verfügbarkeit von Versorgungssystemdienstleistungen.

2) Die Phylogeografie und die genetische Struktur der *T. jarbua* Populationen wurde anhand des Gens der Cytochrom *c* Oxidase Untereinheit I (COI) sowie verschiedener Mikrosatellitenmarker analysiert, wobei zwei unterschiedliche genetische Muster zutage traten. Eine hohe und signifikante genetische Differenzierung existiert auf der geografischen Skala des Indo-Westpazifiks. Drei Populationsgruppen (Cluster) konnten identifiziert werden: eine Gruppe des nordwestlichen Indischen Ozeans (Sokotra, Jemen, Iran), eine Gruppe des westindischen Schelfgebietes und eine Gruppe des Chinesischen Meeres. Die hohe Zahl an Unterschieden in der COI-Nukleotidsequenz ist auffallend und legt die Vermutung nahe, dass es sich trotz der relativ einheitlichen morphologischen Merkmale, insbesondere hinsichtlich des charakteristischen Farbkleids, tatsächlich um einen Artenkomplex handelt könnte, der den indo-

westpazifischen Raum bewohnt und bisher taxonomisch nicht hinreichend erkannt wurde. Auf der kleineren geografischen Skala des nordwestlichen Indischen Ozeans zeigt sich eine geringe aber dennoch signifikante genetische Differenzierung der Populationen, die durch eine Expansion der Populationsgröße in jüngerer Zeit im Anschluss an lokale Kontraktionen während der pleistozänen Glaziale erklärbar ist. Auf der Ebene der Mikrosatelliten ergab die Genotypisierung eine recht hohe und signifikante Differenzierung der ästuaren Populationen Sokotras und der jemenitischen Küste des Golfes von Aden. Die geografische Distanz stellt dabei keinen wesentlichen strukturierenden Faktor dar. Es scheint vielmehr, dass die nahezu obligate Nutzung von TOCEs während der Ontogenie von *T. jarbua* in Verbindung mit der zeitweisen Abgeschlossenheit dieser Lebensräume zu genetischen Flaschenhalseffekten führt, welche die Strukturierung der Populationen auf molekularer Ebene fördert. Auch wenn demgegenüber die monsungetriebenen Strömungssysteme im weiteren Untersuchungsgebiet eher geeignet scheinen, eine Homogenisierung der Gesamtpopulation zu bewirken, könnte die recht kurze pelagische Larvenphase (25 Tage, basierend auf der Otolithen-Mikrostrukturanalyse) und die Rückhaltung von Larven in bestimmten Gebieten diesem Effekt entgegen wirken.

3) Die isotonchemische Analyse der Otolithennuclei deutet auf die Existenz mehrerer mariner Laichgründe hin und unterstützt damit die Ergebnisse der populationsgenetischen Untersuchungen hinsichtlich des regionalen Modells einer Metapopulation, welche sich aus mehreren offen Subpopulationen zusammensetzt, bei verschiedenen Quellen und mehr oder weniger deutlicher Mischung der Ausbreitungsphasen unter raum-zeitlicher Variabilität. The Analyse des Sr:Ba Verhältnisses in einem Transekt entlang der Otolithenwachstumsachse zeigt das klare Muster einer postlarvalen Migration hinein in ästuare Habitate und eines anschließenden Verbleibs in diesen über den Zeitraum von zwei Jahren. Schließlich sind die isotonchemischen Fingerprints der Otolithen hochsignifikant korrelierbar mit den Isotonmustern einzelner Ästuare. Mithilfe dieser Methode könnte in zukünftigen Studien der relative Beitrag der einzelnen Gewässer zum Erhalt der Populationen ermittelt werden und *T. jarbua* als "Proxy" auch für andere, insbesondere ökologisch oder ökonomisch relevante Arten, die auch auf ästuare Habitate angewiesenen sind, eingeführt werden.

## Résumé

La compréhension de la connectivité entre les nourriceries estuariennes et les habitats marins est fondamentale pour l'étude de la dynamique des peuplements et des populations de poissons et pour la conception de stratégies efficaces de conservation et de gestion des pêches. Le but de ce travail était donc de fournir une première référence faunistique et écologique des poissons des estuaires et du lagon de l'île de Socotra (Nord-Ouest de l'Océan Indien) pour les gestionnaires de la zone côtière, avec un accent particulier sur le fonctionnement des populations d'une espèce sentinelle: *Terapon jarbua*. Dans cette étude, une approche multidisciplinaire a été développée afin de comprendre le fonctionnement et l'importance des estuaires (TOCE's : Temporarily Open / Closed Estuaries) et du lagon de l'île de Socotra pour les poissons marins. Différents outils de la biologie et de la chimie (taxonomie, écologie, phylogéographie, génétique des populations, microstructure et microchimie des otolithes) ont été utilisés et les principales conclusions de ce travail sont les suivantes:

1) Les estuaires de Socotra sont composés de 64 espèces dans 30 familles, un chiffre élevé par rapport aux normes régionales. La comparaison avec les inventaires faunistiques d'Afrique du Sud et du Yémen suggère que Socotra joue le rôle de tremplin biogéographique, en permettant la connexion d'une grande variété de groupes taxonomiques provenant de différentes unités biogéographiques. De plus 33 des 64 espèces recensées sont considérées comme importantes pour l'économie locale, soulignant l'importance primordiale des estuaires comme sites de fraie et nourriceries, pour le fonctionnement durable des services écosystémiques.

2) La phylogéographie et la structure génétique des populations de *T. jarbua* ont été analysées considérant des marqueurs de type Cytochrome *c* Oxydase sous-unité I et microsatellites. Une différenciation génétique élevée et significative a été observée à l'échelle de l'Indo-Ouest Pacifique. Trois groupes de populations ont pu être identifiés, le groupe du Nord-Ouest de l'Océan Indien (Socotra, Yémen et Iran), le groupe de l'Ouest de l'Inde et le groupe de la Mer de Chine. Cependant, les grandes différences nucléotidiques observées soulèvent certaines questions concernant l'identification de l'espèce et suggèrent que *T. jarbua* pourrait être en réalité un complexe d'espèces, en dépit du fait que la coloration caractéristique de *T. jarbua* facilite son identification. A l'échelle plus restreinte du Nord-Ouest de l'Océan Indien, une expansion récente de la population de *T. jarbua* après des extinctions locales au cours des glaciations du Pléistocène pourrait expliquer la faible mais significative différenciation génétique. Le génotypage des marqueurs microsatellites souligne une différenciation génétique relativement élevée et significative entre les estuaires, sur le secteur Socotra-Yémen. Si la distance géographique n'est pas un facteur structurant majeur des populations de *T. jarbua* dans

la région du Golfe d'Aden, le lien étroit entre les juvéniles *T. jarbua* et les TOCE, ainsi que les phénomènes d'ouverture associés à de possibles goulots d'étranglement démographiques dans ces systèmes côtiers, peuvent expliquer la mise en place d'une différenciation génétique locale significative entre les estuaires. Bien que l'environnement dynamique de la région puisse limiter la différenciation génétique, la courte durée du stade larvaire de cette espèce (25 jours estimés par la lecture des microstructures de l'otolithe) et la possible rétention des larves dans certains secteurs peuvent réduire l'homogénéisation à plus grande échelle géographique.

3) Les analyses de la composition élémentaire des nucleus d'otolithes suggèrent l'existence de plusieurs zones de fraie marines; ces données confrontées aux résultats des investigations en génétique des populations suggèrent un modèle régional de métapopulation composée de sous-populations ouvertes (sources multiples et mélange plus ou moins marqué des flux larvaires présentant une variabilité spatio-temporelle). De plus, les analyses des ratios Sr:Ba le long de l'axe de croissance des otolithes ont clairement montré des patrons de migrations des post-larves dans les estuaires où les juvéniles resteront deux ans. Enfin, les tests d'assignation d'empreintes géochimiques en bordure d'otolithe à des nourriceries spécifiques se sont avérés être très précis et pourraient conduire à terme à estimer la contribution d'une nourricerie à une population adulte de *T. jarbua* ainsi que d'autres espèces d'importance écologiques et économiques.

*« A cet endroit la Dordogne ne quitte plus son lit. Epaisse et paresseuse, elle fait le tapin sur les berges, mais il n'est jamais que le poisson pour se laisser appâter. »*

**Christian Grené**



## Table of Contents

Table of Contents .....	1
List of Figures .....	3
List of Tables.....	5
List of Acronyms.....	7
<b>Introduction .....</b>	<b>9</b>
<b>Chapter 1 - Diversity and composition of estuarine and lagoon fish assemblages of Socotra Island, including comparative sites over the mainland coast of Yemen .....</b>	<b>25</b>
Summary.....	27
Abstract.....	29
Introduction .....	30
Materials and Methods .....	32
Results .....	36
Discussion.....	43
Conclusions .....	46
Acknowledgments .....	48
Appendix 1 .....	49
Appendix 2 .....	53
Appendix 3 .....	75
<b>Chapter 2 - Length-weight relationship and seasonal effects of the Summer Monsoon on condition factor of <i>Terapon jarbua</i> (Forsskål, 1775) from the wider Gulf of Aden including Socotra Island .....</b>	<b>79</b>
Summary.....	81
Abstract.....	83
Introduction .....	84
Materials and methods.....	84
Results and discussion.....	85
Acknowledgments .....	89

<b>Chapter 3 - Isolation and characterization of nine microsatellite loci of <i>Terapon jarbua</i> (Forsskål, 1775) from Socotra Island (Gulf of Aden) using multiplex PCR.....</b>	<b>91</b>
Summary .....	93
Abstract .....	95
Acknowledgments .....	100
<b>Chapter 4 - Complex genetic structure of <i>Terapon jarbua</i> (Forsskål, 1775) nurseries in temporarily open closed estuaries from the wider Gulf of Aden.....</b>	<b>101</b>
Summary .....	103
Abstract .....	105
Introduction .....	106
Materials and methods .....	108
Results .....	115
Discussion .....	124
Acknowledgments .....	128
<b>Chapter 5 - Early life history of <i>Terapon jarbua</i> (Forsskål, 1775) using microstructures and Laser Ablation ICP-MS elemental composition of otoliths.....</b>	<b>129</b>
Summary .....	131
Abstract .....	133
Introduction .....	134
Materials and methods .....	135
Results .....	142
Discussion .....	146
Acknowledgments .....	149
<b>Conclusion.....</b>	<b>151</b>
<b>References .....</b>	<b>159</b>
<i>Curriculum Vitae</i> .....	191

## List of Figures

### Introduction

Figure 1: Map of the North-Western Indian Ocean and localization of Socotra Archipelago.....	11
Figure 2: Typical trees from Socotra Island.....	13
Figure 3: Underwater survey of Socotra coastal fishes.....	13
Figure 4: Main road network isolating Khor Daneghan from the sea.....	15
Figure 5: Socotra Field Research Station.....	16
Figure 6: Photographs of the main Socotra estuaries.....	18
Figure 7: Freshly caught <i>T. jarbua</i> .....	21
Figure 8: Scientific approach.....	22

### Chapter 1

Figure 1.1: Map of sampling locations.....	33
Figure 1.2: Cumulative frequency of species per family.....	37
Figure 1.3: a) Species rank occurrence curve and b) Frequency distribution of species occurrence .....	38
Figure 1.4: Cumulative species rank abundance curves.....	39
Figure 1.5: Individual based taxon sampling curves for each location.....	39
Figure 1.6: Representation of abundances and alpha diversities per location.....	41
Figure 1.7: a) Ward hierarchical clustering analysis, b), c) and d) Principal Component Analysis based on species Presence / Absence (ANOSIM: $r = 0.87$ , $p < 0.001$ ).....	42
Figure 1.8: a) Ward hierarchical clustering analysis, b), c) and d) Principal Component Analysis based on species abundance (ANOSIM: $r = 0.76$ , $p < 0.001$ ).....	44

### Chapter 2

Figure 2.1: Length-weight relationship of <i>Terapon jarbua</i> from the wider Gulf of Aden.....	86
Figure 2.2: Test plot of $\log(a)$ against $b$ for seven LWRs of <i>Terapon jarbua</i> .....	86
Figure 2.3: Box plot of condition factor K for Khor Dubena during pre- and post- Summer Monsoon periods of 2007 and 2008.....	87
Figure 2.4: Box plot of condition factor per locations during pre- Summer Monsoon periods....	88

### Chapter 3

Figure 3.1: Map of Socotra Archipelago and sampling site location (Matief) .....	97
--	----

### Chapter 4

Figure 4.1: Map of sampling locations .....	108
Figure 4.2: HRM profiles showing three CO1 variants of <i>Terapon jarbua</i> .....	111
Figure 4.3: Haplotype Network of <i>T. jarbua</i> constructed with the parsimony method of Templeton et al. (1992).....	116
Figure 4.4: Multidimensional scaling analyses on CO1 data set .....	118
Figure 4.5: Mismatch distributions .....	119
Figure 4.6: Maximum clade credibility trees .....	120
Figure 4.7: Multidimensional scaling analyses on microsatellite data set .....	124

### Chapter 5

Figure 5.1: Map of sampling locations .....	137
Figure 5.2: Length frequency distribution of <i>T. jarbua</i> .....	138
Figure 5.3: a) Transversal section of a left otolith of <i>Terapon jarbua</i> , b) PLD microincrement counts (green dots) along the otolith growth axis from the core (black spot on the left side) to the settlement-mark (red dot).....	138
Figure 5.4: <i>Terapon jarbua</i> Planktonic Larval Duration .....	142
Figure 5.5: Profiles of Sr:Ba ratios measured along otolith growth axes of <i>Terapon jarbua</i> .....	143
Figure 5.6: Linear Discriminant Function Analysis on the elemental composition of a) otolith edges and b) otolith nuclei .....	145
Figure 5.7: a) Ward hierarchical clustering analysis on $F_{ST}$ , b) Linear Discriminant Function Analysis on the elemental composition of otolith nuclei (Accuracy: 40 %) .....	145

## List of Tables

### Introduction

Table 1: Sampling locations.....	19
----------------------------------	----

### Chapter 1

Table 1.1: Sampling locations.....	34
Table 1.2: List of the ten predominant families sorted by species number.....	37
Table 1.3: List of the 15 most frequent species.....	38
Table 1.4: List of the 15 most abundant species.....	39
Table 1.5: Species richness summary.....	41

### Chapter 2

Table 2.1: Descriptive statistics and estimated parameters of length-weight relationships for <i>Terapon jarbua</i> .....	85
---	----

### Chapter 3

Table 3.1: Multiplex primer-mix.....	98
Table 3.2: Primer sequences for 10 microsatellite loci and allele statistics in one population (N = 22) of <i>Terapon jarbua</i> .....	99

### Chapter 4

Table 4.1: Sampling locations.....	109
Table 4.2: Multiplex Primer-mix.....	110
Table 4.3: CO1 diversity measures for the studied population of <i>T. jarbua</i> .....	117
Table 4.4: CO1 pairwise $\Phi_{ST}$ (below diagonal) and $p$ -values of the pairwise exact tests of population differentiation (above diagonal) in the Indo-West Pacific.....	117
Table 4.5: Estimated parameters from mismatch distribution analysis of <i>T. jarbua</i> .....	119
Table 4.6: Number of alleles ( $N_A$ ), observed ( $H_O$ ) and unbiased expected ( $H_E$ ) heterozygosity and $F_{IS}$ for each location and each locus.....	122
Table 4.7: Microsatellite pairwise $F_{ST}$ and $F_{ST(ENA)}$ (below diagonal) and $p$ -values of the pairwise exact tests of population differentiation (above diagonal) in the wider Gulf of Aden.....	123

### Chapter 5

Table 5.1: Sampling locations.....	136
Table 5.2: Assignment test.....	144



## List of Acronyms

### Institution acronyms

<b>BiK-F</b>	Biodiversity and Climate Research Centre, Frankfurt am Main, Germany
<b>EDSM</b>	Doctoral programme in Marine Sciences, Plouzané, France
<b>EPA</b>	Environment Protection Authority, Yemen
<b>FRS</b>	Socotra Field Research Station, Hadibo, Socotra, Yemen
<b>GEF</b>	Global Environment Facility
<b>GRADE</b>	Graduate Academy of the Goethe University, Frankfurt am Main, Germany
<b>IUEM</b>	European Institute for Marine Studies, Plouzané, France
<b>LEMAR</b>	Marine Environmental Science Laboratory - UMR 6539, Plouzané, France
<b>LOEWE</b>	Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz
<b>MoWE</b>	Ministry of Water and Environment, Yemen
<b>NHMV</b>	National History Museum of Vienna
<b>NIST</b>	National Institute of Standards and Technology
<b>SCDP</b>	Socotra Conservation and Development Programme
<b>SFN</b>	Senckenberg Research Institute, Frankfurt am Main, Germany
<b>UBO</b>	University of Western Brittany, Brest, France
<b>UEB</b>	European University of Brittany, Rennes, France
<b>UNDP</b>	United Nations Development Programme
<b>UNEP</b>	United Nations Environment Programme
<b>UNESCO</b>	United Nations Educational, Scientific and Cultural Organization
<b>USGS</b>	United States Geological Survey
<b>WWF</b>	World Wildlife Fund

## Scientific acronyms

<b>AFLP</b>	Amplified Fragment Length Polymorphism
<b>AMOVA</b>	Analysis of MOlecular VAriance
<b>ANOSIM</b>	ANalysis Of SIMilarities
<b>ANOVA</b>	ANalysis Of VAriance
<b>BEAST</b>	Bayesian Evolutionary Analysis by Sampling Trees
<b>CO1</b>	Cytochrome <i>c</i> Oxydase sub-unit 1
<b>CV</b>	Coefficient of Variation
<b>DNA</b>	Deoxyribose Nucleic Acid or DeoxyriboNucleic Acid
<b>ESS</b>	Effective Sampling Size
<b>FDR</b>	False Discovery Rate
<b><math>F_{IS}</math></b>	Genetic fixation index (or inbreeding index)
<b><math>F_{ST}</math></b>	Genetic differentiation index
<b>FL</b>	Fork Length
<b>HRMA</b>	High Resolution Melting Analysis
<b>HWE</b>	Hardy-Weinberg Equilibrium
<b>IPB</b>	Indo-Pacific Barrier
<b>ITCZ</b>	Inter-Tropical Convergence Zone
<b>IWP</b>	Indo-West Pacific
<b>LA-ICP-MS</b>	Laser Ablation - Inductively Coupled Plasma - Mass Spectrometer
<b>LDFA</b>	Linear Discriminant Function Analysis
<b>LWR</b>	Length-Weight Relationship
<b>MANOVA</b>	Multivariate ANalysis Of VAriance
<b>MDS</b>	MultiDimensional Scaling analysis
<b>mtDNA</b>	mitochondrial DNA
<b>NIST</b>	National Institute of Standards and Technology
<b>PCA</b>	Principal Components Analysis
<b>PCR</b>	Polymerase Chain Reaction
<b>PLD</b>	Planktonic Larval Duration
<b>SL</b>	Standard Length
<b>SNP</b>	Simple Nucleotide Polymorphism
<b>SSCP</b>	Single Strand Conformational Polymorphism
<b>TL</b>	Total Length
<b>TOCE</b>	Temporarily Open / Closed Estuary
<b>UPGMA</b>	Unweighted Pair Group Method with Arithmetic mean

# Introduction



## Introduction

### Socotra Archipelago

The Socotra Archipelago is located in the north-western corner of the Indian Ocean at the junction between the Gulf of Aden and the Arabian Sea at 12°30'N 54°00'E (Fig. 1). It lies on a Palaeozoic granite block which separated from the Southern Arabian peninsula during the opening of the Gulf of Aden around 18 Mya ago (Leroy et al., 2004; Van Damme, 2009). The archipelago includes the main island of Socotra and the three smaller islands of Samha and Darsa, also known as “The Brothers” and Abd al-Kuri. Other minor rock outcrops are Kal Farun two connected rocks to the north of Abd al-Kuri, and Sabuniya two connected rocks to the west of Qalansiya. The 3,695 km<sup>2</sup> of the main island is composed of the igneous Haggier Mountains (maximum altitude 1,526 m), Paleogene karstic limestone plateaus (maximum altitude 1,000 m) and alluvial coastal plains (Scholte et al., 2011).



**Figure 1: Map of the North-Western Indian Ocean and localization of Socotra Archipelago (Source: ReefGIS)**

Socotra Island is populated by at least 50,000 inhabitants (Van Damme and Banfield, 2011), which concentrate mainly in two districts: 32,000 inhabitants for Hadibo (north-east coast), and 12,000 inhabitants for Qalansiya (west coast). The smaller outer islands are much less populated with only 500 inhabitants for Abdul al Kuri, 250 for Samha and no permanent inhabitant for Darsa (Scholte et al., 2011). Since the unification of North and South Yemen in 1990, Socotra Island depends on the mainland Hadhramout governorate and began to open up to the outside world. The “local” population is increasing by mainlander immigration with yearly urban expansion. In addition, with the development of tourism infrastructures, seasonal population has also increased from 140 tourists in 2000 to 4,000 in 2008 (Scholte et al., 2011).

The Archipelago lies close to boundaries among four major biogeographic units of the circum-Arabian seas: the Eritrean, South Arabian and Persian sections of the Arabian subprovince and the Western Indian Ocean subprovince (Kemp, 1998; Zajonz et al., 2000). The Archipelago is characterized by the alternating monsoon seasons in the Northern Indian Ocean driven by the Inter-Tropical Convergence Zone (ITCZ). From October to February the weaker winter or north-east monsoon dominates with a rainy period starting in October and being strongest in November/December. From April/May to September the forceful summer or south-west monsoon blows strong hot winds that generate upwelling of cold nutrient-rich waters on both the north and south coasts of Socotra, and on the south coast of Yemen mainland (Currie et al., 1973; Fleitmann et al., 2004; Fratantoni et al., 2006; Glynn, 1993; Kemp, 1998; Klaus and Turner, 2004; Scholte and De Geest, 2010). Average annual rainfall reaches 216 mm, however it may increase up to 800 mm in the Haggier Mountains. Indeed, this particular climate and the presence of the Haggier Mountains blocking rainy clouds and allowing the fresh water to percolate through the karstic limestone and the formation of wadis running to the coastal waters are the major factors responsible for the unique and high biodiversity of Socotra (Banfield et al., 2011; Scholte and De Geest, 2010). Although freshwater biota endemism is low in comparison to the terrestrial biota, Socotra Island was recognized in 2005 by the World Wildlife Fund (WWF) as one of the world's Freshwater Ecoregions (Thieme, 2005).

### **The biodiversity of the Socotra Archipelago**

Socotra Archipelago high number of both flora and fauna endemic species has been acknowledged worldwide and allowed the Island to be recognized in July 2008 as a natural world heritage site by the United Nations Educational, Scientific and Cultural Organization (UNESCO). Although Socotra is a continental island, its high level of endemism is comparable with other continental islands such as Madagascar or oceanic islands such as the Canary Islands, the Galapagos or Mauritius. Indeed 37 % of the 835 plant species (Fig. 2), 90 % of the 38 reptile species, 90 % of the 101 terrestrial mollusc species, 73 % of the 41 isopod species and 60 % of the 41 arachnid species are endemic to the archipelago (Dixey et al., 1898; Miller and Morris, 2004; Neubert, 2005, 2006, 2009; Platnick, 2011; Taiti and Checcucci, 2009). Moreover the archipelago harbors 192 bird species among which 44 reproduce on the archipelago islands, 300 species of crabs, lobsters and shrimps, 283 species of corals and 726 species of coastal fishes (estimated up to 900, Zajonz pers. com.) (Fig. 3) (DeVantier et al., 2004; Kemp, 1998; UNEP/WCMC, 2008; Zajonz and Khalaf, 2002; Zajonz et al., 2000).



**Figure 2: Typical trees from Socotra Island**

a) The Cucumber Tree – *Dendrosicyos socotrana*, Cucurbitaceae (Photo: L. Banfield), b) The Dragon Blood Tree – *Dracaena cinnabari*, Dracaenaceae (Photo: L. Banfield), c) This tree is a symbol for Socotri people and is present on the 20 Yemeni Rials coin and d-e) The Socotra Bottle Tree or Desert Rose – *Adenium obesum socotranum*, Apocynaceae (Photos: E. Lavergne)



**Figure 3: Underwater survey of Socotra coastal fishes**

Meeting between a large anemone protecting adults *amphiprion sp.* and several juveniles *Dascyllus trimaculatus* and E. Lavergne (Photo: U. Zajonz)

These incredibly rich fish communities have developed across a large variety of biotopes providing different suitable type of habitats: indigenous rock 45 %, sand sediment 10 %, macroalgal communities with interspersed scleractinian corals 25 %, “non-reefal” coral communities 35 % and coral reefs less than 0.5 % (Klaus and Turner, 2004; Klaus et al., 2002). Although no true reefs formed by biogenic accretion is present on the archipelago, many typical reef-associated fish species dominate in occurrence and abundance. These communities may form an important link between Red Sea and Indian Ocean populations, possibly playing a role in maintaining gene flow between the two regions (Kemp, 1998). Moreover Socotra is one of the rare marine location where it is possible to observe sympatry between a number of Indian Ocean species and their Arabian endemic sister taxa such as the pomacentridae *Dascyllus carneus* Fischer, 1885 and *Dascyllus marginatus* (Rüppell, 1829) or the Acanthuridae *Acanthurus sohal* (Forsskål, 1775) and *Acanthurus lineatus* (Linnæus, 1758) (Kemp, 1998). The description of a hybrid species between two Chaetodontidae sympatric species is underway (Zajonz and Lavergne *in prep.*)

### **Threats to the biodiversity of Socotra Island**

The first presence of *Homo* on Socotra dates back to the Lower Stone Age, 1.4- 2.5 million years ago (Sedov et al., 2009). The first human colonization occurred in the early Holocene (~11,000 years ago) from Southern Arabian populations (Cerny et al., 2009). It is only later that human population started to expand, (3,000 and 1,000 years BC), due to better climatic conditions than nowadays, coupled with the development of the agriculture, the introduction and expansion of livestock and the fishery (Cerny et al., 2009; Van Damme and Banfield, 2011). Through trials and errors, often leading to hard episodes of famines during bad climatic conditions thus dramatically reducing the population size, the Socotri have developed their own traditional resource management system (cultivation, nomadic, pastoral and fishing). These first relatively large scale human activities have transformed and impacted somehow Socotra Island pristine ecosystems which have, however, evolved in certain equilibrium with human to form the actual ecosystems (Van Damme and Banfield, 2011).

Nowadays, human activities are seen as the major threats to biodiversity in general and to Island biodiversity in particular, driven by two main mechanisms (Corlett, 2010; Shadbolt and Ragai, 2010): 1) the introduction of non-native species in a particular area might, by direct competition or predation, greatly reduce the effective size of the area for native species and might also facilitate the spread of diseases and 2) habitat loss, degradation and fragmentation even on very small scale is dramatic for biodiversity and in particular for some island endemic species that live in area not bigger than few 100 m<sup>2</sup> (Van Damme and Banfield, 2011). The recent population expansion of Socotra Island was boosted by the erratic development of trade and tourism activities supported by regular flights and boats and a modern asphalt road network (> 900 Km). Such rapid development has an impact on many ecosystems of the island. The large amount of waste (predominately plastic waste) accumulated close to urban areas in fragile ecosystem such as estuaries is one of the conspicuous evidence of pollution directly linked with the rapid population expansion. The development of the road system on Socotra has never taken into account any potential environmental impact such as the construction dust covering shallow coastal areas where corals are growing or the complete isolation of major estuaries from the sea until torrential monsoon floods occur (Fig. 4), thus limiting organism migration between the estuaries and the sea but also retaining stagnant eutrophic water home to mosquitos, potential vector of malaria in the region. Studies assessing the impact of road development on estuarine biodiversity are lacking, however the present research represents a faunistic and ecological baseline of Socotra estuaries and lagoon for the governmental agencies charged with coastal and conservation management on Socotra.



**Figure 4: Main road network isolating Khor Daneghan from the sea**  
The east part of Hadibo is visible in the upright-corner (Photo: Google)

### **Background research program on Socotra Archipelago**

The Ichthyology Section of the Senckenberg Research Institute and Natural History Museum (SFN) is an active research group focusing on 1) taxonomy, systematics and zoogeography of fishes, with a focus on marine fishes of the North-Western Indian Ocean and freshwater fishes of South-West Asia, 2) ecology of Central European freshwater fishes and 3) biodiversity, conservation and environmental research. Besides taxonomic research, ecological field studies of coral-associated fishes are an important part of the section's activities. During various projects, the group has established a network of coral monitoring stations in the Gulf of Aqaba, the Sudanese Red Sea, the Persian/Arabian Gulf, and in the Gulf of Aden including the Socotra Archipelago. At these stations coral associated fish populations are monitored at regular intervals for species presence/absence and abundances along fixed underwater transect lines, allowing drawing a complex picture of the long-term dynamics of fish populations based on a unique set of time-series data. The SFN was one of the two leading institutions involved in the development of the Conservation Zoning and Management Plan for the Socotra Archipelago in the framework of a UNDP-GEF funded multidisciplinary biodiversity project from 1998 to 2000 (Zajonz and Khalaf, 2002; Zajonz et al., 2000) and the World Bank-GEF and EPA Yemen led "Coastal Zone Management Pilot Project" in 2005 (Krupp et al., 2006; Zajonz and Klaus, 2005).

More recently several institutes including the SFN and the Goethe University, Frankfurt (GU) gathered together to form the Biodiversity and Climate Research Centre, Frankfurt (BiK-F). In close cooperation with the Environment Protection Authority (EPA) and the Ministry of Water and Environment (MoWE) of Yemen, a research program was developed to "*study marine biodiversity, ecosystems and living marine resources and predict the impacts of climate change on them, fostering climate-proof conservation and resource management practices*". Three main objectives were defined to reach this goal: 1) to understand key patterns and processes, which are the main drivers for Socotra's wealth of biotopes and ecosystems, and the associated biota and

biological communities, 2) to understand ongoing and predicted impacts of global change, including climate change, on the coastal and marine communities, and the derived ecosystem services, and to develop case studies and models allowing to predict mid and long-term range, phase and community shifts and 3) to contribute to adaptive planning and management of coastal and marine resources, to assist in the preparation of management plans, and to help minimizing socio-economic consequences (Zajonz et al., 2011, unpubl. report).

In addition, to mitigate the hard working conditions in Socotra, a platform for the research activities of the BiK-F was build. The establishment started in March 2009 under the supervision of U. Zajonz and co-supervision of E. Lavergne and H. Pulch and was finished in December 2010. The BiK-F Field Research Station (FRS) is located in Hadibo (Fig. 5) and was planned as a place offering decent working as well as living conditions for research teams working on Socotra. So far it has been used by the BiK-F, the University of Gent, the University of Tübingen and the Royal Botanical Gardens Edinburgh as well as several Yemeni ministries. As all activities of BiK-F in general, the FRS is part and parcel of the Framework Agreement on Scientific and Technical Cooperation between the EPA and the MoWE Yemen and the Memorandum of Agreement between the EPA Socotra, MoWE and BiK-F/SFN (Lavergne et al., 2011).



**Figure 5: Socotra Field Research Station**

a) FRS informal opening ceremony, b) Dormitory House and c) Science Building (Photo: U. Zajonz)

### **Socotra temporarily open/closed estuaries**

Ecologically, an estuary is an ecosystem at the interface between the freshwater and the marine environments, thus presenting a high natural ecological variability and possibly to a certain level of habitat degradation. Socotra temporarily open/closed estuaries (TOCE's) are often separated from the sea by gravelly or sandy berms and some by a road and only get connected to the sea after flash floods during the rainy seasons or by storm surges, thus limiting the in- and out-ward migration of post-larvae, juveniles and mature fishes between the freshwater, brackish and marine environments.

No TOCE was present on any remote islands of the archipelago but the main Island of Socotra. Although several zoological surveys have been conducted on Socotra Island, little is known about its TOCE and lagoon fish communities. Estuaries from Socotra were first sampled during the German Expedition of Riebeck and Schweinfurt in 1881-82 (Taschenberg, 1883) and the Austrian Expedition of Simony in 1898-1899 (Steindachner, 1902, 1903). More recently Krupp and Zajonz (Krupp et al., 2006; Zajonz et al., 2000) initiated marine and coastal expeditions in 1999 and 2000 where estuaries have been investigated, completed by additional surveys undertaken by Lavergne and Zajonz in 2007, 2008 and 2009; it constitutes the present research material. Sampling locations of the present study included one intertidal lagoon (Detwah, Socotra), one very small freshwater stream running from karst caves in the coastal escarpment (Arhen) and the remainder represented TOCE's (Fig. 6, Table 1). A reconnaissance survey of Socotra, funded by the DAAD in the framework of the 2007-2010 project **“Establishment of a Middle Eastern Biodiversity Research, Training, and Conservation Network”** (Krupp et al., 2009), was conducted in order to assess the feasibility of the present research project. Potential study locations (estuaries and lagoon) and the species of interest were identified, and the time that would need to be allocated in the field was estimated. Final location selection was made according to the accessibility, the field time and logistical constraints and the occasional denial of access to certain places by some local village authorities.

### **Life history, population structure and connectivity**

Günter provided the first and one of the most focused studies towards the understanding of the use of estuaries by fish, stating that “the young of many animals usually thought of as marine, require areas of low salinity for nursery grounds” (Günter, 1945, 1967; Pearse and Günter, 1957). Dependence of marine fish on estuarine or freshwater habitats has been studied since, and few so-called “estuary dependent fishes” are, in fact, obligatory users. This observation gave rise to the question “what are the causes and consequences of estuarine habitat use?” and ultimately led to the development of the life history and population connectivity studies (Secor and Rooker, 2005). However, it is only at the Estuarine Research Federation 2003 Seattle Meeting that fish connectivity has been deeply explored. Today connectivity refers to “the demographic connection maintained between nearby, or more distant, local populations of a species due to dispersal of pelagic eggs and larvae or to migrations of individuals, whether these be juveniles or adults” (Mora and Sale, 2002). Estuaries are known to support great productivity, abundance and diversity of fish.



**Figure 6: Photographs of the main Socotra estuaries**  
a) Khor Dubena , b) Khot Delisha, c) Khor Quariya, d) Wadi Quariya,  
e) Khor Matief, f) Wadi Matief (Photo: E. Lavergne),  
g-h) E. Lavergne and his driver Adel fishing in Khor Matief (Photo: U. Zajonz)

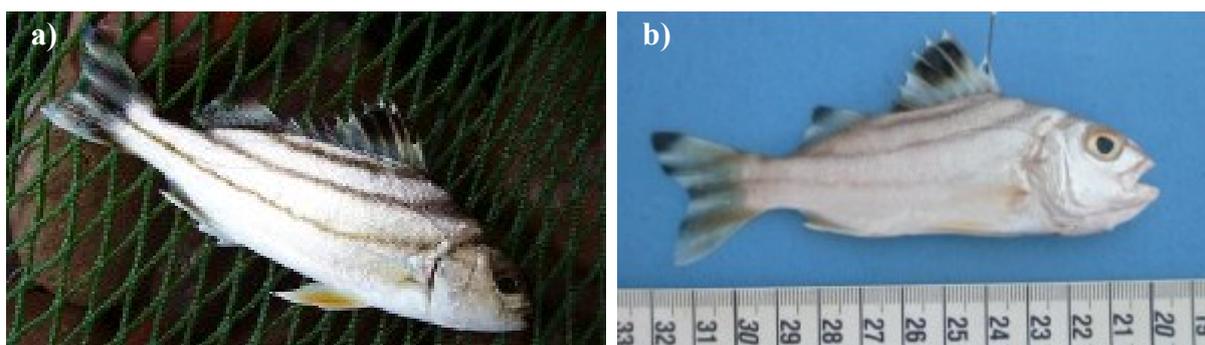
**Table 1: Sampling locations**

Locations	Coordinates (Lat., Long.)	
<b>Socotra Island:</b>		
Khor Delisha	12°41'11.3''N, 54°07'47.8''E	Shallow khor isolated by a sand berm, with a very low water level during the dry period. Very eutrophicated, many <i>Chara</i> sp. and filamentous algae. A "bridge" should allow water to circulate but disintegrating construction material (rocks) reduces significantly the water flow.
Khor Dubena	12°40'16.3''N, 54°09'01.6''E	Shallow khor periodically isolated by a sand berm. Continuous slow flow of very clear fresh to brackish water crossing a date palm plantation.
Khor Quariya	12°38'31.8''N, 54°13'29.1''E	Large khor connected to the sea at the time of the surveys, only rarely isolated by a sand berm. Stagnant to very slow flowing water from the hinterland.
Arhen	12°36'44.0''N, 54°18'16.0''E	Very small freshwater stream running from karst caves in the coastal escarpment.
Khor Matief	12°26'48.5''N, 54°18'17.6''E	Large khor isolated by a gravelly berm resting on a sandy bottom, which may imply slight interstitial water exchange when not connected to the sea. Opened during the monsoon storms and associated floodwaters.
Khor Bidholeh	12°19'45.8''N, 54°00'29.5''E	Khor opened to the sea with highly limited freshwater input, used by local fishermen as a fish landing site.
Khor Hadibo	12°39'17.7''N, 54°01'25.4''E	Large khor next to the largest village of Socotra (Hadibo), filled with sandy-muddy sediments holding eutrophicated stagnant water separated from the sea by a gravelly berm, with many <i>Chara</i> sp. and filamentous algae. Occasionally flooded during the monsoon and home to a large number of birds.
Detwah Lagoon	12°42'29.5''N, 53°30'52.6''E	A very large sandy shallow intertidal lagoon, connected by a permanent tidal channel to the sea.
Khor Quadub	12°39'00.0''N, 53°55'00.0''E	Small lagoon at the sea side, which is rarely flooded during high and storm waters. It used to be the estuary of Wadi Quadub but became separated from it by a road.
Khor Girmah	12°36'30.0''N, 53°46'41.0''E	Large, elongated khor with little freshwater input, with very soft mud bottom, its mouth near a dead mangrove.
Khor Si-irhim	12°39'35.0''N, 54°02'12.8''E	Khor with shallow, stagnant and eutrophicated water, many <i>Chara</i> sp. and filamentous algae. The bottom is composed of coarse sand and rubble.
Khor Daneghan	12°39'34.2''N, 54°02'13.9''E	Khor at the east of Hadibo. Isolated from the sea by the ring road.
<b>Yemen Mainland:</b>		
Khor Ambekha	14°30'18.5''N, 49°04'20.7''E	Khor at the east of Al Mukalla, which was completely blocked for several years during the road construction.
Khor Rukup	14°34'34.5''N, 49°13'43.6''E	Khor periodically isolated by a sand berm. The wadi is crossed up stream by a large road.
Khor Sahier	14°39'55.4''N, 49°24'55.6''E	Khor periodically isolated by a sand berm. The wadi is crossed up stream by a large road.
Khor Dufega	14°45'45.4''N, 49°37'51.2''E	Khor periodically isolated by a sand berm. The wadi is crossed up stream by a large road.

As nurseries are habitats of juveniles that contribute more than other habitats to the adult population (Beck et al., 2001; Beck et al., 2003), the understanding of connectivity between nurseries and marine habitats is fundamental to population dynamics investigations and to settle effective conservation and fisheries management strategies (Gillanders, 2005). Those movements have been inferred predominantly from temporal and spatial abundance estimates coupled with analysis of size-frequency distributions, various tagging methods and the examination of otolith marks (Gillanders and Kingsford, 2003). More recently, natural chemical tracers (“elemental fingerprints” and strontium isotope ratio  $^{87}\text{Sr}:^{86}\text{Sr}$ ) have been used to identify birth site and describe migration patterns of diadromous species (Gillanders, 2005; Kennedy et al., 1997; Kennedy et al., 2002; McCulloch et al., 2005). This approach is largely based on two key assumptions: 1) otoliths are metabolically inert with no evidence that the new material is resorbed or reworked after deposition and 2) otoliths grow continuously throughout the fish lifetime (Campana, 1999). However, the demographic connectivity requires that individuals not only move between habitats, but become participating members of the populations they join, growing, surviving, and reproducing (Sale, 2004). For the last 30 years, attempts have been made to discriminate among fish populations by using molecular markers. Studies on population structure and connectivity are based on a variety of genetic differentiation measures between population units. Genetic differentiation allows identifying partly reproductively isolated sub-populations and estimating gene flow between these sub-populations. Combining markers such as otolith elemental fingerprints and microsatellites would lead to complementary information but also to higher validation and precision (Fromentin et al., 2009).

### **Biological model**

*Terapon jarbua* (Forsskål, 1775) (Terapontidae, Perciformes) locally known as “Dirhar” in Yemen mainland and “Habraham” on Socotra Island, inhabits marine and brackish waters of the Indo-West Pacific (IWP), from the Red Sea and east coast of Africa to Samoa. Its juveniles have been observed to thrive even in coastal freshwater courses. The type locality of the species is Jeddah, Saudi Arabia, and the type series is deposited in the Zoological Museum of Copenhagen (Klausewitz and Nielsen, 1965; Nielsen, 1974). *Terapon jarbua* (Fig. 7) is commonly named, tiger perch because it can be distinguished from all other members of the family by their body coloration of three downwardly curved longitudinal stripes, or grunters in reference to the sound emitted by their unique swimbladder equipped with extrinsic muscles, a specific anatomic characteristic of the family (Vari, 1978). It has a rather compressed body with a strong, powerful spine at the back of the operculum, and a slightly downward-pointing mouth armed with numerous small, sharp teeth (Van der Elst, 1993).



**Figure 7: Freshly caught *T. jarbua***

In their study of the role of South African estuaries in providing nursery habitats for juvenile fish, Wallace and colleagues (1984; 1975) observed that the reproduction, spawning and early larval life of *T. jarbua* is limited to the marine environment but estuarine recruitment seems to take place at an early stage. Underwater observations of Whitfield and Blaber (1978) recorded the feeding behaviour of adult *T. jarbua* under natural conditions and showed that this species is primarily carnivorous. Fish or invertebrate prey would be swallowed if it is much smaller than *T. jarbua*, otherwise only scales, skin or other pieces would be snapped off.

Like the majority of tropical and subtropical marine spawners, they have an extended breeding season and are fractional spawners. To spawn in several batches seems to avoid overcrowding of larvae in order to reduce food competition among the offspring and to allow post larvae to immigrate into TOCE's when connection with seawater occurs (James et al., 2007). Cowley and Whitfield (2001) proposed that such a strategy prevents recruitment failure, and explains the dominance of such species in TOCE's.

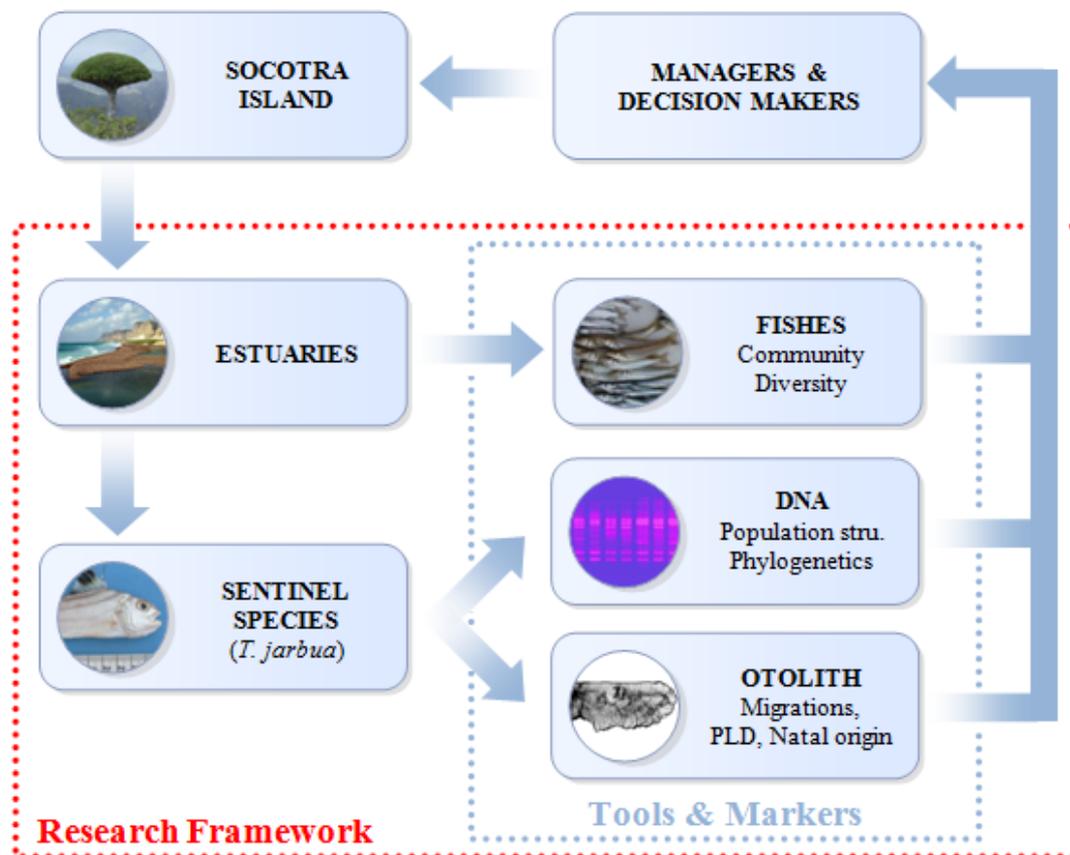
Although advances have been made in the taxonomy and biology of the Terapontidae (Miu et al., 1990; Vari, 1978; Whitfield and Blaber, 1978), no in-depth studies of the reproductive ecology, life history strategy or population structure of *T. jarbua* have been conducted so far. Yet, its wide distribution beyond the study region and its ability to cope with contrasted environments (salinity: 0-39 ‰, temperatures: up to 36°C) indicate that this species can be considered as an excellent sentinel species for the estuaries of the region.

### **Objectives and plan of this thesis**

In this general context the aim of this work is to provide the first faunistic and ecological baseline of Socotra estuaries and lagoon fishes for governmental coastal managers and decision makers, with a particular focus on a sentinel species, *T. jarbua*, to better understand the functioning and the importance of Socotra TOCE system (Fig. 8). To achieve this goal, several objectives have been drawn and sorted in the five different chapters of this document, each of

those part have been written in order to be published separately in peer reviewed international science journals.

- **The first part of this manuscript** presents a preliminary faunistic account of estuarine and lagoon fish species of Socotra Island and the Hadhramout mainland coast of Yemen and describes for the first time fish species diversity and assemblage composition at key sites.
- **The second part** assesses seasonal effects of the Summer Monsoon on Fulton's condition factor K and compares Length-Weight Relationship of the sentinel species *T. jarbua* from the wider Gulf of Aden region vs. other regions.
- **The third part** presents the isolation and characterization of the nine first microsatellite loci of *T. jarbua*, which will be used in the next part.
- **The forth part** explores the phylogenetics and genetic structure of *T. jarbua* in the wider Gulf of Aden including Socotra Island, by considering several genetic markers: the Cytochrome *c* Oxydase sub-unit 1 (CO1) and the nine previously characterized microsatellites.
- **The fifth part** reconstructs migratory pattern and defines natal origins of juvenile *T. jarbua* inhabiting estuaries in an attempt to correlate this results with potential genetic structure.



**Figure 8: Scientific approach**  
\*PLD: Planktonic Larval Duration

Finally a general conclusion is drawn on Socotra estuaries and lagoon functioning, their importance to fish diversity and their fragility face to the climate change and rapid uncontrolled development. Additional perspectives derived from this work are also proposed.

This work was developed in a multidisciplinary approach to understand the functioning and importance of Socotra estuaries and lagoon for fishes. Several tools were used from different field of biology and chemistry: taxonomy, ecology, phylogenetics, population genetics, otolith microstructure and otolith microchemistry. Thus it was natural to involved in the implementation phase of this study a well-equipped and recognized laboratory specialised in marine genetics and otolith analysis: The Marine Environmental Science Laboratory (LEMAR) of the European Institute for Marine Studies (IUEM), Plouzané – France, an institute of the University of Western Brittany (UBO).



# Chapter

# 1

**Diversity and composition of estuarine and lagoon fish assemblages of Socotra Island, including comparative sites over the mainland coast of Yemen**

---



## Summary

**Context:** Socotra Island, located in the North-Western Indian Ocean, is characterized by rainy and dry alternating monsoon seasons and composed by the Haggier Mountains, Paleogene karstic limestone plateaus and alluvial coastal plains (Scholte et al., 2011). Its particular geographical location, relief and climate provide sufficient freshwater input to support a rich biodiversity and a high number of endemic species. Numerous biodiversity surveys have been conducted including marine fishes (Kemp, 1998; Zajonz et al., 2000), however little is known about temporarily open / closed estuary (TOCE) and lagoon fish communities except old specimens (Krupp and Zajonz, 2006; Steindachner, 1902, 1903; Taschenberg, 1883).

**Aim and objectives:** The aim of this study is to provide baseline data on estuarine and lagoon fish diversity, especially in support of informed conservation management. The objectives are 1) to present for the first time a preliminary faunistic account of estuarine fish species of Socotra Island and the Yemen mainland, 2) to describe fish species diversity and assemblage composition and 3) to characterize and compare the fish community structure across sites.

**Materials and methods:** The specimens were collected using seine net during the pre- and post- summer monsoon period from 1999 to 2009, at 15 locations on both Socotra and Yemen mainland. Specimens were preserved and identified. Species richness, Shannon diversity index and Evenness index were calculated to describe assemblages and Ward hierarchical clustering analyses and principal component analyses were performed on species presence / absence and abundance in order to understand differences in estuarine fish community assemblages.

**Results:** A total 5,598 fishes dominated by juvenile size classes, representing 66 species belonging to 38 genera and 31 families, has so far been recorded from estuaries and lagoon during this study spanning a decade of survey. Out of the 66 species, 23 represent new records for Socotra. All recorded specimens are marine or secondary freshwater species. *Terapon jarbua* and Mugilidae sp. are the most abundant and frequent species in the region.

**Conclusion:** Socotra Island appears as a biogeographic “stepping stone” (habitats located between larger habitats) for several species, however for other species it is not possible to bridge the gap between the African coasts and Socotra and the Eastern Arabian coast. Moreover 33 out of 66 species were considered relevant species for the local economy. This underscores the

paramount importance of TOCE as spawning and nursery sites, and for the sustainability of vital provisioning ecosystem services.

**Next chapter:** To better understand TOCE functioning, the next chapters will focus on a sentinel species: *T. jarbua*. The second chapter will assess seasonal effects of the Summer Monsoon on Fulton's condition factor K and compares Length-Weight Relationship of the sentinel species from the wider Gulf of Aden region with that from other regions.

## **Diversity and composition of estuarine and lagoon fish assemblages of Socotra Island, including comparative sites over the mainland coast of Yemen**

*E. Lavergne*<sup>1, 2, 3</sup>, *U. Zajonz*<sup>2, 1</sup>, *F. Krupp*<sup>4, 1</sup>, *F. Naseeb*<sup>5, 2</sup> and *M. S. Aided*<sup>6, 2</sup>

<sup>1</sup> *Senckenberg Forschungsinstitut und Naturmuseum, Sektion Ichthyologie – Senckenberganlage 25, 60325 Frankfurt am Main, Deutschland*

<sup>2</sup> *Biodiversität und Klima Forschungszentrum (BiK-F), Tropical Marine Ecosystems Group – Senckenberganlage 25, 60325 Frankfurt am Main, Deutschland*

<sup>3</sup> *Université de Bretagne Occidentale, UMR 6539, CNRS/IRD/UBO, Laboratoire des Sciences de l'Environnement Marin LEMAR, Institut Universitaire Européen de la Mer, Rue Dumont d'Urville, 29280 Plouzané, France*

<sup>4</sup> *Qatar Natural History Museum, Qatar Museums Authority P.O. Box 2777, Doha, Qatar*

<sup>5</sup> *Environmental Protection Authority, Socotra Branch, Hadiboh, Yemen*

<sup>6</sup> *Hadhramout University of Science and Technology, Dept. of Marine Fisheries and Resources, Marine Biology Division, Al-Mukalla, Yemen*

**Corresponding author:** *E. Lavergne, Tel +33 2 98 49 86 27*

*Email address: edouard.lavergne@gmail.com*

*To be submitted*

### **Abstract**

Estuarine and lagoon surveys of Socotra Island and the Hadhramout coast of Yemen were conducted with the objectives to provide baseline data on estuarine and lagoon fish diversity, especially in support of informed conservation management. A total of 66 species in 31 families have been recorded, among which 64 species in 30 families were from Socotra and 20 species in 13 families were from the mainland. 23 species represent new faunistic records and the most common species is *Terapon jarbua* (Forsskål, 1775). Including the critically assessed historic records the total fish diversity of estuaries and lagoons of Socotra Island is estimated at 75-80 species, which is relatively higher compared with species inventories of well-researched coastal estuaries from South Africa. The high number of economically relevant species of fish recorded to date underscores the paramount importance of these coastal water bodies as spawning and nursery sites, and for the sustainability of vital provisioning ecosystem services.

**Keywords:** Fish community, estuary, diversity, richness, Socotra Island, Gulf of Aden, Yemen.

## Introduction

The Socotra Archipelago lies in a region of still relatively poorly known coastal and marine fish faunas by Indian Ocean standards. Fish assemblages of coastal estuaries and lagoons of the Gulf of Aden, the Arabian Sea coast of Oman and Somalia have received little attention by researchers, especially when compared to the highly monitored coastal estuaries of South-Africa and Mozambique (Cowley and Whitfield, 2001; Harrison and Whitfield, 1995; James et al., 2007; Wallace et al., 1984; Whitfield, 2010; Whitfield and Cowley, 2010). Coastal fish communities of Yemen have been investigated to some degree. Especially the coastal ecosystems of Socotra Archipelago are of regional and global importance as revealed by detailed marine and coastal surveys conducted from 1996-2000 in the framework of the UNDP-GEF and Environmental Protection Authority (EPA) Yemen led project “Conservation and Sustainable Use of Socotra Archipelago” (Kemp, 1998, 2000; Zajonz and Khalaf, 2002; Zajonz et al., 2000; Zajonz and Saeed, 2002). Besides the publications of Kemp, most of the ichthyological results of these surveys are yet to be published (Zajonz, pers. comm.).

The Socotra Archipelago includes the main island of Socotra and the three smaller islands of Samha, Darsa and Abd al-Kuri. Socotra Island lies in the north-western corner of the Indian Ocean, at the junction between the Gulf of Aden and the Arabian Sea at 12°30'N 54°00'E (Fig. 1.1). The Archipelago is characterized by the alternating monsoon seasons in the Northern Indian Ocean driven by the Inter-Tropical Convergence Zone (ITCZ): the weak and wet winter or north-east monsoon (October – February) and the forceful and dry summer or south-west monsoon (Currie et al., 1973; Fleitmann et al., 2004; Fratantoni et al., 2006; Glynn, 1993; Kemp, 1998; Klaus and Turner, 2004; Scholte and de Geest, 2010).

According to Zajonz and colleagues (2000) coastal fish communities of Socotra Archipelago are highly diverse and enriched by species of adjacent biogeographic regions consistent with the archipelago’s position at “biogeographic crossroads” as postulated by various authors (De Vantier et al., 2004; Kemp, 1998; Zajonz et al., 2000). Of the four major surrounding biogeographic units, species of the Eritrean, South Arabian and Persian sections of the Arabian subprovince dominate, but a marked influence of the Western Indian Ocean subprovince, notably of East African species is prevalent too (Zajonz, 2006; Zajonz and Saeed, 2002). Recently, Gill and Zajonz (2011) suggested that the three endemic pseudochromid species described from Socotra so far appear to be more closely related to species clades from East Africa than to clades of the North-Western Indian Ocean within their respective subfamilies.

Fishes were sampled from Socotra Island, including freshwater and estuarine species, for the first time during the German expedition of Riebeck and Schweinfurth in 1881-82, resulting in eight species mentioned by Taschenberg (1883) who, however, did not list their names. Part of

their collections is lost today and cannot be verified. Several specimens were traced by the second author and included three secondary and two primary species of freshwater fishes. Although their historic collection labels refer to the expedition of Riebeck and Schweinfurth it remains still uncertain whether the fishes actually originate from Socotra. The Austrian Expedition to Socotra and South Arabia in 1898-1899, led by Simony, recorded a total of 156 species of fish from “South Arabia”, representing 124 mostly marine species collected at about six sites at the Yemen Gulf of Aden coast and 56 mostly marine and brackish water species collected at about nine sites at the Socotra Archipelago (Steindachner, 1902, 1903). Based on the collection from Socotra, Steindachner described two species *Gerres sokotranus* and *Hirundichthys sokotranus* as new to science. Among the total of 56 species he recorded 28 species sampled in three estuaries.

A total of 215 species were recorded from the Archipelago by (Kemp, 1998). His study, however, was solely based on sightings, thus cannot be verified and did not include estuaries specifically. During the UNDP-GEF project (1998-2000) detailed marine and coastal surveys and extensive sampling were conducted, including a number of estuarine habitats. Zajonz and colleagues (2000, 2002) reported 726 species from the island group but did not list estuarine and lagoon species separately. Combining their estuarine samples with a first systematic, though non-quantitative, survey of estuarine and freshwater fishes conducted in 2000, Krupp et al. (2006) counted 44 species in 22 families without, however, providing a species list. The coastal estuaries of the Hadhramout and Shabwa governorates of Yemen were mapped during the World Bank-GEF and EPA Yemen led “Coastal Zone Management Pilot Project” in 2005 (Zajonz and Klaus, 2005) but were not investigated at any detail concerning their fish inventories before the present study.

The temporarily open/closed estuaries (TOCE's) of Socotra Island and the Yemen mainland are very important ecosystems, especially due to their function as spawning and nursery sites for commercially exploited species of fish and crustaceans and as roosting and breeding sites for coastal birds (Klaus et al., 2003; Krupp et al., 2006; Zajonz and Klaus, 2005). The aim of this study is to provide baseline data on estuarine and lagoon fish diversity, especially in support of informed conservation management. The objectives are 1) to present for the first time a preliminary faunistic account of estuarine fish species of Socotra Island and the Hadhramout mainland coast of Yemen, 2) to describe fish species diversity and assemblage composition at key sites and 3) to characterize and compare the fish community structure across sites.

## **Materials and methods**

### ***Study area***

Socotra Island has about 20 TOCE's which vary greatly in terms of their morphology, water regime and ecological conditions. The particular monsoon climate with dry and rainy seasons contributes to create particular estuarine environments with marked seasonal river flow, salinity and temperature regimes (Krupp et al., 2006). Most estuaries are separated from the sea by gravelly or sandy berms and only get connected to the sea after flush floods during the rainy seasons or by storm surges. Thus the in- and out-ward migration of post-larvae, juveniles and mature fishes between freshwater, brackish, and marine environments is usually limited for long periods during the year. No estuaries or lagoons are found on the islands of Darsa, Samha and Abd al-Kuri and the Hadhramout coast of Yemen has as about 16 coastal estuaries.

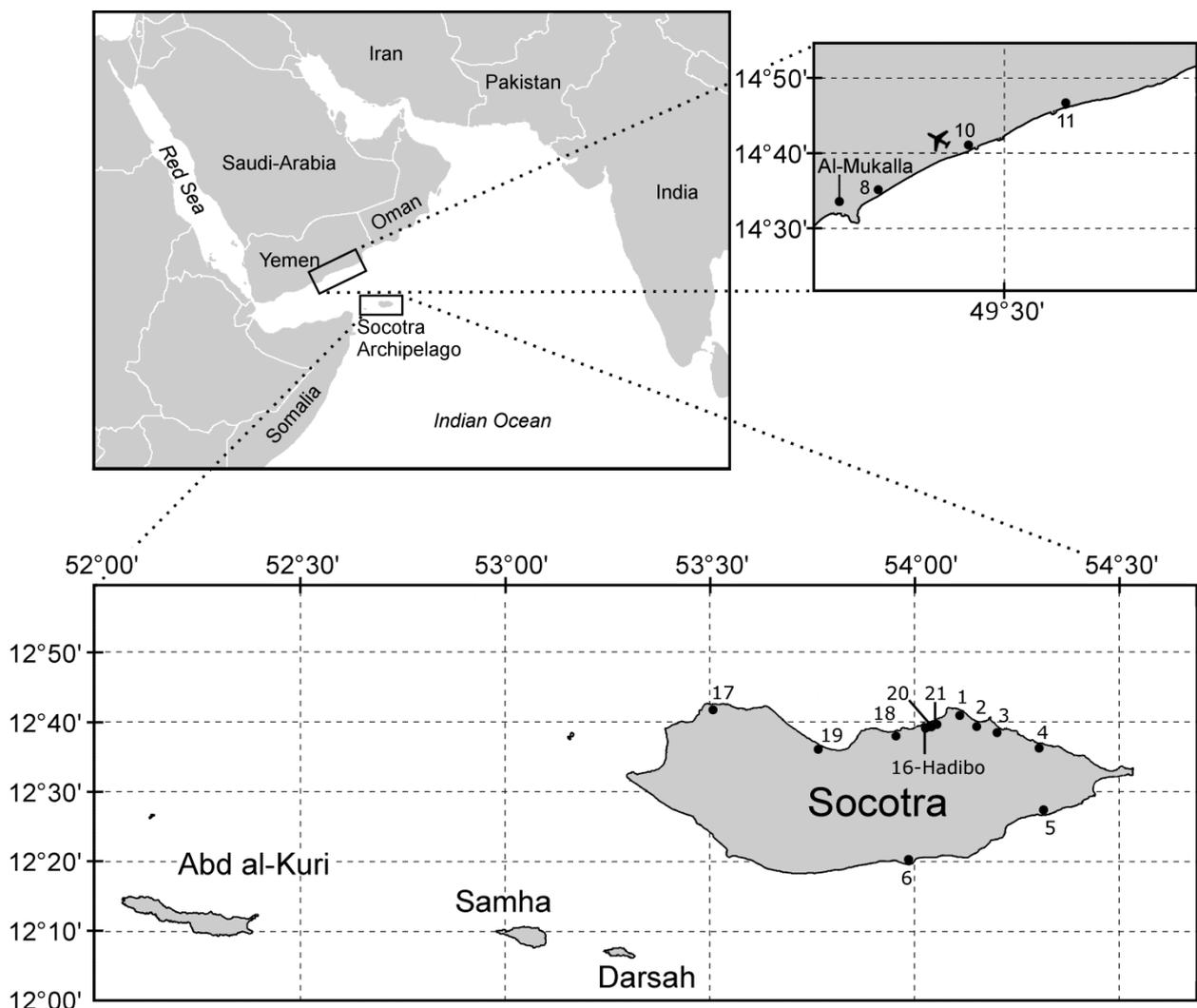
### ***Data collection***

The specimens were collected during the pre- (March-April) and post- (October-December) summer monsoon period of 1999, 2000, 2007, 2008 and 2009, at 15 locations, respectively 12 on Socotra Island and three on Yemen mainland (Table 1.1 and Fig. 1.1). Locations included one intertidal lagoon (Detwah, Socotra), one very small freshwater stream running from karst caves in the coastal escarpment (Arhen) and the remainder represented TOCE's. Sampling was undertaken principally in the morning hours in order to leave sufficient time for subsequent preliminary fish identification, otolith extraction and genetic sample preparation (Lavergne et al., 2011) requiring good light conditions, as electricity supply was highly limited on Socotra. Fishing was performed using a seine net of 30 m length, 1.2 m height and 10 mm mesh size, equipped with an end bag of smaller mesh size which retains the fishes. Although aimed at by the original sampling protocol a standardized sampling effort could not be fully achieved due to field time and logistical constraints and occasional denial of access to certain locations by some local village authorities. Specimens were fixed on site in formalin before being shipped to the Senckenberg Research Institute (Germany) for proper identification and final preservation in 70 % ethanol. Half of the collection will be returned to an appropriate natural history institution in Yemen, according to the research permit issued by the EPA of Yemen.

### ***Taxonomic analysis***

The taxonomic classification used herein follows Eschmeyer (2011). The species recorded during the recent surveys and the earlier surveys of the UNDP-GEF project (Krupp et al., 2006; Zajonz and Khalaf, 2002; Zajonz et al., 2000) were included into the preliminary faunal account in Appendix 1 and the analysis of the diversity of estuarine and lagoon fishes of the region

presented in this study. A preliminary annotated taxonomic inventory of the species is included in Appendix 2. The final positive identification of certain specimens of the collection is however still pending and a full taxonomic account, including a taxonomic revision of previously published collection records (i.e.: of Steindachner 1902, 1903) will be presented in a forthcoming monographical publication. The estuarine species records of Steindachner were, however, critically assessed. Their nomenclatural status was updated and the plausibility of their occurrence was assessed using current knowledge of species distribution ranges (Froese and Pauly, 2011) and unpublished regional record lists of the authors. They were then compared with the species recorded by the present study (Appendix 3) and included in an approximation of the total diversity of estuarine and lagoon fishes of Socotra Island.



**Figure 1.1: Map of sampling locations**

1 – Khor Delisha, 2 – Khor Dubena, 3 – Khor Quariya, 4 – Arhen, 5 – Khor Matief, 6 – Khor Bidholeh, 8 – Khor Rukup, 10 – Khor Sahier, 11 – Khor Dufega, 16 – Khor Hadibo, 17 – Detwah Lagoon, 18 – Khor Quadub, 19 – Khor Girmah, 20 – Khor Si-irhim and 21 – Khor Daneghan. This study is part of a larger research project including the analyses of the genetic structure (Chapter 4) and the otolith microchemistry (Chapter 5) of *T. jarbua*. As it was desirable to use a consistent location numbering across studies and because not all locations of the project were involved in the present study, some locations are not presented here.

**Table 1.1: Sampling locations**

Locations (Fig. 1.1)	Coordinates (Lat., Long.)	
<b>Socotra Island:</b>		
1-Khor Delisha	12°41'11.3''N, 54°07'47.8''E	Shallow khor isolated by a sand berm, with a very low water level during the dry period. Very eutrophicated, many <i>Chara</i> sp. and filamentous algae. A "bridge" should allow water to circulate but disintegrating construction material (rocks) reduces significantly the water flow.
2-Khor Dubena	12°40'16.3''N, 54°09'01.6''E	Shallow khor periodically isolated by a sand berm. Continuous slow flow of very clear fresh to brackish water crossing a date palm plantation.
3-Khor Quariya	12°38'31.8''N, 54°13'29.1''E	Large khor connected to the sea at the time of the surveys, only rarely isolated by a sand berm. Stagnant to very slow flowing water from the hinterland.
4-Arhen	12°36'44.0''N, 54°18'16.0''E	Very small freshwater stream running from karst caves in the coastal escarpment.
5-Khor Matief	12°26'48.5''N, 54°18'17.6''E	Large khor isolated by a gravelly berm resting on a sandy bottom, which may imply slight interstitial water exchange when not connected to the sea. Opened during the monsoon storms and associated floodwaters.
6-Khor Bidholeh	12°19'45.8''N, 54°00'29.5''E	Khor opened to the sea with highly limited freshwater input, used by local fishermen as a fish landing site.
16-Khor Hadibo	12°39'17.7''N, 54°01'25.4''E	Large khor next to the largest village of Socotra (Hadibo), filled with sandy-muddy sediments holding eutrophicated stagnant water separated from the sea by a gravelly berm, with many <i>Chara</i> sp. and filamentous algae. Occasionally flooded during the monsoon and home to a large number of birds.
17-Detwah Lagoon	12°42'29.5''N, 53°30'52.6''E	A very large sandy shallow intertidal lagoon, connected by a permanent tidal channel to the sea.
18-Khor Quadub	12°39'00.0''N, 53°55'00.0''E	Small lagoon at the sea side, which is rarely flooded during high and storm waters. It used to the estuary of Wadi Quadub but became separated from it by a road.
19-Khor Girmah	12°36'30.0''N, 53°46'41.0''E	Large, elongated khor with little freshwater input, with very soft mud bottom, its mouth near a dead mangrove.
20-Khor Si-irhim	12°39'35.0''N, 54°02'12.8''E	Khor with shallow, stagnant and eutrophicated water, many <i>Chara</i> sp. and filamentous algae. The bottom is composed of coarse sand and rubble.
21-Khor Daneghan	12°39'34.2''N, 54°02'13.9''E	Khor at the east of Hadibo. Isolated from the sea by the ring road.
<b>Yemen Mainland:</b>		
8-Khor Rukup	14°34'34.5''N, 49°13'43.6''E	Khor periodically isolated by a sand berm. The wadi is crossed up stream by a large road.
10-Khor Sahier	14°39'55.4''N, 49°24'55.6''E	Khor periodically isolated by a sand berm. The wadi is crossed up stream by a large road.
11-Khor Dufega	14°45'45.4''N, 49°37'51.2''E	Khor periodically isolated by a sand berm. The wadi is crossed up stream by a large road.

This study is part of a larger research project including the analyses of the genetic structure (Chapter 4) and the otolith microchemistry (Chapter 5) of *T. jarbua*. As it was desirable to use a consistent location numbering across studies and because not all locations of the project were involved in the present study, some locations are not presented here.

**Statistical analysis**

Abundance and species richness ( $S$ ) were recorded to calculate the Shannon species entropy ( $H'$ ) (Shannon and Weaver, 1949):

$$H' = - \sum_{i=1}^S [p_i \times \ln(p_i)]$$

where  $p_i$  is the relative abundance of the  $i^{\text{th}}$  species.

Accounting for the bias caused by the differing sampling efforts, individual based taxon sampling curves were used in order to standardize data sets to a common number of individuals for the purposes of comparing diversity indices among locations (Gauthier et al., 2010; Gotelli and Colwell, 2001). Due to low abundance at three locations (less than 30 individuals for Daneghan, Quadub and Si-irhim) those sites were removed from the rarefaction, cluster and ordination analyses. Rarefied species richness and Shannon index were calculated using the function *renyiaccum* of the R package *vegan* using 1,000 permutations (Ihaka and Gentleman, 1996; Liu et al., 2007; Oksanen et al., 2008).

Most diversity indices such as the Shannon index are entropies and not diversities, thus are difficult to interpret. However, all diversity indices can be transformed into true diversities (equivalent number of species), which are the numbers of equally-likely elements needed to produce the given value of the diversity index (Jost, 2006; Jurasinski and Koch, 2011; Moreno and Rodríguez, 2011). Numbers equivalents have the advantage to have the same unit (species), thus to be comparable and to avoid biological misinterpretations due to the nonlinearity of most diversity indices (Jost, 2006). The rarefied Shannon diversity for each location was calculated as  $exp(H')$  (Jost, 2006; Jurasinski and Koch, 2011; Moreno and Rodríguez, 2011) also known as Hill's number which gives the number of abundant species in a sample (Ludwig and Reynolds, 1988). In addition Pielou's evenness index ( $J'$ ), indicating the way in which the total number of individuals is distributed among the total number of species, was calculated as follow (Pielou, 1966):

$$J' = \frac{H'}{\ln(S)}$$

Although permutations during Renyi's calculations allowed the calculation of 95 % confidence intervals for each locations, permutations are not independent from each other and do not allow statistical comparison among locations. However species richness, Shannon diversity ( $exp(H')$ ) and Pielou's evenness will still be suitable descriptors of the lagoon and estuarine fish diversity of the area under study and help elucidating to which extend locations might differ from each other (Jost, 2006).

Beta diversity was investigated using community relatedness between locations. A pairwise distance matrix between location was calculated based on Hellinger's index using the function *decostand* of the R package *vegan* (Legendre and Gallagher, 2001; Oksanen et al., 2008):

$$D_{\text{Hellinger}}(x_1, x_2) = \sqrt{\sum_{i=1}^s [\sqrt{p_{1i}} - \sqrt{p_{2i}}]^2}$$

where  $x_1$  and  $x_2$  are location 1 and 2,  $p_{1i}$  and  $p_{2i}$  are the relative abundance of the  $i^{\text{th}}$  species at location 1 and 2. Hellinger's distance is the Euclidean distance between the square root of the relative abundances of the compared locations (Kindt and Coe, 2005; Legendre and Gallagher, 2001). The Hellinger transformation allows comparisons among locations with varying sampling effort, and also reduces the effect of highly abundant species on the ordination (Legendre, 2005). According to Legendre and Legendre (1998), Hellinger's distance represents the best compromise between linearity and resolution when compared with other distances (e.g.: chi-square distance) for linear ordination. Ward's hierarchical joining clustering analysis based on Hellinger's distances was then used to group locations according to their similarity in fish community composition. Ward's method maximizes the differences among clusters and minimizes the differences within clusters (Kindt and Coe, 2005). In addition, principal components analyses (PCA's) were used to produce ordination graphs that portray Hellinger's distance among locations (Legendre and Gallagher, 2001) on plans in the multidimensional space that will best explain the variation between locations, and group differences were tested using the ANOSIM permutation tests (1,000 permutations) (Clarke and Green, 1988). Analyses were performed using the *anosim* function of the R package *vegan* (Oksanen et al., 2008).

## Results

A total 5,598 fishes dominated by juvenile size classes, representing 66 species belonging to 38 genera and 31 families (Appendix 1), has so far been recorded from estuaries and lagoons during this study spanning a decade of survey work. All recorded specimens are so far marine or secondary freshwater (e.g.: *Aphanius dispar* Rüppell, 1829) species, respectively.

### General diversity

About 64 species from 30 families were caught on Socotra Island (23 new records) and 20 species from 13 families on the Yemen mainland, respectively. The cumulative frequency of species per family is presented in Fig. 1.2. Gobies (Gobiidae) are the most speciose family (i.e: rich in number of species), representing 11.94 % of all species encountered followed by mugilids (Mugillidae). The ten richest families in terms of number of species are listed in Table 1.2

accounting for 40 species, or 59.7 % of all species, respectively. A total of 17 families are represented by a single species and three families by two species only.

A critical assessment of Steindachner's records (1902, 1903) of the Austrian expedition of 1898-99 revealed that about 28 species were collected from three estuarine sites of Socotra, representing the Qalansiyah estuary in the west, Tamarida estuary (Suq) near Hawlaf in the central north, and Pond Lebine near Khor Quariya in the north-east of Socotra, with two, 15 and 20 species, respectively. The updated nomenclature of these records and a comparison with the species account of the present study, including critical remarks, is provided in Appendix 3. Eleven of Steindachner's species were also recorded by the present study, four are considered reliable additional records and twelve nominal species have potentially matching species (i.e.: being closely related) among the present account, therefore requiring taxonomic re-examination of Steindachner's voucher specimens according to current literature. A further three of his records are doubtful for different reasons and require verification as well.

The present study could not confirm the presence of primary freshwater species, in particular not the presence on Socotra of two species belonging to the genera *Capoeta* and *Esomus*, which were traced among the collections of the 1881-82 expedition to Socotra by Riebeck and Schweinfurt (Krupp et al., 2006). Three additional Gobiidae species of this collection potentially represent yet unidentified gobiid species of the present study.

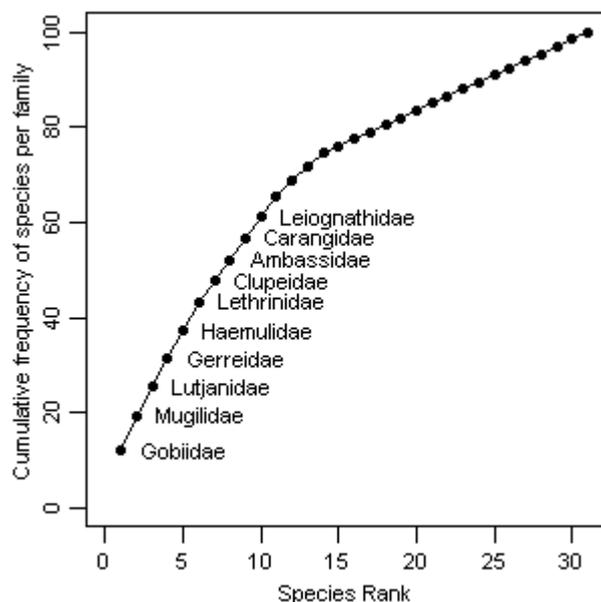


Figure 1.2: Cumulative frequency of species per family

Table 1.2: List of the ten predominant families sorted by species number

Rank	Family	Species no	Species no %
1	Gobiidae	8	11.94
2	Mugilidae	4	5.97
3	Lutjanidae	4	5.97
4	Gerreidae	4	5.97
5	Haemulidae	4	5.97
6	Lethrinidae	4	5.97
7	Clupeidae	3	4.48
8	Ambassidae	3	4.48
9	Carangidae	3	4.48
10	Leionathidae	3	4.48

### *Species occurrence and species abundance*

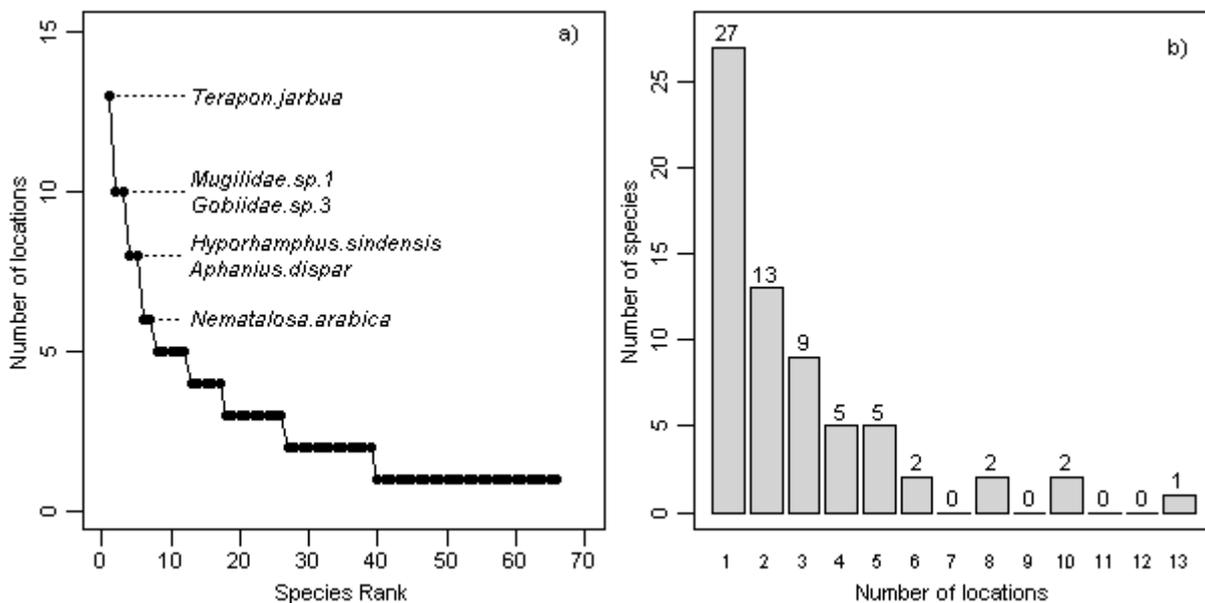
The frequencies of occurrence, based on the number of locations where a species was recorded, were relatively high for five species (*Terapon jarbua*, Mugilidae sp. 1, Gobiidae sp. 3, *Aphanius dispar* and *Hyporhamphus sindensis* Regan, 1905). Those species were present on both

Socotra Island and Yemen mainland, thus revealing their wide distribution throughout the studied region (Table 1.3 and Fig. 1.3a). The distribution of species occurrence frequencies (Fig. 1.3b) shows that a majority of the species is recorded at only few locations. Moreover, a total of 46 species were only recorded at Socotra and, two species (Gobiidae sp. 5 and *Sphyraena jello* Cuvier, 1829) were recorded only at mainland locations.

The four most abundant fish species include one of the four mugilid species (sp. 1), *Terapon jarbua*, *Hyporhamphus sindensis* and *Ambassis dussumieri* Cuvier, 1828 and account for around 60.4 % of the total abundance. With *Terapon jarbua*, Mugilidae sp. 1, and *Hyporhamphus sindensis* three of the five most frequent species in terms of occurrences also dominate the relative abundances, therefore representing superior constituents of the estuarine ecosystems under study. Frequencies of species abundance are presented in Table 1.4 and Fig. 1.4.

**Table 1.3: List of the 15 most frequent species**

Rank	Species	Occ.
1	<i>Terapon jarbua</i>	13
2	<i>Mugilidae</i> sp. 1	10
3	<i>Gobiidae</i> sp. 3	10
4	<i>Hyporhamphus sindensis</i>	8
5	<i>Aphanius dispar</i>	8
6	<i>Nematalosa Arabica</i>	6
7	<i>Ambassis dussumieri</i>	6
8	<i>Mugilidae</i> sp. 2	5
9	<i>Mugilidae</i> sp. 3	5
10	<i>Sillago</i> sp.	5
11	<i>Lutjanus</i>	5
12	<i>Monodactylus argenteus</i>	5
13	<i>Atherinomorus lacunosus</i>	4
14	<i>Gerres filamentosus</i>	4
15	<i>Gerres longirostris</i>	4



**Figure 1.3: a) Species rank occurrence curve and b) Frequency distribution of species occurrence**

Individual based taxon sampling curves (Fig. 1.5) allow comparing diversity profiles. Some curves, however, do not reach their asymptotic maximum (the “true” species richness  $S$ ), indicating that the observed species richnesses underestimate the probable  $S$ . This conclusion is further supported by a large number of low occurrence species (Fig. 1.3b). Indeed the more low occurrence species in a location there are, the more difficult it is for the location-specific

individual based taxon sampling curve to reach its maximum and thus to estimate  $S$ . This underestimation is also depicted in (Fig. 1.6). Occasionally one species dominated the community of a particular location characterized by a relatively high abundance and low Shannon diversity (Fig. 1.6). Khor Bidholeh is dominated at 90.9 % by *Terapon jarbua* and Khor Dufega at 84 % by *Mugilidae* sp. 1.

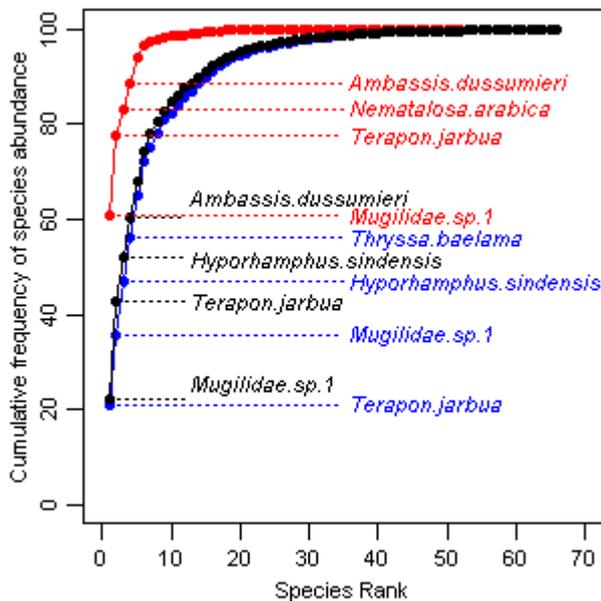


Figure 1.4: Cumulative species rank abundance curves Socotra Island (Red), Yemen mainland (blue) and the whole region (black).

Table 1.4: List of the 15 most abundant

Rank	Species	n	n %
1	<i>Mugilidae</i> sp. 1	1243	22.2
2	<i>Terapon jarbua</i>	1142	20.4
3	<i>Hyporhamphus sindensis</i>	530	9.5
4	<i>Ambassis dussumieri</i>	465	8.3
5	<i>Thryssa baelama</i>	436	7.8
6	<i>Aphanius dispar</i>	354	6.3
7	<i>Mugilidae</i> sp. 2	192	3.4
8	<i>Gobiidae</i> sp. 8	146	2.6
9	<i>Mugilidae</i> sp. 4	121	2.2
10	<i>Nematalosa Arabica</i>	116	2.1
11	<i>Monodactylus argenteus</i>	82	1.5
12	<i>Gobiidae</i> sp. 3	77	1.4
13	<i>Herklostichthys</i>	68	1.2
14	<i>Aurigequula fasciata</i>	68	1.2
15	<i>Mugilidae</i> sp. 3	67	1.2

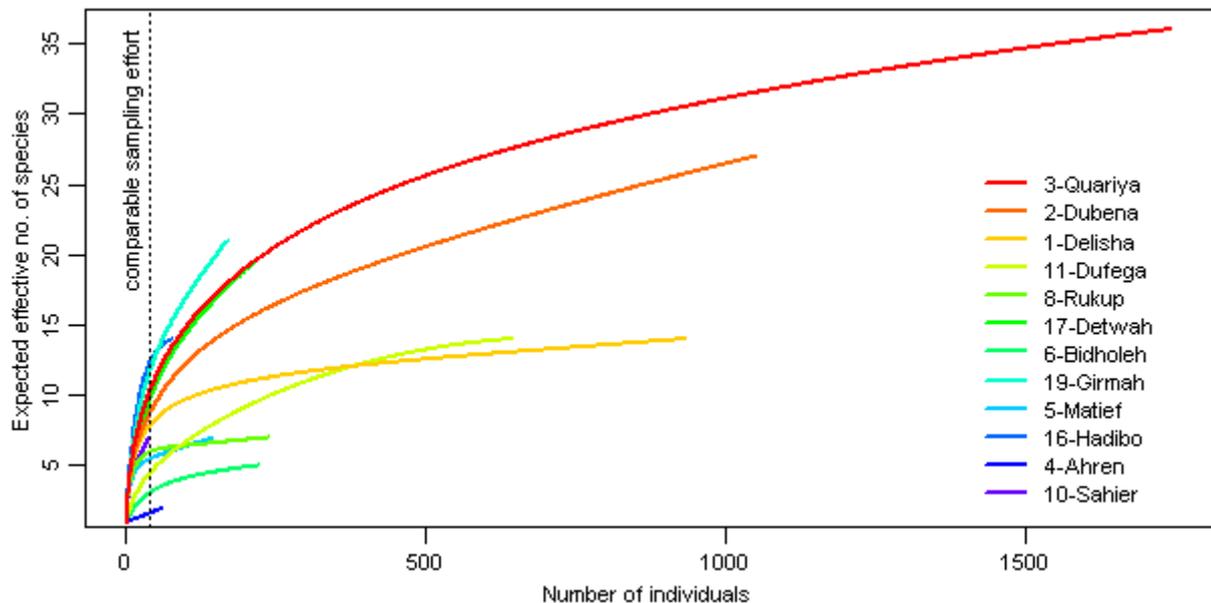


Figure 1.5: Individual based taxon sampling curves for each location

**Richness, Shannon diversity and evenness**

A total of 66 fish species has been recorded in the estuaries and lagoon of the region. On Socotra, a total of 64 species were found, with a mean number of 13 species per site ranging

from 1 (Khor Daneghan) to 36 (Khor Quariya). On Yemen mainland a total of 20 species were found, with a mean number of 9.3 species per site ranging from 7 (Khors Rukup and Sahier) to 14 (Khor Dufega). A summary of estuarine and lagoon species richness observed within the studied region is presented in Table 1.5 and emphasizes the higher diversity of Socotra compared to mainland estuaries, while Fig. 1.6 shows the observed and the expected species richness (rarefied) per location for the selected sampling effort.

The abundances ranged from 39 fishes at Khor Sahier to 1742 fishes at Khor Quariya, and the rarefied Shannon diversity ( $exp(H')$ ) ranged from 1.08 species at Ahren to 9.07 species at Khor Hadibo (Fig. 1.6). Three groups of locations can be drawn from Shannon diversity values, a high diversity group which includes Khors Hadibo, Girmah and Quariya, an intermediate diversity group which includes Khors Dubena, Delisha, Sahier, Matief, Rukup and Detwah lagoon, and a low diversity group that includes Khors Bidholeh, Dufega, and Ahren (Fig. 1.6).

Rarefied evenness ranges from 0.17 at Arhen to 0.88 at Khor Hadibo and the site values can be divided in two groups. The first group includes Khor Bidholeh, Dufega and Arhen and is characterized by small evenness values (0.17-0.42) indicating that the distribution of individuals across species is not even, confirming field observations that those locations are dominated by a single species. The second group presents larger evenness values (0.73-0.88) indicating that the distribution of abundances at those locations is equitable across species.

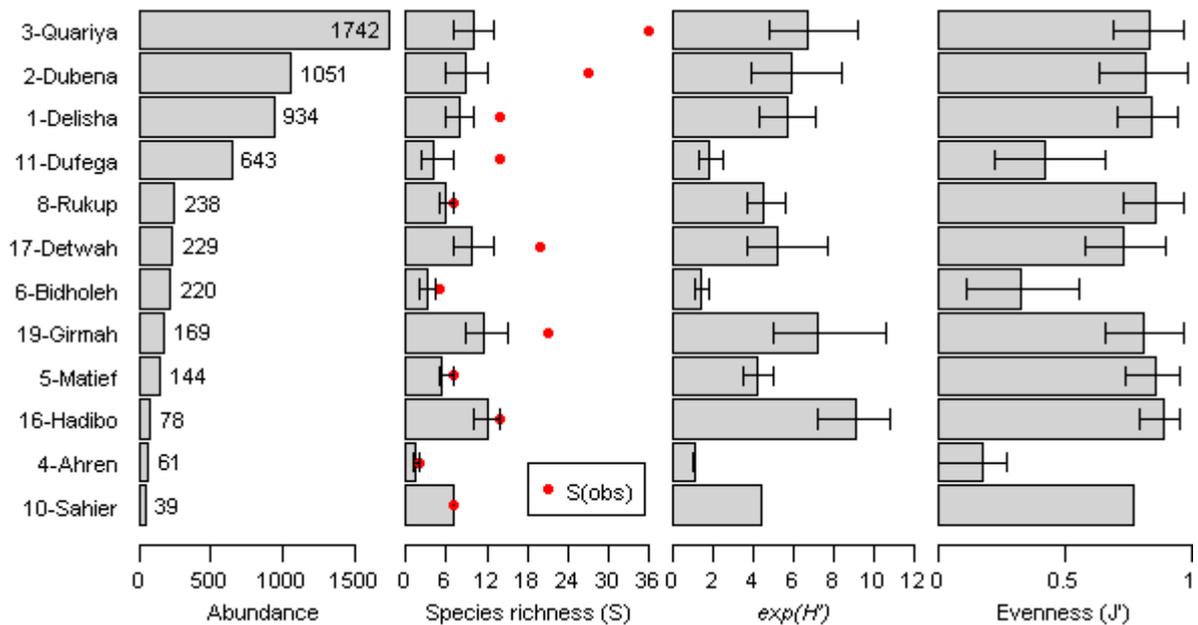
### ***Fish community relatedness among locations***

Ward's hierarchical clustering analysis derived from Hellinger's distances based on species Presence / Absence produced three main groups with Ahren and Detwah lagoon not belonging to any group. Group 1 includes Khors Hadibo, Girmah, Dubena and Quariya, Group 2 includes Khors Delisha, Matief and Bidholeh and Group 3 represents a consistent Yemen mainland community as it includes Khors Dufega, Sahier and Rukup (Fig. 1.7a). Ahren is separated as it hosts only two species while Detwah lagoon is separated as it appears to host marine community of its own kind. The first four axes of the PCA explain 18.1 %, 14.26 %, 13.15 % and 11.31 % respectively of the variance (Fig. 1.7b, c, d), however, it is the first and fourth axes that revealed best the differences in the fish community between the three groups previously determined by the cluster analysis (Fig. 1.7d).

Differences between the groups were supported by ANOSIM ( $r = 0.87, p < 0.001$ ). The first and third axes show that Groups 2 and 3 are characterized by the presence of Mugilidae sp. 1 and *Terapon jarbua*, compared to Group 1 (Fig. 1.7c) and the fourth axis allowed to characterize the Yemen mainland Group 3 by the presence of *Nematalosa arabica* Regan, 1917 at the three locations (Fig. 1.7d).

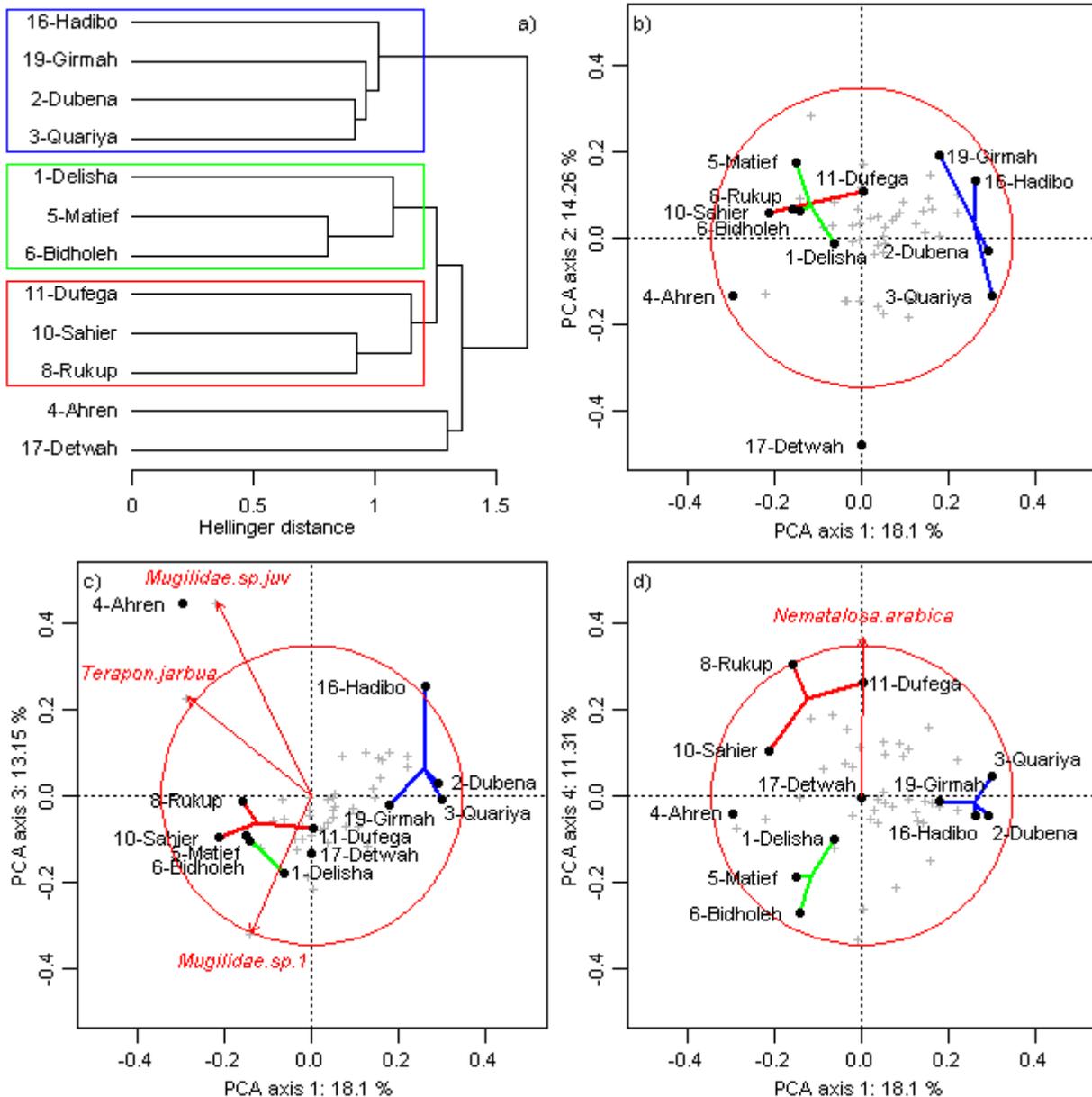
**Table 1.5: Species richness summary**

	Socotra Island	Yemen mainland	All locations
<b>Total species number</b>	64	20	67
<b>Number of sampling locations</b>	12	3	15
<b>Mean species number per location</b>	13.17	9.33	12.40
<b>Maximum species number per location</b>	36	14	36
<b>Minimum species number per location</b>	1	7	1
<b>Standard deviation</b>	10.99	4.04	9.99
<b>Number of families recorded</b>	30	13	31



**Figure 1.6: Representation of abundances and alpha diversities per location**

Alpha diversity (grey bars) represent rarefied values and error bars represent the 95 % confidence interval (1,000 permutations). Species richness (red dots) represent observed values regardless the sampling efforts.



**Figure 1.7: a) Ward hierarchical clustering analysis, b), c) and d) Principal Component Analysis based on species Presence / Absence (ANOSIM:  $r = 0.87$ ,  $p < 0.001$ )**

Analyses were performed after Hellinger transformation calculated from Presence / Absence. Colored rectangles and star like figures represent groups of similar fish communities. Grey crosses represent species, the red circles are the Equilibrium circle and red vectors represent the present species that significantly contributed to the ordination graph (species outside the circle). The equilibrium circle radius and species coordinate have been scaled to fit within the PCA plot dimensions.

Ward's hierarchical clustering analysis derived from Hellinger's distances based on relative species abundance also produced three groups. Group 1 includes Khors Hadibo, Girmah, Dubena and Quariya, Group 2 includes Arhen and Khor Bidholeh and Group 3 includes Khors Delisha, Matief, Dufega, Sahier and Rukup (Fig. 1.8a). Within this last group, the Yemen mainland estuaries cluster again together. The first four axes of the PCA explain 21.16 %, 17.21 %, 15.09 % and 11.63 % respectively of the variance (Fig. 1.8b, c, d), however, it is the first and third axes that revealed best the differences in the fish community between the three groups previously determined by the cluster analysis (Fig. 1.8c). Detwah lagoon appears also here to be isolated from any other locations as shown by the second axis thus confirming its specific fish community dominated by Mugilidae sp. 2 (Fig. 1.8b) and characterized by the presence of reef associated species such as *Gymnothorax thyrsoideus* (Richardson, 1845), *Lethrinus harak* (Forsskål, 1775), *Lethrinus lentjan* (Lacépède, 1802) or *Abudefduf vaigiensis* (Quoy and Gaimard, 1825). Differences between the groups were supported by ANOSIM ( $r = 0.76$ ,  $p < 0.001$ ). To summarize, the first axis describes a gradient of abundance in *Terapon jaubua*, which characterized the three groups, from Group 2 (high abundance) to Group 3 (moderate abundance) and Group 1 (lower abundance) (Fig. 1.8b), while the third axis allows to differentiate the Group 3 from the two others by a higher abundance of Mugilidae sp. 1 (Fig. 1.8c).

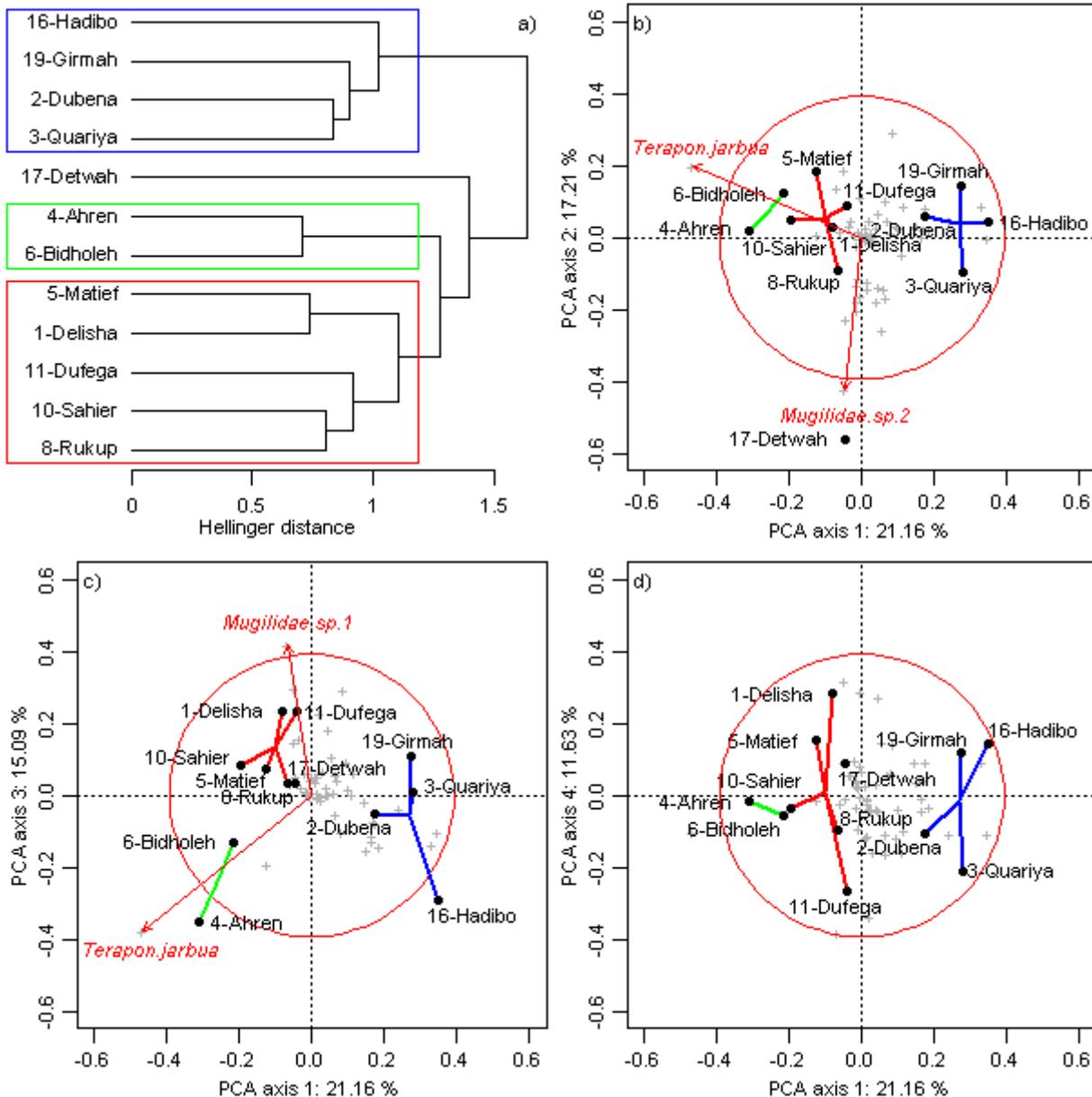
## Discussion

### *Socotra estuarine and lagoon fish community in the context of the Western Indian Ocean*

With some degree of caution due to the different sampling effort, the estuarine and lagoon fish community of Socotra (64 species observed by this study) does not appear to be more diverse than the community of Yemen mainland estuaries (20 species) as the mainland has been sampled at four times less sites than Socotra Island (Table 1.5). However, more species per location were recorded on Socotra Island (13.17) than on Yemen mainland (9.33). In addition, no estuarine species is endemic to Socotra, given that *Gerres socotranus* Steindachner is considered a junior synonym of *G. oyena* (Forsskål, 1775). The actual diversity of Socotra estuaries and lagoons might total 75-80 species. Indeed this tentative estimate considers the additional species included in Steindachner's account and the fact that the individual based taxon-sampling curves indicate insufficient sampling at several sites, thus higher richness than the observed one is expected.

The overall species richness of Socotra is thus marked. However, the highest levels of species richness observed in individual estuaries (21 species in Khor Girmah, 27 in Khor Dubena and 36 in Khor Quariya) are comparable with equivalent subtropical and warm-temperate TOCE's,

e.g.: of the well-researched estuaries of KwaZulu-Natal (South Africa) where Harrison and Whitfield (1995) recorded a total of 68 fish species, with 24 species recorded in Damba, 47 in Mhlanga and 56 in Zotsha.



**Figure 1.8: a) Ward hierarchical clustering analysis, b), c) and d) Principal Component Analysis based on species abundance (ANOSIM:  $r = 0.76, p < 0.001$ )**

Both analyses were performed after Hellinger transformation calculated from the squared root of relative abundances. Colored rectangles and star like figures represent groups of similar fish communities. Grey crosses represent species, the red circles are the Equilibrium circle and red vectors represent species that significantly contributed to the ordination graph (species outside the circle). The equilibrium circle radius and species coordinate have been scaled to fit within the PCA plot dimensions.

The most abundant and frequent taxa of the study region are: *Terapon jarbua* and members of the family Mugilidae. Like the majority of tropical and subtropical marine spawners, they have an extended breeding season and are fractional spawners. To spawn in several batches seems to avoid overcrowding of larvae in order to reduce food competition among the offspring and to allow post larvae to immigrate into TOCE's when connection with seawater occurs (James et al., 2007). Cowley and Whitfield (2001) proposed that such a strategy prevents recruitment failure, and explains the dominance of such species in TOCE's (James et al., 2007). In contrast, many species were present in only a few locations, although they have a wide geographical distribution, indicating an opportunistic behavior in the use of estuaries when their reproductive cycle is in phase with the TOCE's seasonal opening cycle.

Harrison (2005) reviewed the ichthyofauna of 250 coastal outlets in South Africa. His accounts have 15 species in common with our study, thus indicating a wide distribution and a potential connectivity between habitats of these species spanning from the Gulf of Aden to all over the East African coast: *Ambassis dussumieri*, *Sillago* sp., *Caranx heberi* (Bennett, 1830), *Caranx ignobilis* (Forsskål, 1775), *Scomberoides lysan* (Forsskål, 1775), *Leiognathus Equulus* (Forsskål, 1775), *Lutjanus argentimaculatus* (Forsskål, 1775), *Lutjanus fulviflamma* (Forsskål, 1775), *Gerres longirostris* (Lacépède, 1801), *Gerres macracanthus* Bleeker, 1854, *Pomadasys commersonii* (Lacépède, 1801), *Pomadasys kaakan* (Cuvier, 1830), *Monodactylus argenteus* (Linnæus, 1758), *Terapon jarbua* and *Sphyræna jello*. All of these species except *Sphyræna jello* are present in Socotra Island estuaries, while only seven were recorded in Yemen mainland estuaries as well. This provides further support to Socotra's function as a biogeographic "stepping stone" for particular species, as proposed by Kemp (1998), Zajonz et al (2000) and De Vantier et al. (2004). Furthermore, this distribution pattern also suggests that for other species it is not possible to bridge the gap between the African coasts and Socotra and the Eastern Arabian coast. The observation, that about 70% of Socotra's estuarine species have not been recorded from the mainland sites may be attributed to a combination of biogeographic effects, differences in the estuarine ecology, and a sampling bias related to the lower number of study sites at the mainland. Moreover, although this study integrates species accounts from 1999 to 2009, sampling efforts per location and between Socotra and the Yemen mainland were different and restricted to particular seasons (pre- and post-monsoon) due to the difficulty to implement regular surveys. Therefore, conclusions about the absence of particular species should still be taken with caution.

***Comparison of the fish community structure of the estuaries of Socotra and Yemen mainland***

Multivariate techniques of classification and ordination are commonly used to describe species community structure of a particular region (Bennett, 1989; Collie et al., 2008; Nicolas et al., 2010). Results of the present study distinctively differentiated the fish assemblages of Socotra Island and Yemen mainland and clustered them into three groups plus Detwah lagoon, plus Arhen. Presence / Absence analysis reveals a geographical affinity for the three communities: Group 1, a very diverse and evenly distributed community, is restricted to the northern part of Socotra Island; Group 2, a less diverse and evenly distributed community, is restricted to the east and south of the Island, and Group 3 is restricted to the Yemen mainland. The species community analysis based on relative abundance revealed similar patterns, with Group 1 clearly separated from the two others. Clustering patterns for Group 2 and 3 appear to be slightly different between both analyses. This is most probably due to the dominance of few species and the presence of different rare species at some locations. Indeed Presence / Absence based analyses of relatedness grant higher importance to rare species, while abundance based analyses give higher weight to the dominant species. Thus, dominated by *Terapon jarbua*, Arhen and Khor Bidholeh cluster here together in the Group 2. However, locations from Yemen mainland are still clustering together within the Group 3.

Detwah lagoon is the only coastal water basin of Socotra with no freshwater input presenting a unique fish community which strongly differs from all other locations studied on Socotra Island. The high rarefied Shannon diversity value of Khor Hadibo, the most eutrophic estuary studied is presumably related to the presence of *Chara* sp. and filamentous algae, providing hide outs, food and source of prey to Gobiidae and *T. jarbua* (gut content: filamentous algae, fish scales and small crustaceans, personal observation). Surprisingly, the large and permanently open Khor Bidholeh is dominated by *T. jarbua*. This observation casts doubts over the characterization of this species as catadromous species (e.g.: Riede, 2004) since this Khor is a highly energetic coastal indentation with relatively low freshwater input (Salinity: 35 ‰) for most of the year. The previous observation underlines the higher plasticity of *T. jarbua* at the juvenile stage in estuarine systems.

**Conclusions**

The results of this study are the first contribution to the knowledge of estuarine fish community ecology of Socotra Island and Yemen mainland combined with a thorough species inventory. The estuarine fish diversity of Socotra is high by regional comparison and underscores the particular conservation importance of Socotra (Klaus et al., 2003; Simões et al., 2001; Simões and Jones, 2000, Turner et al., 1999), not least in view of its status as UNESCO World Natural

Heritage Site. It mirrors the archipelago's particular position at crossroads between several biogeographical regions and the diversity of the specific ecological conditions of Socotra's estuaries and lagoons. The positive taxonomic identification or revision, respectively, of the existing estuarine fish collections needs to be completed in order to fully appreciate the total diversity and community composition.

The high number of economically relevant species of fish recorded to date, with 18 species being tentatively classified as highly important and 15 as medium important to the local fishery, underscores the paramount importance of these coastal water bodies as spawning and nursery sites, and for the sustainability of vital provisioning ecosystem services. This aspect appears to be poorly understood yet and requires further studies of the general and functional estuarine ecology and fisheries biology in support of appropriate management. Seasonal and annual variation of species assemblages and recruitment patterns need to be investigated in detail in relation to the monsoon regime, depending on meteorological pattern inducing the opening or closing of the estuaries towards the sea.

At present day many of the estuaries appear to come under increasing threat by coastal degradation related to development, road construction isolating them from the sea and eutrophication from household sewerage, requiring remedial action and improved resource use practices. To this end this study represents a faunistic and ecological baseline for the governmental agencies charged with coastal and conservation management on Socotra. The local communities which partly depend on the estuarine resources need to be informed accordingly.

## **Acknowledgments**

The present study was mainly funded by the Total Foundation, Paris. It was partially conducted at the Socotra Field Research Station of the Biodiversity and Climate Research Centre (BiK-F), Frankfurt a.M., based on financial support of the research-funding programme "LOEWE – Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz" of Hesse's Ministry of Higher Education, Research, and the Arts. Additional mobility funds were provided by scholarships from the GRADE - Goethe Graduate Academy of the Goethe University Frankfurt a.M. and the International Doctoral College of the European University of Brittany (UEB). His Excellency the former Minister of Water and Environment of the Republic of Yemen, Eng. Abdul-Rahman F. Al-Eryani, and His Excellency the Chairman of the Environment Protection Authority, Eng. Mahmoud Shidiwa, are cordially acknowledged for their continued support and for granting research and sample export permits. The Socotra Conservation and Development Program (SCDP-UNDP) is thanked for providing indispensable support during the field work. We would like to thank the People of Socotra and in particular the members of the coastal communities which kindly facilitated field work and provided access to the areas in their care. We wish to express our gratitude to Olivier Gauthier for his comments on the ecological statistic work. Jean Laroche is cordially acknowledged for his support to the Ph.D. project of the first author and valuable comments improving the quality of the manuscript.

# Appendix

# 1

**Preliminary species list and abundance per  
location**

---

## Appendix 1: Preliminary species list and abundance per location

Species list	Locations														
	Socotra Island											Yemen mainland			
	1	2	3	4	5	6	16	17	18	19	20	21	8	10	11
<i>S</i>	14	27	36	2	7	5	14	20	3	21	8	1	7	7	14
<i>N</i>	934	1051	1742	61	144	220	78	229	18	169	29	3	238	39	643
<b>Dasyatidae</b>															
<i>Himantura gerrardi</i> (Gray, 1851)	★	.	1	.	.	.	.	.	.	.	.	.	.	.	.
<b>Anguillidae</b>															
<i>Anguilla bicolor</i> McClelland, 1844	★	.	.	.	1	.	.	.	.	.	.	.	.	.	.
<b>Muraenidae</b>															
<i>Gymnothorax</i> sp. Bloch, 1795	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.
<i>Gymnothorax thyrsoideus</i> (Richardson 1845)	★	.	.	.	.	.	.	1	.	.	.	.	.	.	.
<b>Engraulidae</b>															
<i>Thryssa baelama</i> (Forsskål, 1775)	★	.	436	.	.	.	.	.	.	.	.	.	.	.	.
<b>Clupeidae</b>															
<i>Herklotsichthys lossei</i> Wongratana, 1983	★	7	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Herklotsichthys quadrimaculatus</i> (Rüppell, 1837)	★	60	4	.	.	.	4	.	.	.	.	.	.	.	.
<i>Nematalosa arabica</i> Regan, 1917	★	1	58	.	.	.	.	.	.	5	.	.	20	6	26
<b>Plotosidae</b>															
<i>Plotosus lineatus</i> (Thunberg, 1787)	★	.	.	.	.	.	.	.	.	8	.	.	.	.	.
<b>Mugilidae</b>															
<i>Gen. sp. 1</i>	51	202	409	12	6	.	1	.	2	.	.	.	16	4	540
<i>Gen. sp. 2</i>	30	.	4	.	.	.	.	109	.	.	1	.	48	.	.
<i>Gen. sp. 3</i>	.	11	9	.	.	.	20	.	.	25	2	.	.	.	.
<i>Gen. sp. 4</i>	.	116	.	.	.	.	.	.	.	4	.	.	.	.	1
<i>Gen. sp. juv.</i>	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
<b>Atherinidae</b>															
<i>Atherinomorus lacunosus</i> (Forster, 1801)	★	20	15	.	.	.	.	.	7	.	.	.	.	.	2
<b>Hemiramphidae</b>															
<i>Hyporhamphus sindensis</i> (Regan, 1905)	★	194	171	52	32	2	.	.	.	63	6	.	.	.	10
<b>Cyprinodontidae</b>															
<i>Aphanius dispar</i> (Rüppell, 1828)	★	302	.	.	11	2	.	.	.	14	.	3	12	8	2
<b>Syngnathidae</b>															
<i>Gen. sp.</i>	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
<b>Ambassidae</b>															
<i>Ambassis dussumieri</i> (Lacepède, 1802)	★	24	358	.	.	.	14	.	.	16	1	.	52	.	.
<b>Sillaginidae</b>															
<i>Sillago sp.</i> (Forsskål, 1775)	.	9	1	2	.	.	.	.	44	.	1	.	.	.	.
<i>Gen. sp. juv.</i>	.	2	3	.	.	.	.	.	2	.	.	.	.	.	.
<b>Carangidae</b>															
<i>Caranx heberi</i> (Bennett, 1828)	★	20	.	.	.	.	6	.	.	.	.	.	.	.	.
<i>Caranx ignobilis</i> (Forsskål, 1775)	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1
<i>Scomberoides lysan</i> (Forsskål, 1775)	★	.	8	.	.	.	.	.	.	.	.	.	.	.	3
<b>Leiognathidae</b>															
<i>Aurigequula fasciata</i> (Lacepède, 1803)	★	.	67	.	.	.	.	.	1	.	.	.	.	.	.
<i>Leiognathus equulus</i> (Forsskål, 1775)	★	.	.	.	.	.	.	.	.	1	.	.	.	.	.
<i>Gen. sp.</i>	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
<b>Lutjanidae</b>															
<i>Lutjanus argentimaculatus</i> (Forsskål, 1775)	.	1	7	1	.	4	.	.	.	1	.	.	.	.	.
<i>Lutjanus ehrenbergii</i> (Peters, 1879)	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.
<i>Lutjanus fulviflamma</i> (Forsskål, 1775)	★	4	2	.	.	.	.	.	.	1	.	.	.	.	.
<i>Lutjanus fulvus</i> (Foster, 1801)	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.

## Appendix 1 (continued)

Species list	Locations											Yemen mainland					
	Socotra Island											8	10	11			
	1	2	3	4	5	6	16	17	18	19	20				21		
<b>Gerreidae</b>																	
<i>Gerres filamentosus</i> Cuvier, 1829	.	16	26	.	.	11	.	.	.	6	.	.	.	.	.	.	.
<i>Gerres longirostris</i> (Lacepède, 1801)	1	.	8	.	.	.	1	.	.	1	.	.	.	.	.	.	.
<i>Gerres macracanthus</i> Bleeker, 1854	★	1	1	.	.	.	.	.	6	.	.	.	.	.	.	.	.
<i>Gerres oyena</i> (Forsskål, 1775)	.	.	2	.	.	.	.	19	.	.	.	.	.	.	.	1	.
<b>Haemulidae</b>																	
<i>Pomadasys commersonii</i> (Lacepède, 1801)	★	.	1	5	.	.	.	.	5	.	.	.	.	.	.	.	.
<i>Pomadasys kaakan</i> (Cuvier, 1830)	★	.	.	17	.	.	.	.	.	.	2	.	.	.	.	.	2
<i>Pomadasys punctulatus</i> (Rüppell, 1838)	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Pomadasys</i> sp. juv. Lacepède, 1802	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
<b>Lethrinidae</b>																	
<i>Lethrinus harak</i> (Forsskål, 1775)	★	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
<i>Lethrinus lentjan</i> (Lacepède, 1802)	★	.	.	.	.	.	.	10	.	.	.	.	.	.	.	.	.
<i>Lethrinus nebulosus</i> (Forsskål, 1775)	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<b>Sparidae</b>																	
<i>Acanthopagrus berda</i> (Forsskål, 1775)	.	.	8	.	.	.	2	.	.	1	1	.	.	.	.	.	.
<i>Acanthopagrus bifasciatus</i> (Forsskål, 1775)	.	1	11	.	.	.	4	.	.	.	1	.	.	.	.	.	.
<i>Crenidens crenidens</i> (Forsskål, 1775)	★	.	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.
<b>Mullidae</b>																	
<i>Parupeneus</i> sp. Bleeker, 1863	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<b>Monodactylidae</b>																	
<i>Monodactylus argenteus</i> (Linnaeus, 1758)	.	1	70	.	.	.	6	.	.	1	.	.	.	.	.	.	4
<b>Terapontidae</b>																	
<i>Terapon jarbua</i> (Forsskål, 1775)	143	373	129	60	57	200	8	9	.	5	5	.	89	18	46	.	.
<b>Kuhliidae</b>																	
<i>Kuhlia mugil</i> (Forster, 1801)	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<b>Pomacentridae</b>																	
<i>Abudefduf sordidus</i> (Forsskål, 1775)	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Abudefduf vaigiensis</i> (Quoy & Gaimard, 1825)	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.
<b>Scaridae</b>																	
<i>Gen.</i> sp. juv.	.	.	1	.	.	.	.	2	.	.	.	.	.	.	.	.	.
<b>Blenniidae</b>																	
<i>Alticus</i> sp. Lacepède, 1800	.	.	.	.	.	.	.	1	15	.	.	.	.	.	.	.	.
<i>Istiblennius</i> sp. Whitley, 1943	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
<b>Eleotridae</b>																	
<i>Eleotris</i> sp. Bloch & Schneider, 1801	.	6	19	.	.	.	2	.	.	.	.	.	.	.	.	.	.
<b>Gobiidae</b>																	
<i>Gen.</i> sp. 1	35	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
<i>Gen.</i> sp. 2	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Gen.</i> sp. 3	20	6	2	.	30	1	3	1	.	1	12	.	.	.	.	1	.
<i>Gen.</i> sp. 4	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Gen.</i> sp. 5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
<i>Gen.</i> sp. 6	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.
<i>Gen.</i> sp. 7	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Gen.</i> sp. 8	136	.	.	.	.	.	.	.	.	.	10	.	.	.	.	.	.
<b>Sphyraenidae</b>																	
<i>Sphyraena jello</i> Cuvier, 1829	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
<b>Bothidae</b>																	
<i>Bothus</i> sp. Rafinesque, 1810	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.
<b>Tetraodontidae</b>																	
<i>Gen.</i> sp.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.

★ New records for Socotra Island



# Appendix

# 2

**Fish species inventory of Socotra Island and  
Yemen mainland estuaries and lagoon**

---



## Appendix 2: Fish species inventory of Socotra Island and Yemen mainland estuaries and lagoon

### Family **Dasyatidae** (whiptail stingrays)

#### ***Himantura gerrardi*** (Gray, 1851)

*Trygon gerrardi* Gray, 1851. – List of the specimens of fish in the collection of the British Museum. Part I. Chondropterygii. London. Type locality: India.

*Dasyatis gerrardi*. – Dor, 1984; Qing-chao, 1997.

*Himantura gerrardi*. – Bonfil and Abdallah, 2004; Randall and Hoover, 1995.

SPECIMENS EXAMINED: (i) SMF 33652, 1 spm, 285 mm, Khor Quariya, 06/04/2008, leg. E. Lavergne and M. S. Aideed.

Distribution range: from Socotra Island to New Guinea and Japan.

### Family **Anguillidae** (freshwater eels)

#### ***Anguilla bicolor*** McClelland, 1844

*Anguilla bicolor* McClelland, 1844. – Apodal fishes of Bengal. Calcutta Journal of Natural History **5(18)**: 151-226. Type locality: Sandoway, Malay coast, India.

*Anguilla bicolor*. – Morgan et al., 2011; Seegers et al., 2003; Teng et al., 2009).

SPECIMENS EXAMINED: (i) SMF 33653, 1 spm, 174.3 mm, Khor Matief, 16/04/2007, leg. E. Lavergne and U. Zajonz.

Distribution range: from Africa to Western Australia.

### Family **Muraenidae** (moray eels)

#### ***Gymnothorax sp.*** Bloch, 1795

*Gymnothorax sp.* Bloch, 1795. – Naturgeschichte der ausländischen Fische. Berlin (9).

SPECIMENS EXAMINED: (i) SMF 33654, 1 spm, 176.2 mm, Khor Quadub, 18/04/2008, leg. U. Zajonz, (ii) SMF 33655, 1 spm, 231.8 mm, Khor Rukup (Yemen Mainland), 19/04/2008, leg. E. Lavergne and M. S. Aideed.

#### ***Gymnothorax thyrsoideus*** (Richardson, 1845)

*Muraena thyrsoidea* Richardson, 1845. – Ichthyology - Part 2. In Hinds R. B. (Ed.): The zoology of the voyage of H. M. S. Sulphur, under the command of Captain Sir Edward Belcher during the years 1836-42, (9). London: Smith, Elder & Co. Type locality: Canton, Guangdong Province, China, South China Sea, Western Pacific.

*Siderea thyrsoideus*. – Paxton et al., 1989.

*Siderea thyrsoidea*. – Allen and Swainston, 1988; Randall et al., 1997.

*Gymnothorax thyrsoideus*. – Masuda et al., 1984; Randall and Lim, 2000.

SPECIMENS EXAMINED: (i) SMF 33656, 1 spm, 900 mm (size record), Detwah Lagoon, 22/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: Indo-West Pacific.

Family **Engraulidae** (anchovies)

***Thryssa baelama*** (Forsskål, 1775)

*Clupea baelama* Forsskål, 1775. – Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit... Post mortem auctoris edidit Carsten Niebuhr. Hauniae. No locality stated (Red Sea). No types known.

*Thrissina baelama*. – Dor, 1984.

*Thryssa baelama*. – Fischer and Bianchi, 1984; Randall and Hoover, 1995; Whitehead et al., 1988.

SPECIMENS EXAMINED: (i) SMF 33657, 5(18) spms, 55.6-81.5 mm, Khor Quariya, 18/04/2007, leg. E. Lavergne and U. Zajonz, (ii) SMF 33658, 5(18) spms, 39.8-79.4 mm, Khor Quariya, 28/11/2008, leg. E. Lavergne, (iii) SMF 33659/SMF 33560/SMF 33661, 5(>200) spms, 47.1-87.3 mm, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from the Red Sea and East Africa to Australia, New Caledonia and Samoa.

Family **Clupeidae** (herrings)

***Herklotsichthys lossei*** Wongratana, 1983

*Herklotsichthys lossei* Wongratana, 1983. – Diagnoses of 24 new species and proposal of a new name for a species of Indo-Pacific clupeoid fishes. Japanese Journal of Ichthyology, 29(4):385-407. Type locality: Arabian Gulf (Persian Gulf 30°08'N, 46°54'E).

*Herklotsichthys lossei*. – Carpenter et al., 1997; Fischer and Bianchi, 1984; Goren and Dor, 1994; Randall and Hoover, 1995; Smith et al., 2003; Whitehead et al., 1985.

SPECIMENS EXAMINED: (i) SMF 33662, 7 spms, 75.9-84.1 mm, Khor Dubena, 27/11/2008, leg. E. Lavergne.

Remark: According to Randall (1995) *Herklotsichthys lossei* might only be distinct from *H. punctulatus* at the subspecies level.

Distribution range: from the Red Sea to the Arabian Gulf (Persian Gulf).

***Herklotsichthys quadrimaculatus*** (Rüppell, 1838)

*Clupea quadrimaculata* Rüppell, 1838. – Neue Wirbelthiere zu der Fauna von Abyssinien gehörig. Fische des Rothen Meeres. Frankfurt-am-Main. pp. 148. Type locality: Bay of Massawa, Eritrea, Red Sea.

*Herklotsichthys quadrimaculatus*. – Fischer and Bianchi, 1984; Fricke et al., 2009; Randall and Hoover, 1995; Smith et al., 2003; Whitehead et al., 1985.

SPECIMENS EXAMINED: (i) SMF 33663, 4 spms, 60.7-89.5 mm, Shore at Khor Hadibo, 02/1999, leg. U. Zajonz and M. Khalaf, (ii) SMF 33664/SMF 33665/SMF 33666, 5(58) spms, 82-108.4 mm, Khor Dubena, 01/12/2007, leg. E. Lavergne and M. S. Aideed, (iii) SMF 33667, 4 spms, 74.2-79 mm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed.

Distribution range: from the Red Sea, East and South Africa to Japan and the Hawaiian Islands.

***Nematalosa arabica* Regan, 1917**

*Nematalosa arabica* Regan, 1917. – A revision of the clupeoid fishes of the genera *Pomolobus*, *Brevoortia* and *Dorosoma* and their allies. *Annals and Magazine of Natural History (Series 8)* , 19(112):297-316. Type locality: Muscat, Oman, Gulf of Oman, Arabian Sea, North-Western Indian Ocean.

*Nematalosa arabica*. – Fischer and Bianchi, 1984; Nelson and McCarthy, 1995; Nelson and Rothman, 1973; Randall and Hoover, 1995; Smith et al., 2003; Whitehead et al., 1985.

SPECIMENS EXAMINED: (i) SMF 33668, 5 spms, 61.8-111.2 mm, Khor Girmah, 27/02/1999, leg. U. Zajonz and M. Khalaf, (ii) SMF 33669, 5(9) spms, 50.4-67.5 mm, Khor Quariya, 18/04/2007, leg. E. Lavergne and U. Zajonz, (iii) SMF 33670, 1 spm, 144.4 mm, Khor Dubena, 01/12/2007, leg. E. Lavergne and M. S. Aideed, (iv) SMF 33671, 2 spms, 92.8-99.8 mm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (v) SMF 33672, 5(20) spms, 35.6-102.3 mm, Khor Rukup (Yemen Mainland), 19/04/2008, leg. E. Lavergne and M. S. Aideed, (vi) SMF 33673, 6 spms, 91.3-104.7 mm, Khor Sahier (Yemen Mainland), 21/04/2008, leg. E. Lavergne and M. S. Aideed, (vii) SMF 33674, 5(26) spms, 61.6-70.9 mm, Khor Dufega (Yemen Mainland), 24/04/2008, leg. E. Lavergne and M. S. Aideed, (viii) SMF 33675, 5(36) spms, 44.4-52.9 mm, Khor Quariya, 28/11/2008, leg. E. Lavergne, (ix) SMF33676, 5(11) spms, 54.6-106.1 mm, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: North-Western Indian Ocean.

Family **Plotosidae** (eeltail catfishes)

***Plotosus lineatus* (Thunberg, 1787)**

*Silurus lineatus* Thunberg, 1787. – *Museum naturalium Academiae Upsaliensis*. Type locality: Eastern Indian Ocean.

*Plotosus lineatus*. – Fischer and Bianchi, 1984; Golani, 2002; Randall and Hoover, 1995.

SPECIMENS EXAMINED: (i) SMF 33677, 5(8) spms, 33.5-36.5 mm, Khor Girmah, 22/10/2000, leg. F. Krupp and F. Nasseeb.

Distribution range: from the Red Sea, East and South Africa to Japan and New Caledonia; Golani (2002) has reported the species as Lessepsian migrant to the Eastern Mediterranean.

Family **Mugilidae** (mulletts)

***Mugilidae sp. 1***

SPECIMENS EXAMINED: (i) SMF 33678, 5 spm, Khor Girmah, 27/02/1999, leg. U. Zajonz and M. Khalaf, (ii) SMF 33679, 1 spm, Khor Girmah, 12/04/1999, leg. U. Zajonz, (iii) SMF 33680, 54 spms, Khor Dubena, 04/04/2007, leg. E. Lavergne and U. Zajonz, (iv) SMF 33681, 17 spms, Khor Delisha, 05/04/2007, leg. E. Lavergne and U. Zajonz, (v) SMF 33682, 21 spms, Khor Dubena, 05/04/2007, leg. E. Lavergne and U. Zajonz, (vi) SMF 33683/ SMF 33684, 21 spms, Khor Delisha, 09/04/2007, leg. E. Lavergne and U. Zajonz, (vii) SMF 33685, 77 spms, Khor Quariya, 18/04/2007, leg. E. Lavergne and U. Zajonz, (viii) SMF 33686, 7 spms, Khor Dubena, 01/12/2007, leg. E. Lavergne and M. S. Aideed, (ix) SMF 33687, 3 spms, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (x) SMF 33688, 9 spms, Khor Matief, 11/12/2007, leg. E. Lavergne and M. S. Aideed, (xi) SMF 33689, >100 spms, Khor Quariya, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (xii) SMF 33690, 20 spms, Khor Dubena, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (xiii) SMF 33691/ SMF 33692, 9 spms, Khor Delisha, 07/04/2008, leg. E. Lavergne and M. S. Aideed, (xiv) SMF 33693, 3 spms, Khor Matief, 13/04/2008, leg. E. Lavergne and M. S. Aideed, (xv) SMF 33694, 6 spms, Khor Bidholeh, 13/04/2008, leg.

E. Lavergne and M. S. Aideed, (xvi) SMF 33695, 16 spms, Khor Rukup (Yemen Mainland), 19/04/2008, leg. E. Lavergne and M. S. Aideed, (xvii) SMF 33696, 4 spms, Khor Sahier (Yemen Mainland), 21/04/2008, leg. E. Lavergne and M. S. Aideed, (xviii) SMF 33697/SMF 33698, 540 spms, Khor Dufega (Yemen Mainland), 24/04/2008, leg. E. Lavergne and M. S. Aideed, (xix) SMF 33699, >100 spms, Khor Dubena, 27/11/2008, leg. F. Krupp and F. Nasseeb, (xx) SMF 33700, 129 spms, Khor Quariya, 28/11/2008, leg. E. Lavergne, (xxi) SMF 33701, 4 spms, Khor Delisha, 29/11/2008, leg. E. Lavergne, (xxii) SMF 33702, 1 spm, Detwah Lagoon, 22/03/2009, leg. E. Lavergne and U. Zajonz, (xxiii) SMF 33703, >100 spms, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

### **Mugilidae sp. 2**

SPECIMENS EXAMINED: (i) SMF 33704, 58 spms, Detwah Lagoon, 20/04/1999, leg. E. Lavergne and M. S. Aideed, (ii) SMF 33705, >50 spms, Detwah Lagoon, 19/04/2000, leg. U. Zajonz and F. A. Saleh, (iii) SMF 33706, 1 spms, Khor Si-irhim (east of Hadibo), 28/10/2000, leg. F. Krupp and F. Nasseeb, (iv) SMF 33707, 30 spms, Khor Delisha, 09/04/2007, leg. E. Lavergne and U. Zajonz, (v) SMF 33708, 2 spms, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (vi) SMF 33709, 48 spms, Khor Rukup (Yemen Mainland), 19/04/2008, leg. E. Lavergne and M. S. Aideed, (vii) SMF 33710, 5 spms, Detwah Lagoon, 12/03/2009, leg. E. Lavergne and U. Zajonz, (viii) SMF 33711, 2 spms, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

### **Mugilidae sp. 3**

SPECIMENS EXAMINED: (i) SMF 33712, 25 spms, Khor Girmah, 22/10/2000, leg. F. Krupp, F. Nasseeb and A. Plaga, (ii) SMF 33713, 3 spms, Khor Quariya, 24/10/2000, leg. F. Krupp and F. Nasseeb, (iii) SMF 33714, 20 spms, Khor Hadibo, 28/10/2000, leg. F. Krupp and F. Nasseeb, (iv) SMF 33715, 2 spms, Khor Si-irhim, 28/10/2000, leg. F. Krupp and F. Nasseeb, (v) SMF 33716, 6 spms, Khor Quariya, 29/10/2000, leg. F. Krupp and F. Nasseeb, (vi) SMF 33717, 7 spms, Khor Dubena, 29/10/2000, leg. F. Krupp and F. Nasseeb, (vii) SMF 33718/ SMF 33719, >50 spms, Khor Dubena, 01/12/2007, leg. E. Lavergne and M. S. Aideed.

### **Mugilidae sp. 4**

SPECIMENS EXAMINED: (i) SMF 33720/SMF 33721, 4 spms, Khor Girmah, 12/04/1999, leg. U. Zajonz, (ii) SMF 33722, 116 spms, Khor Dubena, 05/04/2007, leg. E. Lavergne and U. Zajonz, (iii) SMF 33723, 1 spm, Khor Dufega (Yemen Mainland), 24/04/2008, leg. E. Lavergne and M. S. Aideed.

### **Mugilidae sp. juv.**

SPECIMENS EXAMINED: (i) SMF 33724, 1 spm, IT-A7/N49, 07/02/1999, leg. U. Zajonz, (ii) SMF 33725, 1 spm, Khor Arhan, 18/04/2007, leg. E. Lavergne and U. Zajonz.

## Family **Atherinidae** (Old World silversides)

### ***Atherinomorus lacunosus*** (Forster, 1801)

*Atherina lacunosa* Forster, 1801. – in: Bloch, M. E. and Schneider J. G. (Eds.) (1801): Systema Ichthyologiae. Type locality: Balade, Province Nord, North-Eastern Grande Terre, New Caledonia, South-Western Pacific.

*Atherinomorus lacunosus*. – Fischer and Bianchi, 1984; Masuda et al., 1984; Randall and Hoover, 1995. Carpenter et al., 1997; Goren and Dor, 1994.

SPECIMENS EXAMINED: (i) SMF 33726, 5(17) spms, 71.3-80.8 mm, Khor Dubena, 01/12/2007, leg. E. Lavergne, (ii) SMF 33727, 5(15) spms, 34.8-68.8 mm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (iii) SMF 33728, 1 spm, 45.3 mm, Khor Dubena, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (iv) SMF 33729, 2 spms, 38 mm, Khor Dufega (Yemen Mainland), 24/04/2008, leg. E. Lavergne and M. S. Aideed, (v) SMF 33730, 2 spms, 354.9-35.9 mm, Khor Dubena, 27/11/2008, leg. E. Lavergne, (vi) SMF 33731, 5(7) spms, 53.5-59.3 mm, Detwah Lagoon, 22/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from the Red Sea and East Africa to Japan and the Hawaiian Islands; (2002; Bucciarelli et al., ) and (2006; Ben Souissi et al., ) have reported the species as Lessepsian migrant to the Eastern and central Mediterranean.

### Family **Hemiramphidae** (halfbeaks)

#### ***Hyporhamphus sindensis*** (Regan, 1905)

*Hemirhamphus sindensis*, Regan, 1905. – On fishes from the Persian Gulf, the Sea of Oman, and Karachi, collected by Mr. F. W. Townsend. Journal of the Bombay Natural History Society, **16**:318–333. Type locality: Karachi, Pakistan.

*Hemirhamphus sindensis*. – Coad, 1991.

*Hyporhamphus sindensis*. – Carpenter et al., 1997; Collette, 2004; Parin et al., 1980; Randall and Hoover, 1995.

SPECIMENS EXAMINED: (i) SMF 33732/SMF 33733, 10(51) spms, 24.3-104.6 mm, Khor Girmah, 27/02/1999, leg. U. Zajonz and M. Khalaf, (ii) SMF 33734, 5(11) spms, 47.6-90.8 mm, Khor Girmah<sup>2</sup>, 13/04/1999, leg. U. Zajonz, (iii) SMF 33735, 1 spm, 108.2 mm, Khor Girmah, 22/10/2000, leg. F. Krupp and F. Nasseeb, (iv) SMF 33736, 5 spms, 62.3-73.72 mm, Khor Si-irhim (east of Hadibo), 28/10/2000, leg. F. Krupp and F. Nasseeb, (v) SMF 33737, 1 spm, 94.44 mm, Khor Si-irhim, 28/10/2000, leg. F. Krupp and F. Nasseeb, (vi) SMF 33738, 1 spm, 98.7 mm, Khor Dubena, 04/04/2007, leg. E. Lavergne and U. Zajonz, (vii) SMF 33739, 5(26) spms, 63.7-132.1 mm, Khor Dubena, 05/04/2007, leg. E. Lavergne and U. Zajonz, (viii) SMF 33740, 5(12) spms, 62.1-124.1 mm, Khor Delisha, 05/04/2007, leg. E. Lavergne and U. Zajonz, (ix) SMF 33741, 1 spm, 79.2 mm, Khor Quariya, 18/04/2007, leg. E. Lavergne and U. Zajonz, (x) SMF 33742, 5 spms, 76.4-100.4 mm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (xi) SMF 33743, 5(10) spms, 60.9-113.9 mm, Khor Matief, 11/12/2007, leg. E. Lavergne and M. S. Aideed, (xii) SMF 33744, 5(44) spms, 43.3-119.9 mm, Khor Dubena, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (xiii) SMF 33745, 5(>100) spms, 54-111.6 mm, Khor Delisha, 07/04/2008, leg. E. Lavergne and M. S. Aideed, (xiv) SMF 33746, 2 spms, 54-72.1 mm, Khor Bidholeh, 13/04/2008, leg. E. Lavergne and M. S. Aideed, (xv) SMF 33747, 5(22) spms, 68.2-102.5 mm, Khor Matief, 13/04/2008, leg. E. Lavergne and M. S. Aideed, (xvi) SMF 33748, 5(10) spms, 27.9-61.3 mm, Khor Dufega (Yemen Mainland), 24/04/2008, leg. E. Lavergne and M. S. Aideed, (xvii) SMF 33749, 5(10) spms, 71-90.9 mm, Khor Dubena, 27/11/2008, leg. E. Lavergne, (xviii) SMF 33750, 5(26) spms, 44.6-109.84 mm, Khor Quariya, 28/11/2008, leg. E. Lavergne, (xix) SMF 33751, 5(10) spms, 64.7-134.3 mm, Khor Delisha, 29/11/2008, leg. E. Lavergne, (xx) SMF 33752, 5(20) spms, 80.8-96.2 mm, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from Socotra Island to the Arabian Sea and Persian Gulf (Pakistan).

Family **Cyprinodontidae** (pupfishes)

***Aphanius dispar*** (Rüppell, 1829)

*Lebias dispar* Rüppell, 1829. – Atlas zu der Reise im nördlichen Afrika. Fische des Rothen Meers. Frankfurt am Main (Heinrich Ludwig Brönnner), 1-141. Type locality: Red Sea.

*Lebias dispar*. – Bilecenoglu et al., 2002; Coad, 1996.

*Aphanius dispar*. – Banister and Clarke, 1977; Carpenter et al., 1997; Coad, 1991; Dor, 1984; Goren and Dor, 1994; Krupp, 1983, 1988; Krupp and Schneider, 1989; Randall and Hoover, 1995.

SPECIMENS EXAMINED: (i) SMF 33753, 5(11) spms, 23.9-44.7 mm, Khor Girmah, 27/02/1999, leg. U. Zajonz and M. Khalaf, (ii) SMF 33754, 2 spms, 38.3-39.5 mm, Khor Girmah, 12/04/1999, leg. M. Apel, (iii) SMF 33755, 1 spm, 32.8 mm, Khor Girmah, 14/04/1999, leg. U. Zajonz, (iv) SMF 33756, 3 spms, 25.6-28.7 mm, Wadi Daneghan,, 21/10/2000, leg. F. Krupp and F. Nasseeb, (v) SMF 33757, 2 spms, 28.2-38.8 mm, Khor Hadibo, 28/10/2000, leg. F. Krupp and F. Nasseeb, (vi) SMF 33758, 5(47) spms, 19.4-46.7 mm, Khor Delisha, 05/04/2007, leg. E. Lavergne and U. Zajonz, (vii) SMF 33759, 5(28) spms, 21.4-52.6 mm, Khor Delisha, 09/04/2007, leg. E. Lavergne and U. Zajonz, (viii) SMF 33760, 5(103) spms, 24.2-48.8 mm, Khor Delisha, 03/12/2007, leg. E. Lavergne and M. S. Aideed, (ix) SMF 33761, 1 spm, 27.7 mm, Khor Matief, 11/12/2007, leg. E. Lavergne and M. S. Aideed, (x) SMF 33762, 5(105) spms, 12.9-55.6 mm, Khor Delisha, 07/04/2008, leg. E. Lavergne and M. S. Aideed, (xi) SMF 33763, 5(10) spms, 28.63-88.9 mm, Khor Matief, 13/04/2008, leg. E. Lavergne and M. S. Aideed, (xii) SMF 33764, 5(12) spms, 19.16-86.1 mm, Khor Rukup (Yemen Mainland), 19/04/2008, leg. E. Lavergne and M. S. Aideed, (xiii) SMF 33765, 5(8) spms, 18.7-42.4 mm, Khor Sahier (Yemen Mainland), 21/04/2008, leg. E. Lavergne and M. S. Aideed, (xiv) SMF 33766, 2 spms, 40.19-43.8 mm, Khor Dufega (Yemen Mainland), 24/04/2008, leg. E. Lavergne and M. S. Aideed, (xv) SMF 33767, 5(19) spms, 36.2-51.2 mm, Khor Delisha, 29/11/2008, leg. E. Lavergne.

Distribution range: from the Mediterranean Sea to the Red Sea and the Northern Indian Ocean; *A. dispar* was considered to be a Lessepsian migrant but (1976; Kornfield and Nevo, demonstrated through electrophoretic analysis of Red Sea and Mediterranean Sea populations that its presence in the Mediterranean Sea preceded the opening of the Suez Canal.

Family **Syngnathidae** (pipefishes and seahorses)

**Syngnathidae** *Sp.*

SPECIMENS EXAMINED: (i) SMF 33768, 1 spm, 1 mm, Detwah Lagoon, 19/04/2000, leg. U. Zajonz and F. A. Saleh.

Family **Ambassidae** (Asiatic glassfishes)

***Ambassis dussumieri*** Cuvier, 1828

*Ambassis dussumieri*, Cuvier in: Cuvier and Valenciennes, 1828. – Histoire naturelle des poissons - Tome 2. Des poissons de la famille des perches, ou des percoides, xxi-490 pp. Type locality: Malabar, India.

*Ambassis dussumieri*. – Allen in: Anderson and Heemstra, 2003; Harrison, 2005; Heemstra and Heemstra, 2004; Manilo and Bogorodsky, 2003; Randall and Lim, 2000.

SPECIMENS EXAMINED: (i) SMF 33769, 5(15) spms, 45.7-60.5 mm, Khor Girmah, 27/02/1999, leg. U. Zajonz and M. Khalaf, (ii) SMF 33770, 1 spm, 37.8 mm, Khor Girmah, 22/10/2000, leg. F. Krupp and F. Nasseeb, (iii) SMF 33771, 1 spm, 53.2 mm, Khor Si-irhim (east of Hadibo), 28/10/2000, leg. F. Krupp and F. Nasseeb, (iv) SMF 33772, 5(14) spms, 49.4-60.65 mm, Khor Hadibo, 28/10/2000, leg. F. Krupp and F. Nasseeb, (v) SMF 33773, 5(24) spms, 37.1-43.3 mm, Khor Dubena, 29/10/2000, leg. F. Krupp and F. Nasseeb, (vi) SMF 33774, 5(102) spms, 31.7-57.9 mm, Khor Quariya, 18/04/2007, leg. E. Lavergne and U. Zajonz, (vii) SMF 33775, 5(101) spms, 32.3-56.4 mm, Khor Quariya, 18/04/2007, leg. E. Lavergne and U. Zajonz, (viii) SMF 33776, 7 spms, 40.6-53.3 mm, Khor Quariya, 18/04/2007, leg. E. Lavergne and U. Zajonz, (ix) SMF 33777, 5(50) spms, 46.4-58.9 mm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (x) SMF 33778, 5(38) spms, 46.7-58.5 mm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (xi) SMF 33779, 1 spm, 56.1 mm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (xii) SMF 33780, 5(12) spms, 46.8-59.1 mm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (xiii) SMF 33781, 5(16) spms, 39.1-54.4 mm, Khor Quariya, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (xiv) SMF 33782, 4 spms, 39.5-55.6 mm, Khor Quariya, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (xv) SMF 33783, 5(45) spms, 40.3-52.1 mm, Khor Rukup (Yemen Mainland), 19/04/2008, leg. E. Lavergne and M. S. Aideed, (xvi) SMF 33784, 7 spms, 40.2-51.4 mm, Khor Rukup (Yemen Mainland), 19/04/2008, leg. E. Lavergne and M. S. Aideed, (xvii) SMF 33785, 5(27) spms, 29.0-57.4 mm, Khor Quariya, 28/11/2008, leg. E. Lavergne.

Distribution range: from the Red Sea, East and South Africa to China.

#### Family **Sillaginidae** (sillagos)

##### ***Sillago* sp.** Cuvier, 1816

*Sillago* sp. Cuvier, 1816. – Le Règne Animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Edition1, xviii-532 pp.

SPECIMENS EXAMINED: (i) SMF 33786, 12 spms, Detwah Lagoon, 19/04/2000, leg. U. Zajonz and F. A. Saleh, (ii) SMF 33787, 1 spm, Khor Girmah, 22/10/2000, leg. F. Krupp and F. Nasseeb, (iii) SMF 33788, 1 spm, Khor Dubena, 04/04/2007, leg. E. Lavergne and U. Zajonz, (iv) SMF 33789, 9 spms, Khor Delisha, 05/04/2007, leg. E. Lavergne and U. Zajonz, (v) SMF 33790, 2 spms, Khor Quariya, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (vi) SMF 33791, 32 spms, Detwah Lagoon, 22/03/2009, leg. E. Lavergne and U. Zajonz.

Remark: Specimens are probably *Sillago sihama* (Forsskål, 1775) and/or *Sillago arabica* McKay and McCarthy, 1989, precise identification requires specimen dissection. Moreover (2011; Golani et al., ) have recently rehabilitated *Sillago erythraea* Cuvier, 1829 and redescribed *Sillago sihama*. Additional work on the specimens is required.

##### ***Sillago* sp. juv.** Cuvier, 1816

*Sillago* sp. Cuvier, 1816. – Le Règne Animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Edition1, xviii-532 pp.

SPECIMENS EXAMINED: (i) SMF 33792, 2 spms, Detwah Lagoon, 19/04/2000, leg. U. Zajonz and F. A. Saleh, (ii) SMF 33793, 2 spms, Khor Dubena, 27/11/2008, leg. E. Lavergne, (iii) SMF 33794, 3 spms, Khor Quariya, 28/11/2008, leg. E. Lavergne.

Family **Carangidae** (jacks and pompanos)

***Caranx heberi*** (Bennett, 1830)

*Scomber heberi* (Bennett, 1830). – A selection from the most remarkable and interesting fishes found on the coast of Ceylon. First Edition. London. No types known.

*Caranx heberi*. – Carpenter et al., 1997; Fischer and Bianchi, 1984; Khalaf and Krupp, 2003; Motomura et al., 2007; Randall and Hoover, 1995.

SPECIMENS EXAMINED: (i) SMF 33795, 6 spms, 138.6-183.1 mm, Khor Hadibo, 28/10/2000, leg. F. Krupp and F. Nasseeb, (ii) SMF 33796, 1 spm, 67.1 mm, Khor Dubena, 04/04/2007, leg. E. Lavergne and U. Zajonz, (iii) SMF 33797, 1 spm, Khor Dubena, 05/04/2007, leg. E. Lavergne and U. Zajonz, (iv) SMF 33798, 5(9) spms, 81.3-92.9 mm, Khor Dubena, 01/12/2007, leg. E. Lavergne and M. S. Aideed, (v) SMF 33799, 1 spm, 98.4 mm, Khor Dubena, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (vi) SMF 33800, 5(8) spms, 140.0-171.5 mm, Khor Dubena, 27/11/2008, leg. E. Lavergne.

Distribution range: from the Red Sea, East and South Africa to Australia and Japan.

***Caranx ignobilis*** (Forsskål, 1775)

*Scomber ignobilis* Forsskål, 1775. – Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit... Post mortem auctoris edidit Carsten Niebuhr. Hauniae. Type locality: Jeddah, Saudi Arabia, Red Sea; Al-Luhayya, Yemen, Red Sea.

*Caranx ignobilis*. – Carpenter et al., 1997; Dor, 1984; Goren and Dor, 1994; Kyushin et al., 1977; Randall, 2007; Randall and Hoover, 1995.

SPECIMENS EXAMINED: (i) SMF 33801, 1 spm, 102.2 mm, Khor Quariya, 04/12/2007, leg. E. Lavergne and M. S. Aideed, (ii) SMF 33802, 1 spm, Khor Dufega, 24/04/2008, leg. E. Lavergne and M. S. Aideed.

Distribution range: from the Red Sea and East Africa to Japan, Australia and the Hawaiian Islands.

***Scomberoides lysan*** (Forsskål, 1775)

*Scomber lysan* Forsskål, 1775. – Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit... Post mortem auctoris edidit Carsten Niebuhr. Hauniae. Type locality: Jeddah, Saudi Arabia, Red Sea, or Al-Luhayya, Yemen, Red Sea.

*Scomberoides lysan*. – Dor, 1984; Ho and Shao, 2011; Paxton et al., 1989; Randall, 2007; Randall and Hoover, 1995; Smith-Vaniz and Staiger, 1973.

SPECIMENS EXAMINED: (i) SMF 33803, 1 spm, 137.1 mm, Khor Quariya, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (ii) SMF 33804, 3 spms, 37.1-57.48 mm, Khor Dufega (Yemen Mainland), 24/04/2008, leg. E. Lavergne and M. S. Aideed, (iii) SMF 33805, 4 spms, 71.8-79.97 mm, Khor Quariya, 25/11/2008, leg. E. Lavergne, (iv) SMF 33806, 3 spms, 101.6-123.9 mm, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from the Red Sea, East and South Africa to Australia, Japan and the Hawaiian Islands.

Family **Leiognathidae** (ponyfishes, slimys, or slipmouths)

***Leiognathus Equulus*** (Forsskål, 1775)

*Scomber equula* Forsskål, 1775. – Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit... Post mortem auctoris edidit Carsten Niebuhr. Haunia. Type locality: Al-Luhayya, Yemen, Red Sea.

*Leiognathus Equulus*. – Abraham et al., 2011; Chakrabarty et al., 2009; Chakrabarty et al., 2010; Dor, 1984; Fischer and Bianchi, 1984; Goren and Dor, 1994; Harrison, 2005; Randall and Hoover, 1995.

SPECIMENS EXAMINED: (i) SMF 33807, 1 spm, 113.3 mm, Khor Girmah, 27/02/1999, leg. U. Zajonz and M. Khalaf.

Distribution range: from the Red Sea, East and South Africa to Australia and Japan.

***Aurigequula fasciata*** (Lacépède, 1803)

*Clupea fasciata* Lacépède, 1803. – Histoire naturelle des poissons. v.5, pp 803. Type locality: Mauritius, Mascarenes, south-Western Indian Ocean.

*Leiognathus fasciatus*. – Coad, 1991; Dor, 1984; Fischer and Bianchi, 1984; Goren and Dor, 1994; Kyushin et al., 1977; Randall and Hoover, 1995.

*Aurigequula fasciata*. – Abraham et al., 2011; Chakrabarty et al., 2009; Chakrabarty et al., 2010.

SPECIMENS EXAMINED: (i) SMF 33808, (5)21 spms, 27.8-63.69 mm, Khor Quariya, 18/04/2007, leg. E. Lavergne and U. Zajonz, (ii) SMF 33809, 1 spm, 94.3 mm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (iii) SMF 33810, 5(45) spms, 32.7-74.5 mm, Khor Quariya, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (iv) SMF 33811, 1 spm, Detwah Lagoon, 22/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from the Red Sea, East Africa to Australia, Samoa and Japan.

***Leiognathidae sp.***

SPECIMENS EXAMINED: (i) SMF 33812, 1 spm, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

Family **Lutjanidae** (snappers)

***Lutjanus argentimaculatus*** (Forsskål, 1775)

*Sciaena argentimaculata* Forsskål, 1775. – Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit... Post mortem auctoris edidit Carsten Niebuhr. Haunia. Type locality: Red Sea. No types known.

*Lutjanus argentimaculatus*. – Allen, 1985; Carpenter et al., 1997; Dor, 1984; Fischer and Bianchi, 1984; Goren and Dor, 1994; Kyushin et al., 1977; Randall and Hoover, 1995; Smith et al., 2003.

SPECIMENS EXAMINED: (i) SMF 33813, 1 spm, 91.8 mm, Khor Girmah, 22/10/2000, leg. F. Krupp and F. Nasseeb, (ii) SMF 33814, 4 spms, 77.1-102.8 mm, Khor Hadibo, 28/10/2000, leg. F. Krupp and F. Nasseeb, (iii) SMF 33815, 3 spms, 56.1-95.1 mm, Khor Quariya, 29/10/2000, leg. F. Krupp and F. Nasseeb, (iv) SMF 33816, 1 spm, 216 mm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (v) SMF 33817, 1 spm, 148.4 mm, Khor Matief, 11/12/2007, leg. E. Lavergne and M. S. Aideed, (vi) SMF 33818, 2 spms, 136.8-158.8 mm, Khor Quariya, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (vii) SMF 33819, 1 spm, 182 mm, Khor Dubena, 27/11/2008, leg. E. Lavergne, (viii) SMF 33820, 1 spm, 152.8 mm, Khor Quariya, 28/11/2008, leg. E. Lavergne.

Distribution range: from the Red Sea and East Africa to Australia to Japan; Golani (1998) has reported the species as Lessepsian migrant to the Eastern Mediterranean.

***Lutjanus ehrenbergii*** (Peters, 1869)

*Mesoprion ehrenbergii* Peters, 1869. – Über neue oder weniger bekannte Fische des Berliner Zoologischen Museums. Monatsberichte der Königlich Preuss[ischen] Akademie der Wissenschaften zu Berlin, 703-711. Type locality: Massawa, Eritrea, Red Sea.

*Lutjanus ehrenbergii*. – Allen, 1985; Carpenter et al., 1997; Dor, 1984; Fischer and Bianchi, 1984; Goren and Dor, 1994; Randall and Hoover, 1995; Smith et al., 2003.

SPECIMENS EXAMINED: (i) SMF 33821, 2 spms, 80.6-93.3 mm, Khor Hadibo, 28/10/2000, leg. F. Krupp and F. Nasseeb.

Distribution range: from the Red Sea and East Africa to Australia, Fiji and Japan.

***Lutjanus fulviflamma*** (Forsskål, 1775)

*Sciaena fulviflamma* Forsskål, 1775. – Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit... Post mortem auctoris edidit Carsten Niebuhr. Hauniae. No locality stated (Red Sea).

*Lutjanus fulviflamma*. – Allen, 1985; Dor, 1984; Fischer and Bianchi, 1984; Goren and Dor, 1994; Harrison, 2005; Masuda et al., 1984; Randall and Hoover, 1995; Smith et al., 2003.

SPECIMENS EXAMINED: (i) SMF 33822, 1 spm, 72 mm, Khor Girmah, 22/10/2000, leg. F. Krupp and F. Nasseeb, (ii) SMF 33823, 3 spms, 107.6-119.4 mm, Khor Dubena, 05/04/2007, leg. E. Lavergne and U. Zajonz, (iii) SMF 33824, 1 spm, 101.3 mm, Khor Quariya, 04/12/2007, leg. E. Lavergne and M. S. Aideed, (iv) SMF 33825, 1 spm, 103.4 mm, Khor Quariya, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (v) SMF 33826, 1 spm, 121.3 mm, Khor Dubena, 27/11/2008, leg. E. Lavergne.

Distribution range: from the Red Sea, South and East Africa to Australia, Japan and Tonga.

***Lutjanus fulvus*** (Forster, 1801)

*Holocentrus fulvus* Forster, 1801. – In: Bloch M. E. and Schneider J. G. (Eds.): Systema Ichthyologiae. Type locality: Tahiti, Society Islands, French Polynesia, South Pacific.

*Lutjanus fulvus*. – Allen, 1985; Fischer and Bianchi, 1984; Goren and Dor, 1994; Masuda et al., 1984; Randall, 2007; Randall and Hoover, 1995; Smith et al., 2003.

SPECIMENS EXAMINED: (i) SMF 33827, 1 spm, 87.4 mm, Khor Quariya, 04/12/2007, leg. E. Lavergne and M. S. Aideed.

Distribution range: from East Africa to Australia, Japan and the Hawaiian Islands.

### Family **Gerreidae** (mojarras)

#### ***Gerres filamentosus*** Cuvier, 1829

*Gerres filamentosus* Cuvier, 1829. – Le Règne Animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Edition 2, xv-406. Type locality: Vanikoro Island, Santa Cruz Islands, Solomon Islands, South-Western Pacific (11°37'S, 166°58'E).

*Gerres filamentosus*. – Allen, 1985; Allen, 1991; Carpenter et al., 1997; Dor, 1984; Fischer and Bianchi, 1984; Goren and Dor, 1994; Iwatsuki et al., 1996; Iwatsuki et al., 2001b; Randall and Hoover, 1995; Smith et al., 2003.

SPECIMENS EXAMINED: (i) SMF 33828, 6 spms, 40.2-59.4 mm, Khor Girmah, 27/02/1999, leg. U. Zajonz and M. Khalaf, (ii) SMF 33829, 5 spms, 51.7-55.9 mm, Khor Dubena, 04/04/2007, leg. E. Lavergne and U. Zajonz, (iii) SMF 33830, 4 spms, 55.3-68.8 mm, Khor Dubena, 05/04/2007, leg. E. Lavergne and U. Zajonz, (iv) SMF 33831, 12 spms, 31.3-36.8 mm, Khor Quariya, 18/04/2007, leg. E. Lavergne and U. Zajonz, (v) SMF 33832, 1 spm, 138.9 mm, Khor Dubena, 01/12/2007, leg. E. Lavergne and M. S. Aideed, (vi) SMF 33833, 3 spms, 90.5-104.4 mm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (vii) SMF 33834, 6 spms, 55.2-69.4 mm, Khor Dubena, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (viii) SMF 33835, 5 spms, 44.5-61.4 mm, Khor Quariya, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (ix) SMF 33836, 11 spms, 40.2-59.4 mm, Khor Bidholeh, 13/04/2008, leg. E. Lavergne and M. S. Aideed, (x) SMF 33837, 6 spms, 34.3-72.5 mm, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from the Red Sea and East Africa to Australia, Japan and Fiji.

#### ***Gerres longirostris*** (Lacépède, 1801)

*Labrus ngirostris* Lacépède, 1801. – Histoire naturelle des poissons, pp 558. Type locality: Madagascar, Western Indian Ocean.

*Gerres acinaces*. - Bleeker 1854 #4 /noper} Carpenter et al., 1997; Dor, 1984; Fischer and Bianchi, 1984; Goren and Dor, 1994; Iwatsuki et al., 1999a; Masuda et al., 1984; Randall and Hoover, 1995.

*Gerres argyreus*. – Forster, 1801, Woodland in: Carpenter and Niem, 1999; Fischer and Bianchi, 1984.

*Gerres longirostris*. – Allen and Adrim, 2003; Harrison, 2005; Heemstra and Heemstra, 2004; Iwatsuki and Heemstra, 2001, 2007; Iwatsuki et al., 2001c; Randall, 2005; Randall et al., 2003.

SPECIMENS EXAMINED: (i) SMF 33838, 1 spm, 89.1 mm, Khor Girmah, 27/02/1999, leg. U. Zajonz and M. Khalaf, (ii) SMF 33839, 1 spm, 94 mm, Khor Hadibo, 28/10/2000, leg. F. Krupp and F. Nasseeb, (iii) SMF 33840, 7 spms, 54.2-82.0 mm, Khor Quariya, 29/10/2000, leg. F. Krupp and F. Nasseeb, (iv) SMF 33841, 1 spm, 73.7 mm, Khor Delisha, 09/04/2007, leg. E. Lavergne and U. Zajonz, (v) SMF 33842, 11 spms, 25.3-91.1 mm, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from the Red Sea, East and South Africa to Australia, Japan and Tonga.

#### ***Gerres macracanthus*** Bleeker, 1854

*Gerres macracanthus* Bleeker, 1854. – *Spéciés piscium bataviensium novae vel minus cognitae*. *Natuurkundig Tijdschrift voor Nederlandsch Indië*, vol. 6, 191-202. Type Locality: Jakarta, Java, Indonesia, Java Sea, Eastern Indian Ocean.

*Gerres macracanthus*. – Allen and Adrim, 2003; Fischer and Bianchi, 1984; Harrison, 2005; Heemstra and Heemstra, 2004; Iwatsuki et al., 2000; Iwatsuki and Heemstra, 2007; Iwatsuki et al., 1996; Iwatsuki et al., 2001b; Iwatsuki and Kimura, 1998, 1998; Iwatsuki et al., 2001a; Kimura et al., 2009; Kyushin et al., 1982.

SPECIMENS EXAMINED: (i) SMF 33843, 6 spms, 44.9-53.8 mm, Detwah Lagoon, 19/04/2000, leg. U. Zajonz and F. A. Saleh, (ii) SMF 33844, 1 spm, 85.6 mm, Khor Delisha, 05/04/2007, leg. E. Lavergne and U. Zajonz, (iii) SMF 33845, 1 spm, 77.1 mm, Khor Dubena, 06/04/2008, leg. E. Lavergne and M. S. Aideed.

Distribution range: from the Red Sea, East and South Africa to Australia, Japan and Tonga.

### ***Gerres oyena* Forsskål, 1775,**

*Labrus oeyena* Forsskål, 1775. – Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit... Post mortem auctoris edidit Carsten Niebuhr. Hauniae. Type locality: Al-Luhayya, Yemen, Red Sea; Suez, Egypt, Red Sea; Jeddah, Saudi Arabia, Red Sea.

*Gerres oyena*. – Allen and Adrim, 2003; Allen et al., 1997; Carpenter et al., 1997; Dor, 1984; Fischer and Bianchi, 1984; Goren and Dor, 1994; Heemstra and Heemstra, 2004; Iwatsuki et al., 2000; Iwatsuki et al., 1998, 2001b; Iwatsuki et al., 2002; Kimura et al., 2009; Masuda et al., 1984; Randall et al., 1997; Randall and Hoover, 1995.

SPECIMENS EXAMINED: (i) SMF 33846, 2 spms, 65.8-83.2 mm, Khor Quariya, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (ii) SMF 33847, 1 spm, 102.6 mm, Khor Sahier (Yemen Mainland), 21/04/2008, leg. E. Lavergne and M. S. Aideed, (iii) SMF 33848, 19 spms, 16.6-90.2 mm, Detwah Lagoon, 22/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from the Red Sea, East and South Africa to Australia, Japan and Tonga.

## Family **Haemulidae** (grunts)

### ***Pomadasys commersonnii* (Lacépède, 1801)**

*Labrus commersonnii* Lacépède, 1801. – Histoire naturelle des poissons, 558 pp. No types known.

*Pomadasys commersonnii*. – Carpenter et al., 1997; Fischer and Bianchi, 1984; Heemstra and Heemstra, 2004; Randall and Hoover, 1995; Smith and Heemstra, 1986.

SPECIMENS EXAMINED: (i) SMF 33851, 5 spms, 94.1-108.0 mm, Detwah Lagoon, 19/04/2000, leg. U. Zajonz and F. A. Saleh, (ii) SMF 33852, 1 spm, 110.7 mm, Khor Dubena, 05/04/2007, leg. E. Lavergne and U. Zajonz, (iii) SMF 33853, 5 spms, 53.0-88.9 mm, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from East and South Africa to the Arabian Sea coast of India.

### ***Pomadasys kaakan* (Cuvier, 1830)**

*Pristipoma kaakan* Cuvier in Cuvier and Valenciennes, 1830. – Histoire naturelle des poissons, 499 pp. Type locality: Arian River, Coupang, Timor; Pondicherry and Mahé, India.

*Pomadasys kaakan*. – Allen et al., 1997; Carpenter et al., 1997; Carpenter and Niem, 1999; Fischer and Bianchi, 1984; Goren and Dor, 1994; Heemstra and Heemstra, 2004; Kimura et al., 2009; Randall and Hoover, 1995; Smith et al., 2003.

SPECIMENS EXAMINED: (i) SMF 33854, 2 spms, 113.0-117.5 mm, Khor Girmah, 27/02/1999, leg. U. Zajonz and M. Khalaf, (ii) SMF 33855, 3 spms, 88.5-116.3 mm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (iii) SMF 33856, 1 spm, 148.6 mm, Khor Quariya, 04/12/2007, leg. E. Lavergne and M. S. Aideed, (iv) SMF 33857,

1 spm, 73.1 mm, Khor Quariya, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (v) SMF 33858, 2 spms, 62.7-87.4 mm, Khor Dufega (Yemen Mainland), 24/04/2008, leg. E. Lavergne and M. S. Aideed, (vi) SMF 33859, 12 spms, 38.8-150.6 mm, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from the Red Sea and East Africa to Australia.

***Pomadasys punctulatus* (Rüppell, 1838)**

*Pristipoma punctulatum* Rüppell, 1838. – Neue Wirbelthiere zu der Fauna von Abyssinien gehörig. Fische des Rothen Meeres. Frankfurt-am-Main, 148 pp. Type locality: Massawa, Eritrea, Red Sea.

*Pomadasys punctulatus*. – Fischer and Bianchi, 1984; Iwatsuki et al., 1999b; Randall and Hoover, 1995.

SPECIMENS EXAMINED: (i) SMF 33860, 1 spm, 98.21 mm, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from the Red Sea to the Western Indian Ocean.

***Pomadasys sp.* Lacépède, 1802**

*Pomadasys sp.* Lacépède, 1802. – Histoire naturelle des poissons, xliv-728 pp.

SPECIMENS EXAMINED: (i) SMF 33861, 2 spms, 54.6-63.8 mm, Khor Dubena, 04/04/2007, leg. E. Lavergne and U. Zajonz, (ii) SMF 33862, 2 spms, 22.3-48.4 mm, Khor Dufega (Yemen Mainland), 24/04/2008, leg. E. Lavergne and M. S. Aideed.

Family **Lethrinidae** (emperors or emperor breams)

***Lethrinus harak* (Forsskål, 1775)**

*Sciaena harak* Forsskål, 1775. – Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit... Post mortem auctoris edidit Carsten Niebuhr. Hauniae. No locality stated (Red Sea).

*Lethrinus harak*. – Carpenter and Allen, 1989; Carpenter and Niem, 1999; Dor, 1984; Fischer and Bianchi, 1984; Goren and Dor, 1994; Heemstra and Heemstra, 2004; Randall, 2005; Randall and Hoover, 1995; Smith and Heemstra, 1986.

SPECIMENS EXAMINED: (i) SMF 33864, 1 spm, 105.6 mm, Detwah Lagoon, 19/04/2000, leg. U. Zajonz and F. A. Saleh.

Distribution range: from the Red Sea and East Africa to Australia, Japan and Tonga.

***Lethrinus lentjan* (Lacépède, 1802)**

*Bodianus lentjan* Lacépède, 1802. – Histoire naturelle des poissons, xliv-728 pp. No locality stated (probably Java, Indonesia, Eastern Indian Ocean).

*Lethrinus lentjan*. – Carpenter and Allen, 1989; Carpenter et al., 1997; Dor, 1984; Fischer and Bianchi, 1984; Goren and Dor, 1994; Kyushin et al., 1977; Kyushin et al., 1982; Randall, 2005; Randall and Hoover, 1995; Smith and Heemstra, 1986.

SPECIMENS EXAMINED: (i) SMF 33865, 10 spms, 37.3-75.5 mm, Detwah Lagoon, 22/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from the Red Sea and East Africa to Australia, Japan and Tonga.

***Lethrinus nebulosus*** (Forsskål, 1775)

*Sciaena nebulosa* Forsskål, 1775. – Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit... Post mortem auctoris edidit Carsten Niebuhr. Hauniae. Type locality: Red Sea.

*Lethrinus nebulosus*. – Carpenter and Allen, 1989; Carpenter et al., 1997; Dor, 1984; Fischer and Bianchi, 1984; Goren and Dor, 1994; Heemstra and Heemstra, 2004; Randall, 2005; Randall and Hoover, 1995; Sato, 1978; Smith and Heemstra, 1986.

SPECIMENS EXAMINED: (i) SMF 33866, 1 spm, 140.4 mm, Khor Dubena, 27/11/2008, leg. E. Lavergne.

Distribution range: from the Red Sea and East Africa to Australia, Japan and Tonga.

***Lethrinus sp. juv.*** Cuvier, 1829

*Lethrinus sp. juv.* Cuvier, 1829. – Le Règne Animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Edition 2, xv-406.

SPECIMENS EXAMINED: (i) SMF 33867, 1 spm, IT-169/MAP292, 12/04/1999, leg. U. Zajonz.

Family **Sparidae** (Porgies)

***Acanthopagrus berda*** (Forsskål, 1775)

*Sparus berda* Forsskål, 1775. – Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit... Post mortem auctoris edidit Carsten Niebuhr. Hauniae. Type locality: Al-Luhayya, Yemen, Red Sea (15°41'52"N, 41°41'07"E)

*Sparus berda*. – Kuang, 1986; Pan et al., 1991.

*Acanthopagrus berda*. – Carpenter et al., 1997; Carpenter and Niem, 1999; Coad, 1991; Dor, 1984; Goren and Dor, 1994; Heemstra and Heemstra, 2004; Iwatsuki and Heemstra, 2010; Masuda et al., 1984; Randall and Lim, 2000; Randall, 2005; Randall and Hoover, 1995; Roberts, 1978; Smith and Heemstra, 1986.

SPECIMENS EXAMINED: (i) SMF 33868, 1 spm, 89.1 mm, Khor Girmah, 27/02/1999, leg. U. Zajonz and M. Khalaf, (ii) SMF 33869, 1 spm, 90.8 mm, Khor Si-ifhim, 28/10/2000, leg. F. Krupp and F. Nasseeb, (iii) SMF 33870, 2 spms, 114.6-120.5 mm, Khor Hadibo, 28/10/2000, leg. F. Krupp and F. Nasseeb, (iv) SMF 33871/SMF 33872, 2 spm, 86.3-95.2 mm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (v) SMF 33873, 1 spm, 139.8 mm, Khor Quariya, 04/12/2007, leg. E. Lavergne and M. S. Aideed, (vi) SMF 33874, 5 spms, 53.5-57.8 mm, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from the Red Sea, East and South Africa to Malaysia and Singapore.

***Acanthopagrus bifasciatus*** (Forsskål, 1775)

*Chaetodon bifasciatus* Forsskål, 1775. – Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit... Post mortem auctoris edidit Carsten Niebuhr. Type locality: Jeddah, Saudi Arabia, Red Sea.

*Neosparus bifasciatus*. – Akazaki, 1994; Manilo and Bogorodsky, 2003.

*Acanthopagrus bifasciatus*. – Carpenter et al., 1997; Dor, 1984; Fischer and Bianchi, 1984; Goren and Dor, 1994; Heemstra and Heemstra, 2004; Iwatsuki et al., 2010; Iwatsuki and Carpenter, 2009; Randall and Hoover, 1995; Smith and Heemstra, 1986.

SPECIMENS EXAMINED: (i) SMF 33875/33876, 4 spms, 101.6-128.2 mm, Khor Hadibo, 28/10/2000, leg. F. Krupp and F. Nasseeb, (ii) SMF 33877, 1 spm, 99.7 mm, Khor Si-irhim (east of Hadibo), 28/10/2000, leg. F. Krupp and F. Nasseeb, (iii) SMF 33878, 1 spm, 84.5 mm, Khor Quariya, 29/10/2000, leg. F. Krupp and F. Nasseeb, (iv) SMF 33879, 1 spm, 100.5 mm, Khor Dubena, 05/04/2007, leg. E. Lavergne and U. Zajonz, (v) SMF 33880, 1 spm, 93.4 mm, Khor Quariya, 28/11/2008, leg. E. Lavergne, (vi) SMF 33881, 9 spms, 66.4-114.5 mm, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from the Red Sea, East and South Africa to the Arabian (Persian) Gulf.

### ***Crenidens crenidens*** (Forsskål, 1775)

*Sparus crenidens* Forsskål, 1775. – Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit... Post mortem auctoris edidit Carsten Niebuhr. Type locality: Jeddah, Saudi Arabia, Red Sea; Egypt, Gulf of Suez, Red Sea.

*Crenidens crenidens*. – Tortonese In: Ben-Tuvia, 1973; Hureau and Monod, 1973 {Carpenter et al., 1997; Dor, 1984; Fischer and Bianchi, 1984; Golani, 1998; Goren and Dor, 1994; Heemstra and Heemstra, 2004; Randall and Hoover, 1995; Smith and Heemstra, 1986.

SPECIMENS EXAMINED: (i) SMF 33883, 6 spms, 48.8-63.7 mm, Detwah Lagoon, 19/04/2000, leg. U. Zajonz and F. A. Saleh.

Distribution range: from the Red Sea, East and South Africa to the Arabian (Persian) Gulf; (1973; Ben-Tuvia, has reported the species as Lessepsian migrant to the Eastern Mediterranean.

## Family **Mullidae** (goatfishes)

### ***Parupeneus* sp.** Bleeker, 1863

*Parupeneus* sp. Bleeker, 1863. – Onzième notice sur la faune ichthyologique de l'île de Ternate. Nederlandsch Tijdschrift voor de Dierkunde **1**:228–238.

SPECIMENS EXAMINED: (i) SMF 33884, 1 spm, Khor Quariya, 04/12/2007, leg. E. Lavergne and M. S. Aideed.

## Family **Monodactylidae** (moonfishes)

### ***Monodactylus argenteus*** (Linnæus, 1758)

*Chaetodon argenteus* Linnæus, 1758. – Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata, 824 pp. Holmiæ. (Salvius). Type locality: India.

*Monodactylus argenteus*. – Allen and Swainston, 1988; Allen et al., 1997; Dor, 1984; Fischer and Bianchi, 1984; Goren and Dor, 1994; Heemstra and Heemstra, 2004; Krupp et al., 2000; Kuang, 1986; Masuda et al., 1984; Randall, 2005; Randall and Hoover, 1995; Smith and Heemstra, 1986).

SPECIMENS EXAMINED: (i) SMF 33885, 1 spm, 75.3 mm, Khor Girmah, 27/02/1999, leg. U. Zajonz and M. Khalaf, (ii) SMF 33886, 6 spms, 56.9-85.9 mm, Khor Hadibo, 28/10/2000, leg. F. Krupp and F. Nasseeb, (iii) SMF 33887, 1 spm, 91.1 mm, Khor Dubena, 04/04/2007, leg. E. Lavergne and U. Zajonz, (iv) SMF 33888, 5(14) spms, 45.5-108.2 mm, Khor Quariya 18/04/2007, leg. E. Lavergne and U. Zajonz, (v) SMF 33889, 3 spms, 84.3-92.3 mm, Khor Quariya, 12/12/2007, leg. E. Lavergne and M. S. Aideed, (vi) SMF 33890, 5(10) spms, 39.7-105.6 mm, Khor Quariya, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (vii) SMF 33891, 4 spms, 48-63.5 mm, Khor Dufega

(Yemen Mainland), 24/04/2008, leg. E. Lavergne and M. S. Aideed, (viii) SMF 33892, 1 spm, 56.5 mm, Khor Quariya, 28/11/2008, leg. E. Lavergne, (ix) SMF 33893, 5(42) spms, 50.5-98.3 mm, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from the Red Sea, East and South Africa to Australia, Japan and Samoa.

### Family **Terapontidae** (grunters or tigerperches)

#### ***Terapon jarbua*** (Forsskål, 1775)

*Sciaena jarbua* Forsskål, 1775. – Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit... Post mortem auctoris edidit Carsten Niebuhr. Type locality: Jeddah, Saudi Arabia, Red Sea.

*Therapon jarbua*. – Dor, 1984; Kuang, 1986.

*Terapon jarbua*. – Allen and Swainston, 1988; Allen, 1991; Carpenter et al., 1997; Fischer and Bianchi, 1984; Goren and Dor, 1994; Heemstra and Heemstra, 2004; Khalaf and Disi, 1997; Khalaf and Zajonz, 2007; Kyushin et al., 1982; Masuda et al., 1984; Paxton et al., 1989; Randall, 2005; Randall and Hoover, 1995; Vari, 1978.

SPECIMENS EXAMINED: (i) SMF 33894, 4 spms, 31.2-15.9 mm, IT-A7/N49, 07/02/1999, leg. U. Zajonz, (ii) SMF 33895, 5(10) spms, 45.6-69.8 mm, Khor Quariya, 27/02/1999, leg. U. Zajonz, (iii) SMF 33896, 1 spm, 72.1 mm, Khor Girmah, 12/04/1999, leg. U. Zajonz, (iv) SMF 33897, 7 spms, 34.1-63.7 mm, Detwah Lagoon, 19/04/2000, leg. U. Zajonz and F. A. Saleh, (v) SMF 33898/SMF 33899, 4 spms, 62.1-64.3 mm, Khor Girmah, 22/10/2000, leg. F. Krupp and F. Nasseeb, (vi) SMF 338900, 2 spms, 64.8-98.8 mm, Khor Si-irhim (east of Hadibo), 28/10/2000, leg. F. Krupp and F. Nasseeb, (vii) SMF 33901, 8 spms, 64.8-78.4 mm, Khor Hadibo, 28/10/2000, leg. F. Krupp and F. Nasseeb, (viii) SMF 33902, 3 spms, 51.2-64.8 mm, Khor Si-irhim, 28/10/2000, leg. F. Krupp and F. Nasseeb, (ix) SMF 33903, 2 spms, 81.4-85.1 mm, Khor Dubena, 29/10/2000, leg. F. Krupp and F. Nasseeb, (x) SMF 33904, 1 spm, 67.8 mm, Khor Quariya, 29/10/2000, leg. F. Krupp and F. Nasseeb (xi) SMF 33905, 8 spms, Khor Arhan, 18/04/2007, leg. E. Lavergne and U. Zajonz, (xii) SMF 33906/SMF 33907/SMF 33908, 15(30) spms, 8.2-101.1 mm, Khor Dubena, 01/12/2007, leg. E. Lavergne and M. S. Aideed, (xiii) SMF 33909, 5(10) spms, 64.2-84.3 mm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (xiv) SMF 33910/SMF 33911/SMF 33912, 15(>80) spms, 25.8-56.1 mm, Khor Dubena, 06/04/2008, leg. E. Lavergne and M. S. Aideed, (xv) SMF 33913, 1 spm, 112.6 mm, Khor Delisha, 07/04/2008, leg. E. Lavergne and M. S. Aideed, (xvi) SMF 33914/SMF 33915, 10(>150) spms, 15.3-55.6 mm, Khor Bidholeh, 13/04/2008, leg. E. Lavergne and M. S. Aideed, (xvii) SMF 33917(13) spms, 27.5-119.8 mm, Khor Quariya, 28/11/2008, leg. E. Lavergne, (xviii) SMF 33918, 1 spm, 104.5 mm, Khor Delisha, 29/11/2008, leg. E. Lavergne, (xix) SMF 33919, 2 spms, 65.3-67.4 mm, Detwah Lagoon, 22/03/2009, leg. E. Lavergne and U. Zajonz, (xx) SMF 33920, 8 spms, 32.4-49.8 mm, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from the Red Sea and East Africa to Australia, Japan and Tonga.

### Family **Kuhliidae** (flagtails)

#### ***Kuhlia mugil*** (Forster, 1801)

*Sciaena jarbua* Forster, 1801. – In: Bloch and Schneider (1801): Systema Ichthyologiae, ix-584. Type locality: Otahaite, Tahiti, Society Islands, French Polynesia, South Pacific. No types preserved.

*Kuhlia mugil.* – Dor, 1984; Fischer and Bianchi, 1984; Goren and Dor, 1994; Heemstra and Heemstra, 2004; Masuda et al., 1984; Randall, 2005; Randall and Hoover, 1995.

SPECIMENS EXAMINED: (i) SMF 33922, 5 spms, 68.1-77.7 mm, Samha Island ,01/03/2007, leg. E. Lavergne and U. Zajonz, (ii) SMF 33923, 7 spms, 104.2-125.3 mm, Khor Delisha, 07/04/2008, leg. E. Lavergne and M. S. Aided.

Distribution range: from the Red Sea, East and South Africa to Australia and Japan.

#### Family **Pomacentridae** (damsel-fishes)

##### ***Abudefduf sordidus*** (Forsskål, 1775)

*Chaetodon sordidus* Forsskål, 1775. – Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit... Post mortem auctoris edidit Carsten Niebuhr. Type locality: Jeddah, Saudi Arabia, Red Sea.

*Abudefduf sordidus.* – Allen and Swainston, 1988; Allen, 1991; Dor, 1984; Fischer and Bianchi, 1984; Goren and Dor, 1994; Heemstra and Heemstra, 2004; Masuda et al., 1984; Randall, 2005, 2007; Randall and Hoover, 1995; Smith and Heemstra, 1986.

SPECIMENS EXAMINED: (i) SMF 33924, 1 spm, 55.4 mm, Khor Dubena, 05/04/2007, leg. E. Lavergne and U. Zajonz, (ii) SMF 33925/SMF 33926, 4 spms, 88.4-155.2 mm, Khor Delisha, 07/04/2008, leg. E. Lavergne and M. S. Aided.

Distribution range: from the Red Sea and East Africa to Australia, Japan and the Hawaiian Islands.

##### ***Abudefduf vaigiensis*** (Quoy and Gaimard, 1825)

*Glyphisodon vaigiensis* Quoy and Gaimard, 1825. – Description des Poissons. Chapter IX. In: de Freycinet, L. – Voyage autour du Monde...Paris, 192-401. Type locality: Pulau Waigeo, Papua Barat, Indonesia, Western Pacific.

*Abudefduf vaigiensis.* – Allen and Swainston, 1988; Allen, 1991; Carpenter et al., 1997; Dor, 1984; Fischer and Bianchi, 1984; Goren and Dor, 1994; Heemstra and Heemstra, 2004; Masuda et al., 1984; Randall, 2005, 2007; Randall and Hoover, 1995; Smith and Heemstra, 1986.

SPECIMENS EXAMINED: (i) SMF 33927, 2 spms, 76.83-85.3 mm, Detwah Lagoon, 22/03/2009, leg. E. Lavergne and U. Zajonz.

Distribution range: from the Red Sea, East and South Africa, Australia, Japan and the Hawaiian Islands; Goren and Galil (1998) have reported the species as Lessepsian migrant to the Eastern Mediterranean.

#### Family **Scaridae** (parrotfishes)

##### ***Scaridae sp. juv.***

SPECIMENS EXAMINED: (i) SMF 33928, 2 spms, Detwah Lagoon, 22/03/2009, leg. E. Lavergne and U. Zajonz, (ii) SMF 33929, 1 spm, Khor Quariya, 25/03/2009, leg. E. Lavergne and U. Zajonz.

#### Family **Blenniidae** (combtooth blennies)

##### ***Alticus sp.*** Lacépède, 1800

*Alticus sp.* Lacépède, 1800. – Histoire naturelle des poissons vol. 2, lxiv-632.

SPECIMENS EXAMINED: (i) SMF 33930, 10 spms, 10 Km east of Rhiy di-Qatanhin Nogid (12° 18' 26.88" N, 53° 39' 30.18" E), 15/02/1999, leg. U. Zajonz, (ii) SMF 33931, 1 spm, IT-93/N186, 01/03/1999, leg. U. Zajonz, (iii) SMF 33932, 15 spms, Khor Quadub, 18/03/1999, leg. U. Zajonz, (iv) SMF 33933, 1 spm, Detwah Lagoon, 22/03/2009, leg. E. Lavergne and U. Zajonz.

***Istiblennius sp.*** Whitley, 1943

*Istiblennius sp.* Whitley, 1943. – Ichthyological notes and illustrations (Part 2). Australian Zoologist **10**: 167–187.

SPECIMENS EXAMINED: (i) SMF 33934, 1 spm, 104.2-125.3 mm, Khor Girmah, 22/10/2000, leg. F. Krupp and F. Nasseeb.

Family **Eleotridae** (sleepers)

***Eleotris sp.*** Bloch and Schneider, 1801

*Eleotris sp.* Bloch and Schneider, 1801. – Systema Ichthyologiae, ix-584.

SPECIMENS EXAMINED: (i) SMF 33935, 2 spms, Khor Hadibo, 28/10/2000, leg. F. Krupp and F. Nasseeb, (ii) SMF 33936, 19 spms, Khor Quariya, 29/10/2000, leg. F. Krupp and F. Nasseeb, (iii) SMF 33937, 6 spms, Khor Dubena, 29/10/2000, leg. F. Krupp and F. Nasseeb.

Family **Gobiidae** (gobies)

***Gobiidae sp. 1***

SPECIMENS EXAMINED: (i) SMF 33938, 35 spms, Khor Delisha, 09/04/2007, leg. E. Lavergne and U. Zajonz, (ii) SMF 33939, 2 spms, Khor Dufega, 24/04/2008, leg. E. Lavergne and M. S. Aideed.

***Gobiidae sp. 2***

SPECIMENS EXAMINED: (i) SMF 33940, 1 spm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (ii) SMF 33941, 1 spm, Khor Delisha, 03/12/2007, leg. E. Lavergne and M. S. Aideed.

***Gobiidae sp. 3***

SPECIMENS EXAMINED: (i) SMF 33942, 1 spm, west of Rhiy di-Diblih Nogid (12° 24' 07.7" N, 54° 13' 15.1" E), 17/02/1999, leg. U. Zajonz, (ii) SMF 33943, 1 spm, Khor Girmah, 27/02/1999, leg. M. Appel and N. Simoes, (iii) SMF 33944, 1 spm, IT-169/MAP292, 12/04/1999, leg. U. Zajonz, (iv) SMF 33945, 1 spm, Detwah Lagoon, 19/04/2000, leg. U. Zajonz and F. A. Saleh, (v) SMF 33946, 3 spms, Khor Hadibo, 28/10/2000, leg. F. Krupp and F. Nasseeb, (vi) SMF 33947, 8 spms, Khor Si-irhim (east of Hadibo), 28/10/2000, leg. F. Krupp and F. Nasseeb, (vii) SMF 33948, 4 spms, Khor Si-irhim, 28/10/2000, leg. F. Krupp and F. Nasseeb, (viii) SMF 33949, 6 spms, Khor Dubena, 29/10/2000, leg. F. Krupp and F. Nasseeb, (ix) SMF 33950, 2 spms, Khor Quariya, 29/10/2000, leg. F. Krupp and F. Nasseeb, (x) SMF 33951, 17 spms, Khor Delisha, 05/04/2007, leg. E. Lavergne and U. Zajonz, (xi) SMF 33952, 1 spm, Khor Delisha, 09/04/2007, leg. E. Lavergne and U. Zajonz, (xii) SMF 33953, 2 spms, Khor Matief, 11/12/2007, leg. E. Lavergne and M. S. Aideed, (xiii) SMF 33954, 1 spm, Khor Bidholeh, 13/04/2008, leg. E. Lavergne and M. S. Aideed, (xiv) SMF 33955, 28 spms, Khor Matief, 13/04/2008, leg. E. Lavergne and M. S. Aideed, (xv) SMF 33956, 1 spm, Khor Sahier, 21/04/2008, leg. E. Lavergne and M. S. Aideed, (xvi) SMF 33957, 2 spms, Khor Delisha, 29/11/2008, leg. E. Lavergne.

**Gobiidae sp. 4**

SPECIMENS EXAMINED: (i) SMF 33958, 1 spm, Khor Dubena, 29/10/2000, leg. F. Krupp and F. Nasseeb.

**Gobiidae sp. 5**

SPECIMENS EXAMINED: (i) SMF 33959, 1 spm, west of Rhiy di-Diblih Nogid (12° 24' 07.7" N, 54° 13' 15.1" E), 17/02/1999, leg. U. Zajonz, (ii) SMF 33960, 1 spm, Khor Sahier, 21/04/2008, leg. E. Lavergne and M. S. Aideed.

**Gobiidae sp. 6**

SPECIMENS EXAMINED: (i) SMF 33961, 2 spms, Khor Quadub, 18/03/1999, leg. U. Zajonz.

**Gobiidae sp. 7**

SPECIMENS EXAMINED: (i) SMF 33962, 1 spm, Khor Girmah,, 12/04/1999, leg. U. Zajonz, (ii) SMF 33963, 1 spm, Khor Dubena, 29/10/2000, leg. F. Krupp and F. Nasseeb.

**Gobiidae sp. 8**

SPECIMENS EXAMINED: (i) SMF 33964, 10 spms, Khor Girmah, 27/02/1999, leg. M. Appel and N. Simoes, (ii) SMF 33965/SMF 33966, 65 spms, Khor Delisha, 05/04/2007, leg. E. Lavergne and U. Zajonz, (iii) SMF 33967/SMF 33968, 26 spms, Khor Delisha, 03/12/2007, leg. E. Lavergne and M. S. Aideed, (iv) SMF 33969, 16 spms, Khor Delisha, 07/04/2008, leg. E. Lavergne and M. S. Aideed, (v) SMF 33970/SMF 33971, 29 spms, Khor Delisha, 29/11/2008, leg. E. Lavergne and M. S. Aideed.

Family **Sphyraenidae** (barracudas)

***Sphyraena jello*** Cuvier, 1829

*Sphyraena jello* Cuvier, 1829. – In: Cuvier G. and Valenciennes A., Histoire naturelle des poissons - Tome 3. Des percoïdes à dorsale unique à sept rayons branchiaux et à dents en velours ou en cardes, xxviii-500.

*Sphyraena jello*. – Carpenter et al., 1997; Dor, 1984; Goren and Dor, 1994; Heemstra and Heemstra, 2004; Kyushin et al., 1977; Kyushin et al., 1982; Pastore, 2009; Randall, 2005; Randall and Hoover, 1995; de Sylva, 1975.

SPECIMENS EXAMINED: (i) SMF 33972/SMF 33973, 2 spms, 270.5-343.5 mm, Khor Dufega, 24/04/2008, leg. E. Lavergne and M. S. Aideed.

Distribution range: from the Red Sea, East and South Africa to Australia, Taiwan and Tonga.

Family **Bothidae** (lefteye flounders)

***Bothus sp.*** Rafinesque, 1810

*Bothus sp.* Rafinesque, 1810. – Caratteri di alcuni nuovi generi e nuove specie di animali e piante della Sicilia, con varie osservazioni sopra i medisimi, 105 pp.

SPECIMENS EXAMINED: (i) SMF 33974, 1 spm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed, (ii) SMF 33975, 1 spm, Detwah Lagoon, 22/03/2009, leg. E. Lavergne and U. Zajonz.

Family **Tetraodontidae** (puffers)

***Tetraodontidae sp.***

SPECIMENS EXAMINED: (i) SMF 33976, 1 spm, Khor Quariya, 02/12/2007, leg. E. Lavergne and M. S. Aideed,  
(ii) SMF 33977, 1 spm, Khor Quariya, 04/12/2007, leg. E. Lavergne and M. S. Aideed.

# Appendix

# 3

**Comparison of estuarine species accounts of  
the present study and Steindachner (1902,  
1903)**

---

### Appendix 3: Comparison of estuarine species accounts of the present study and Steindachner (1902, 1903)

Steindachner's original species account	Present nomenclatoric status	Recorded in the present study	Reliable additional records	Potentially matching records in the present study	Doubtful records	Additional unpublished records available, supporting the general presence on Socotra
<b>Carchariidae</b>	<b>Carcharhinidae</b>	11	4	12	3	16
<i>Carcharias (Prionodon) melanopterus</i>	<i>Carcharhinus melanopterus</i> (Quoy & Gaimard, 1824)	.	.	.	1	1
Uncertain whether collected from inside or outside Tamarida (= Suq) estuary; but the general presence on Socotra is confirmed						
<b>Trygonidae</b>	<b>Dasyatidae</b>					
<i>Trygon uarnak</i>	<i>Himantura uarnak</i> (Gmelin, 1789)	.	.	1	.	1
Identification to be verified at NHM Vienna; easily confused with other similarity colored species; but also recorded from Darsa						
<b>Muraenidae</b>	<b>Muraenidae</b>					
<i>Muraena (Gymnothorax) richardsoni</i>	<i>Gymnothorax richardsonii</i> (Bleeker, 1852)	.	.	1	.	.
Identification to be verified at NHM Vienna						
<b>Clupeidae</b>	<b>Clupeidae</b>					
<i>Dorosoma nasus</i>	<i>Nematolosa nasus</i> (Bloch, 1795)	.	.	1	.	.
Might represent <i>N. arabicus</i> as recorded in this study; identification to be verified at NHM Vienna						
<b>Mugilidae</b>	<b>Mugilidae</b>					
<i>Mugil tade</i>	<i>Chelon planiceps</i> (Valenciennes, 1836)	.	.	1	.	.
Identification to be verified at NHM Vienna						
<i>Mugil crenilabris</i>	<i>Crenimugil crenilabris</i> (Forsskål, 1775)	.	.	1	.	.
Identification to be verified at NHM Vienna						
<i>Mugil seheli</i>	<i>Moolgarda seheli</i> (Forsskål, 1775)	.	.	1	.	.
Identification to be verified at NHM Vienna						
<i>Mugil oeur</i>	<i>Mugil cephalus</i> Linnaeus, 1758	.	.	1	.	.
Identification to be verified at NHM Vienna						
<b>Ambassidae</b>	<b>Ambassidae</b>					
<i>Ambassis gymnocephalus</i>	<i>Ambassis gymnocephalus</i> (Lacépède, 1802)	.	.	1	.	.
Might represent <i>A. dussumieri</i> as recorded in this study; identification to be verified at NHM Vienna.						
<b>Carangidae</b>	<b>Carangidae</b>					
<i>Caranx (Carangoides) latus</i>	<i>Caranx latus</i> Agassiz, 1831	.	.	1	1	.
Very unlikely to occur as it is an Atlantic species. It might represent <i>C. heberi</i> whose presence is certain; identification to be verified at NHM Vienna.						
<i>Trachinotus baillonii</i>	<i>Trachinotus baillonii</i> (Lacépède, 1801)	.	1	.	.	1
Possible confusion with <i>T. botla</i> , thus identification to be verified at NHM Vienna.						
<b>Lutjanidae</b>	<b>Lutjanidae</b>					
<i>Lutjanus argentimaculatus</i>	<i>Lutjanus argentimaculatus</i> (Forsskål, 1775)	1	.	.	.	1
<i>Lutjanus ehrenbergii</i>	<i>Lutjanus ehrenbergii</i> (Peters, 1869)	1	.	.	.	1

## Appendix 3 (continued)

Steindachner's original species account	Present nomenclatoric status	Recorded in the present study	Reliable additional records	Potentially matching records in the present study	Doubtful records	Additional unpublished records available, supporting the general presence on Socotra
<b>Gerridae</b>	<b>Gerridae</b>					
<i>Gerres filamentosus</i>	<i>Gerres filamentosus</i> Cuvier, 1829	1	.	.	.	1
<i>Gerres acinaces</i>	<i>Gerres longirostris</i> (Lacepède, 1801)	1	.	.	.	.
<i>Gerres socotranus</i> [n.sp.]	<i>Gerres oyena</i> (Forsskål, 1775)	1	.	.	.	1
<b>Pristipomatidae</b>	<b>Haemulidae</b>					
<i>Pomadasys argenteus</i>	<i>Pomadasys argenteus</i> (Forsskål, 1775)	.	1	.	.	1
<i>Pomadasys punctulatus</i>	<i>Pomadasys punctulatus</i> (Rüppell, 1838)	1	.	.	.	.
<b>Sparidae</b>	<b>Lethrinidae</b>					
<i>Lethrinus acutus</i>	<i>Lethrinus microdon</i> Valenciennes 1830	.	1	.	.	1
<b>Sparidae</b>	<b>Sparidae</b>					
<i>Sparus</i> [ <i>Chrysophrys</i> ] <i>berda</i>	<i>Acanthopagrus berda</i> (Forsskål, 1775)	1	.	.	.	1
<i>Sparus</i> [ <i>Chrysophrys</i> ] <i>bifasciatus</i>	<i>Acanthopagrus bifasciatus</i> (Forsskål, 1775)	1	.	.	.	1
<i>Crenidens indicus</i>	<i>Crenidens crenidens</i> (Forsskål, 1775) [ssp. "indicus" Day, 1873?]	.	.	1	.	1
Taxonomic validity of <i>C. indicus</i> Day, 1873 not fully resolved; identification to be verified at NHM Vienna.						
<i>Pagellus affinis</i>	<i>Pagellus affinis</i> Boulenger, 1888	.	1	.	.	.
Identification to be verified at NHM Vienna, but likely to occur.						
<b>Psettidae</b>	<b>Monodactylidae</b>					
<i>Psettus argenteus</i>	<i>Monodactylus argenteus</i> (Linnaeus, 1758)	1	.	.	.	1
<b>Theraponidae</b>	<b>Terapontidae</b>					
<i>Therapon jarbua</i>	<i>Terapon jarbua</i> (Forsskål, 1775)	1	.	.	.	1
<b>Kuhliidae</b>	<b>Kuhliidae</b>					
<i>Kuhlia taeniura</i>	<i>Kuhlia mugil</i> (Forster, 1801)	1	.	.	.	1
<b>Gobiidae</b>	<b>Gobiidae</b>					
<i>Gobius arabicus</i>	<i>Cryptocentroides arabicus</i> (Gmelin, 1789)	.	.	1	1	.
Identification to be verified at NHM Vienna. Species is unlikely to occur in freshwater pools, as reported by Steindachner.						
<i>Eleotris fusca</i>	<i>Eleotris fusca</i> (Schneider & Forster, 1801)	.	.	1	.	1
Probably also present among the Riebeck & Schweinfurth material; identification to be verified at NHM Vienna, but likely to occur.						



# Chapter

# 2

**Length-weight relationship and seasonal effects of the Summer Monsoon on condition factor of *Terapon jarbua* (Forsskål, 1775) from the wider Gulf of Aden including Socotra Island**

---



## Summary

**Context:** The last chapter provided baseline data on Socotra Island and Yemen mainland estuarine and lagoon fish diversity, showing that Socotra estuarine fish diversity is high by regional comparison and that the island appears as a biogeographic “stepping stone” for several species in the region, thus underscoring the particular conservation importance of Socotra. Moreover, half of the recorded estuarine species were considered relevant species for the local economy. As Socotra estuaries are under increasing anthropogenic threat, the need to better understand TOCE’s functioning in this complex monsoon driven climate environment become increasingly essential.

**Aims:** The aims of this study are 1) to assess seasonal effects of the Summer Monsoon on Fulton’s condition factor K and 2) to compare Length-Weight Relationship (LWR) of the sentinel species (*Terapon jarbua*) from the wider Gulf of Aden region with that from other regions.

**Materials and methods:** A total of 620 specimens collected in estuaries and at sea were measured and weighted during field surveys carried out in 2007 and 2008 during pre- and post-South-Western monsoon periods. LWR analysis was performed for the whole data set and compared with that from other regions after applying unit measurement corrections. Fulton’s condition factor was calculated and temporal (only for one location) and spatial (only for the pre-monsoon period) comparisons were investigated using Kruskal-Wallis tests (Kruskal and Wallis, 1952).

**Results:** The length-weight relationship of the studied populations of *T. jarbua* is determined as  $W = 0.0288 \times SL^{2.99}$ , with  $r^2 = 0.96$  and is consistent with existing data on the species from other regions. Significant seasonal differences were found in Fulton’s condition factor of *T. jarbua*.

**Conclusion:** The high K values during the post- Summer Monsoon period are the direct consequences of the seasonal upwelling responsible of higher productivity and food availability. Indeed, strong coastal wind and wave action establishing connections between estuaries and the fertile ocean water masses are responsible of higher food availability, thus allowing fishes to increase in weight in a short period of time. This study highlights the important role that plays the monsoon system in TOCE’s functioning and in the biology of estuarine fishes.

**Next chapter:** To improve the understanding of TOCE's functioning and their fish population structure and dynamics based on *T. jarbua*, the third chapter will present the isolation and characterization of the nine first microsatellite loci of *T. jarbua*, which will be used in the fourth chapter.

## **Length-weight relationship and seasonal effects of the Summer Monsoon on condition factor of *Terapon jarbua* (Forsskål, 1775) from the wider Gulf of Aden including Socotra Island**

E. Lavergne<sup>1,2,3</sup>, U. Zajonz<sup>2,1</sup>, L. Sellin<sup>3</sup>

<sup>1</sup> Senckenberg Forschungsinstitut und Naturmuseum, Sektion Ichthyologie – Senckenberganlage 25, 60325 Frankfurt am Main, Deutschland

<sup>2</sup> Biodiversität und Klima Forschungszentrum (BiK-F) – Senckenberganlage 25, 60325 Frankfurt am Main, Deutschland

<sup>3</sup> Université de Bretagne Occidentale, UMR 6539, CNRS/IRD/UBO, Laboratoire des Sciences de l'Environnement Marin LEMAR, Institut Universitaire Européen de la Mer, Rue Dumont d'Urville, 29280 Plouzané, France

**Corresponding author:** E. Lavergne, Tel +33 2 98 49 86 27

Email address: [edouard.lavergne@gmail.com](mailto:edouard.lavergne@gmail.com)

**Published as:** Lavergne, E., Zajonz, U., Sellin, L. (2012). Length-weight relationship and seasonal effects of the Summer Monsoon on condition factor of *Terapon jarbua* (Forsskål, 1775) from the wider Gulf of Aden including Socotra Island. *Journal of Applied Ichthyology*. DOI: [10.1111/j.1439-0426.2012.02018.x](https://doi.org/10.1111/j.1439-0426.2012.02018.x).

### **Abstract**

The present study investigates the length-weight relationship and the condition factor of populations of the Indo-Pacific fish *Terapon jarbua* (Forsskål, 1775) collected in the wider Gulf of Aden, notably from Socotra Island and the Hadhramout coast of Yemen. This region displays a monsoon climate, with wide seasonal variation affecting estuarine habitats. A total of 620 specimens collected in estuaries and at sea were measured and weighted during field surveys carried out in 2007 and 2008 during pre- and post- South-Western monsoon periods. The length-weight relationship of the studied populations of *Terapon jarbua* is determined as  $W = 0.0288 \times SL^{2.99}$ , with  $r^2 = 0.96$  and is consistent with existing data on the species from other regions. Significant seasonal differences were found in Fulton's condition factor of *Terapon jarbua*.

**Keywords:** *Terapon jarbua*, length-weight relationship, condition factor, monsoon, Gulf of Aden, Socotra Island

## Introduction

The grunter *Terapon jarbua* (Terapontidae, Perciformes) locally known as “Dirhar” in Yemen mainland and “Habraham” on Socotra Island, inhabits marine and brackish waters of the Indo-West Pacific (Klausewitz and Nielsen, 1965; Nielsen, 1974; Vari, 1978) and was recently observed in the Eastern Mediterranean (Golani and Appelbaum-Golani, 2010). Estimates on length-weight relationships (LWR) for this species have been reported from populations in Thailand (Yanagawa, 1994), Indonesia (Pauly et al., 1996), New Caledonia (Kulbicki et al. 2005; Letourneur et al., 1998), South Africa (Harrison, 2001), China (Zhang et al., 2002).

The climate of the studied region is characterized by the alternating monsoon seasons in the Northern Indian Ocean driven by the Inter-Tropical Convergence Zone (ITCZ). From October to February the weaker Winter or north-east Monsoon dominates with a rainy period starting in October and being strongest in November/December. From April/May to September the forceful Summer or south-west monsoon blows strong hot winds that generate upwelling of cold nutrient-rich waters on both the north and south coasts of Socotra, and on the south coast of Yemen mainland (Fleitmann et al., 2004; Fratantoni et al., 2006; Klaus and Turner, 2004; Scholte and De Geest, 2010). The objective of the present study is to compare LWR of *Terapon jarbua* from the wider Gulf of Aden region with that from other regions and to assess seasonal effects of the Summer Monsoon on Fulton’s condition factor K (Froese, 2006; Muchlisin et al., 2010; Pauly, 1984).

## Materials and methods

### *Sampling and measurements*

620 specimens of *Terapon jarbua* were sampled using a 30 m seine net (10 mm mesh size) at different locations in the wider Gulf of Aden region including Socotra Island and the Hadhramout coast of Yemen from 2007 to 2008 during pre- and post- south-western monsoon periods. The Standard Length (SL) of all observed specimens ranged from 4.7 to 27.9 cm, with a mean value of 8.7 cm. All specimens were measured to the nearest 0.1 cm and weighed (W) to the nearest gramme.

### *Length-weight relationship*

The sex was not differentiated in this study. Although most of the samples were juveniles it is appreciated that sex may have affected the LWR. The LWR was determined by the equation  $W = a \times SL^b$ . Both parameters  $a$  and  $b$  were estimated by ordinary least squares regression through a logarithmic transformation of the data:  $\log(W) = \log(a) + b \times \log(SL)$  where  $\log(a)$  is the intercept and  $b$  the slope of the regression line (Clark, 1928; Froese, 2006; Keys, 1928;

Kulbicki et al., 2005). The hypothesis of isometric growth was tested by Student's *t*-test. To compare the estimates found in this study with those reported by other authors in different areas of the Indo-West Pacific region (Table 2.1), Froese (2006) proposed to correct parameter *a* by applying the following formula:  $a' = a \times 10^b$  (from data in mm and g to data in cm and g).

**Table 2.1: Descriptive statistics and estimated parameters of length-weight relationships for *T. jarbua***

	<i>n</i>	Length (cm)			LWR Parameters				
		Min	Max		<i>a</i>	<i>a</i> CI 95%	<i>b</i>	<i>b</i> CI 95%	<i>r</i> <sup>2</sup>
<b>Present study</b>	<b>620</b>	<b>4.7</b>	<b>27.9</b>	<b>SL</b>	<b>0.0288</b>	<b>0.0262- 0.0318</b>	<b>2.99</b>	<b>2.95- 3.04</b>	<b>0.96</b>
Kulbicki et al. 2005 *	87	2.0	28.5	FL	0.0132	-	3.13	-	0.98
Zhang et al. 2002 *	-	-	-	-	0.0389	-	2.87	-	-
Harrison 2001**	70	1.0	14.8	SL	0.0340	-	2.94	-	0.99
Letourneur et al. 1998 *	97	2.0	28.5	FL	0.0154	-	3.08	-	0.98
Pauly et al. 1996*	-	8.0	19.0	FL	0.0748	-	2.52	-	0.98
Yanagawa 1994 *	6	9.6	26.8	TL	0.0222	-	2.88	-	0.99

N, sample size; Min, minimum; Max, maximum; FL, Fork Length; SL, Standard Length; TL, Total Length

\* Data collected from FishBase (Froese and Pauly, 2011)

\*\* Original length was in mm and weight in g, parameter *a* was corrected using the following equation:  
 $a' = a \times 10^b$  (Froese, 2006)

### ***Fulton's condition factor***

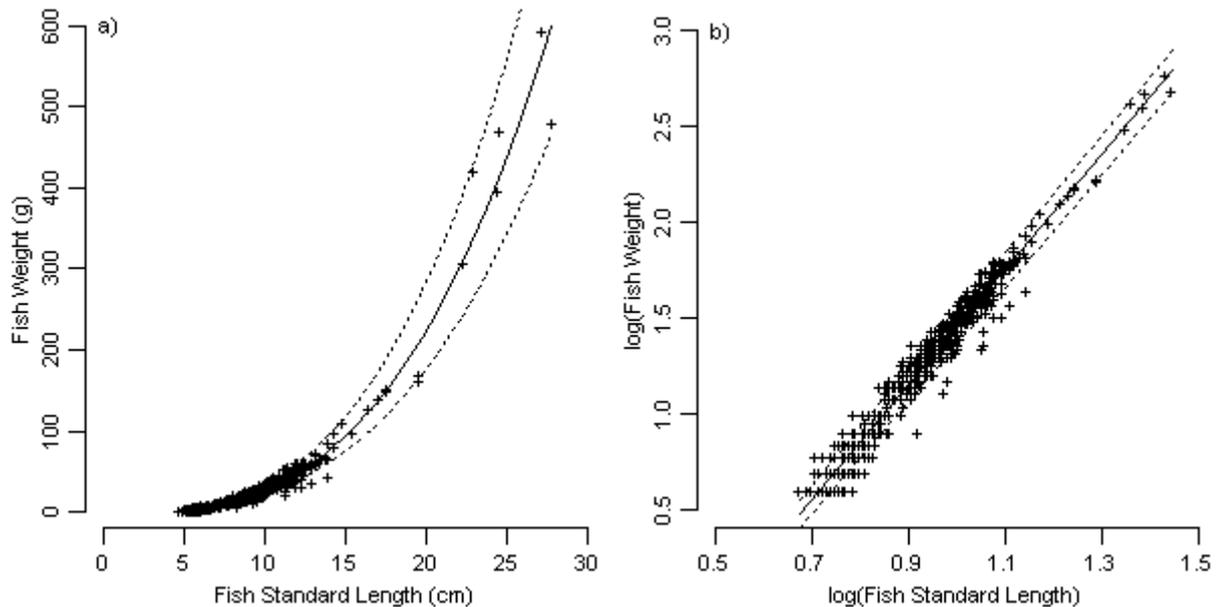
The Fulton's condition factor was calculated for each individual fish according to the equation:  $K = 100 \times W \times SL^{-3}$  (Froese, 2006; Muchlisin et al., 2010; Pauly, 1984), and since  $b = 2.99$  close to 3, condition factor could be compared for different length (Froese, 2006). As the hypotheses of normality (Shapiro and Wilk, 1965) and homoscedasticity (Bartlett, 1937) were not met for all populations ( $p < 0.05$ ), differences in K were investigated using Kruskal-Wallis tests (Kruskal and Wallis, 1952). Due to time restrictions and site access denied by some local village authorities, seasonal comparison was only possible for Khor Dubena (Khor = estuary or coastal lagoon) and spatial comparison was only possible for the pre-monsoon periods. Additionally Nemenyi-Damico-Wolfe-Dunn post-hoc tests (Hollander and Wolfe, 1999) were performed to identify among which seasons and among which locations differences occur. All statistical analyses were performed using the function *shapiro.test*, *bartlett.test* and *kruskal.test* of the R package *stats* and the function *oneway\_test* of the R package *coin* (Ihaka and Gentleman, 1996).

## **Results and discussion**

### ***Length-weight relationship***

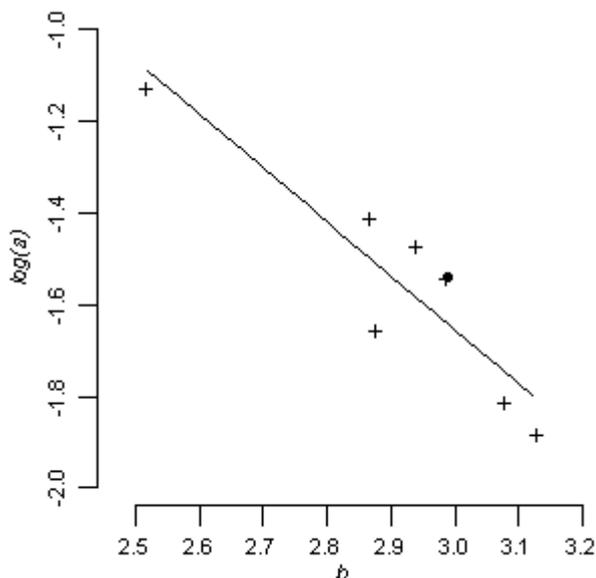
The LWR of *Terapon jarbua* is  $W = 0.0288 \times SL^{2.99}$ , with  $r^2 = 0.96$  as represented in Fig. 2.1. Descriptive statistics and estimated LWR parameters of *T. jarbua* from this study and from other studies are summarized in Table 2.1. The value of the parameter *b* in the present study was not

significantly different from three ( $t = -0.314$ ,  $p > 0.05$ ); therefore the hypothesis of isometric growth for *T. jarbua* in the wider Gulf of Aden was not rejected (Froese, 2006; Giacalone et al., 2010; Harrison, 2001). Different types of length measurements (Standard Length, Total Length and Fork Length) used by the different authors might have altered the estimation of parameter  $a$  but not  $b$  (Froese, 2006). In order, however, to compare the estimates found in this study with other authors' estimates, the  $\log(a)$  was plotted against  $b$  (Fig. 2.2) and proved to be consistent with existing data for *Terapon jarbua*.



**Figure 2.1: Length-weight relationship of *T. jarbua* from the wider Gulf of Aden**

a) Regression of Fish Standard Length vs. Fish Weight, the plain curve represents the LWR regression curve  $W = 0.0288 \times SL^{2.99}$ ,  $r^2 = 0.96$  and the dotted curves represent the upper and lower 95 % confidence limits of the LWR Regression curve. b) Linear regression of the log transformed data presented in a).

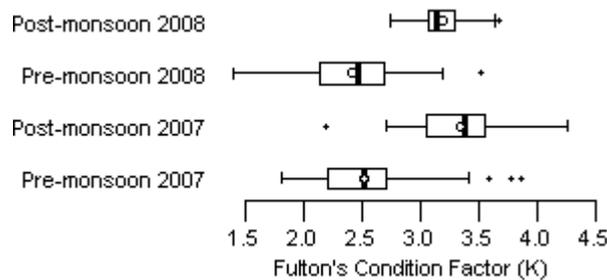


**Figure 2.2: Test plot of  $\log(a)$  against  $b$  for seven LWRs of *T. jarbua***

The black dot identifies the present study parameters. The crosses represent the parameters of the six other studies (Table 2.1). The plain line represents the regression line,  $r^2 = 0.84$ . The extreme point on the left might be seen as an outlier, possibly because it includes a narrow range of juveniles

**Fulton's condition factor**

The values for K ranged from 1.399 to 4.523. At Khor Dubna, significant differences in K between pre- and post-monsoon samples in 2007 and 2008 ( $p < 0.01$ ) were found with K mean values higher during the post-monsoon than the pre-monsoon periods. No difference was found between years (Fig. 2.3). Seasonal changes in body weight and in protein, lipid and water contents in fishes as been reported in several studies (Weatherley and Gill, 1987) and is usually driven by the food availability, the environmental conditions and the reproductive status of the fishes; this last parameter being not considered in the data mainly measured on juveniles. The high K values during the post- Summer Monsoon period are the direct consequences of the upwelling responsible of higher productivity and food availability. Indeed upwelling systems of cold nutrient-rich waters are formed, promoting high primary and secondary productivity (Klaus and Turner, 2004). Strong coastal wind and wave action establish connections between estuaries and the fertile ocean water masses which are otherwise often partly or fully isolated from each other. Thus, the high availability of nutrition, and the favorable environmental conditions during the south-west monsoon (e.g.: lower water temperatures and salinity, higher oxygenation levels) allow fishes to increase in weight in a short period of time. By contrast the low K values during the pre- Summer Monsoon period can be explained by the degradation of environmental conditions (e.g.: higher water temperatures and salinity up to 39 ‰, lower oxygenation levels) and nutritional impoverishment in the estuaries.

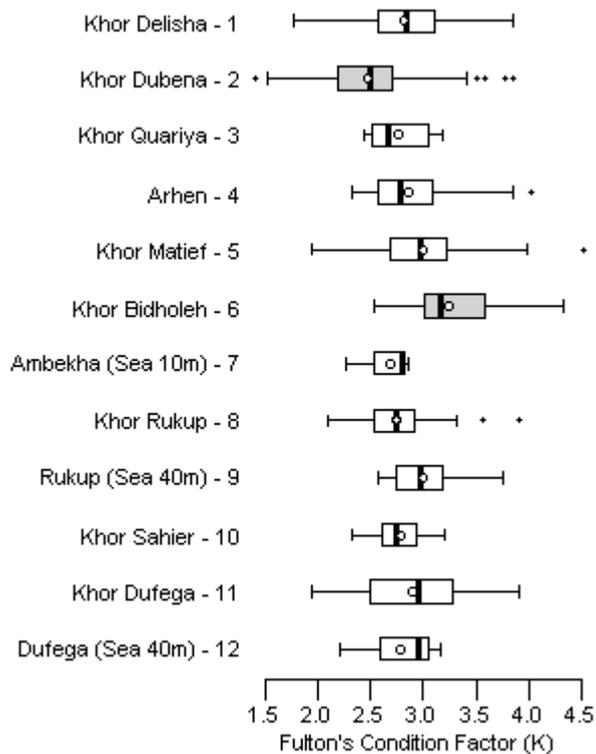


**Figure 2.3: Box plot of condition factor K for Khor Dubena during pre- and post- Summer Monsoon periods of 2007 and 2008**

The open circles represent the mean condition factor, the vertical dark bars represent the median condition factor, boxes encompass 50 % of the data, whiskers encompass 95 % and small crosses represent outliers. Only differences between seasons are significant ( $p < 0.01$ ).

The null hypothesis of no differences between fish condition factors during the same season at different locations could not be rejected for most locations. However, two locations Khor Dubena and Khor Bidholeh both located on Socotra Island were significantly different in K ( $p < 0.01$ ) than all other locations (Fig. 2.4). The low K values of *T. jarbua* individuals at Khor Dubena can probably be explained (1) by the high fish diversity (27 species) inducing a high inter-specific competition for food and (2) by the high abundance of large predators such as the jack *Caranx heberi* (Bennett, 1830), the snappers *Lutjanus argentimaculatus* (Forsskål, 1775) and *Lutjanus fulviflamma* (Forsskål, 1775) and the emperor *Lethrinus nebulosus* (Forsskål, 1775).

Moreover this estuary is often closed from the sea for several months with only occasional water exchange with the ocean thus further reducing food availability for *T. jarbua* during these periods. The high K values at Khor Bidholeh could be related to the presence of a small fish landing site. Indeed, fish wastes have been observed as being directly discarded into the estuary and could represent a non negligible source of food for *T. jarbua* which constitute the dominant species of this estuary.



**Figure 2.4: Box plot of condition factor K per locations during pre-Summer Monsoon periods**

The open circles represent the mean condition factor, the vertical dark bars represent the median condition factor, boxes encompass 50 % of the data, whiskers encompass 95 % and small crosses represent outliers. The light grey boxes represent the locations that are significantly different ( $p < 0.01$ ) from all other locations.

*Terapon jarbua* is a temporal resident of coastal estuaries in the study area and occasionally targeted in the local subsistence fisheries. More generally, over the Indo-West Pacific, juveniles of *T. jarbua* are abundant in brackish waters as in the mangroves of Madagascar (Laroche et al., 1997), where this species represent 16% of the catch (i.e.: the second rank after the Gerreidae). The present study provides basic information on the LWR and seasonal condition of *T. jarbua* populations in the wider Gulf of Aden region in support of sustainable management of the species and especially of the estuaries of the coasts of Socotra Island and the Hadhramout, Yemen.

### **Acknowledgments**

The present study was mainly funded by the Total Foundation, Paris. It was partially conducted at the Socotra Field Research Station of the Biodiversity and Climate Research Centre (BiK-F), Frankfurt a.M., based on financial support of the research-funding programme “LOEWE – Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz” of Hesse's Ministry of Higher Education, Research, and the Arts. Additional mobility funds were provided by scholarships from the GRADE - Goethe Graduate Academy of the Goethe University Frankfurt a.M. and the International Doctoral College of the European University of Brittany (UEB). His Excellency the former Minister of Water and Environment of the Republic of Yemen, Eng. Abdul-Rahman F. Al-Eryani, and His Excellency the Chairman of the Environment Protection Authority, Eng. Mahmoud Shidiwa, are cordially acknowledged for their continued support and for granting research and sample export permits. The Socotra Conservation and Development Program (SCDP-UNDP) is thanked for providing indispensable support during the field work. We would like to thank the People of Socotra and in particular the members of the coastal communities which kindly facilitated field work and provided access to the areas in their care. We wish to express our gratitude to Fouad Naseeb and Motea Sheikh Aideed for their efficient assistance in the field, to Dr. El-Mashjary and Dr. Ali of the Hadhramout University for granting the authors access to the University wet laboratory, to Louis Quiniou and Jacques Baron for their advice concerning the statistical treatment of the data and to Friedhelm Krupp and Jean Laroche for their support to the Ph.D. project of the first author.



# Chapter

# 3

**Isolation and characterization of nine  
microsatellite loci of *Terapon jarbua* (Forsskål,  
1775) from Socotra Island (Gulf of Aden) using  
multiplex PCR**

---



## Summary

**Context:** Although advances have been made in the taxonomy and biology of the Terapontidae (Miu, 1990; Vari, 1978; Whitfield and Blaber, 1978), and the last chapter provided essential information on the important role of the monsoon to the fitness of juveniles *Terapon jarbua*, no in-depth studies of the life history strategy, phylogeography and population structure of *T. jarbua* have been conducted so far.

**Aim:** The aim of this study is to identify and characterize ten polymorphic microsatellite loci from 22 individuals of *T. jarbua* from Socotra Island.

**Materials and methods:** DNA libraries for *T. jarbua* were constructed and polymerase chain reaction (PCR) primers were designed by Genetic Identification Services. Genomic DNA was extracted from 22 individuals collected in March 2007 by seine net at Khor Matief on Socotra Island. DNA extractions were performed following the protocol developed by Ivanova et al. (2006). After optimization, PCR reactions were multiplexed in order to avoid the expenses of using specific fluorescent primers. Touchdown PCR conditions consisted of an initial denaturing step at 95°C (15') followed by 11 cycles at 94°C (30''), 63-53°C (1'30'') and 72°C (1'), followed by 25 cycles at 94°C (30''), 53°C (1'30'') and 72°C (1'). A final elongation step at 60°C (30 min) ended the PCR. Microsatellite alleles were visualized on an ABI 3130 Genetic Analyzer (Applied Biosystems™) and scored using GeneMapper® Software v4.0 (Applied Biosystems™).

**Results and conclusion:** Microsatellite polymorphism was tested, revealing 4 to 19 alleles per locus. The observed heterozygosity values ranged from 0.318 to 0.909. Nine loci out of ten conformed to Hardy-Weinberg proportions and did not show evidence for null alleles and gametic disequilibrium.

**Next chapter:** These newly developed loci coupled with Cytochrome *c* Oxydase sub-unit 1 (CO1) sequences will be used in the next chapter to explore the phylogeography of *T. jarbua* at both the Indo-West Pacific and the North-Western Indian Ocean and the genetic structure of *T. jarbua* in the wider Gulf of Aden including Socotra Island.



## **Isolation and characterization of nine microsatellite loci of *Terapon jarbua* (Forsskål, 1775) from Socotra Island (Gulf of Aden) using multiplex PCR**

E. Lavergne<sup>1, 2, 3</sup>, I. Calves<sup>3</sup>, U. Zajonz<sup>2, 1</sup> and J. Laroche<sup>3</sup>

<sup>1</sup> Senckenberg Forschungsinstitut und Naturmuseum, Sektion Ichthyologie – Senckenberganlage 25, 60325 Frankfurt am Main, Deutschland

<sup>2</sup> Biodiversität und Klima Forschungszentrum (BiK-F) – Senckenberganlage 25, 60325 Frankfurt am Main, Deutschland

<sup>3</sup> Université de Bretagne Occidentale, UMR 6539, CNRS/IRD/UBO, Laboratoire des Sciences de l'Environnement Marin LEMAR, Institut Universitaire Européen de la Mer, Rue Dumont d'Urville, 29280 Plouzané, France

**Corresponding author:** E. Lavergne, Tel +33 2 98 49 86 27

Email address: [edouard.lavergne@gmail.com](mailto:edouard.lavergne@gmail.com)

**Published as:** Lavergne, E., Calves, I., Zajonz, U., Laroche, J. (2011). Isolation and characterization of nine microsatellite loci of *Terapon jarbua* (Forsskål, 1775) from Socotra Island (Gulf of Aden) using multiplex PCR. Electronic supplement to Agostini et al. Permanent Genetic Resources added to Molecular Ecology Resources Database 1 October 2010-30 November 2010. *Molecular Ecology Resources*, **11**:418–421.

[DOI: 10.1111/j.1755-0998.2010.02970.x](https://doi.org/10.1111/j.1755-0998.2010.02970.x).

### **Abstract**

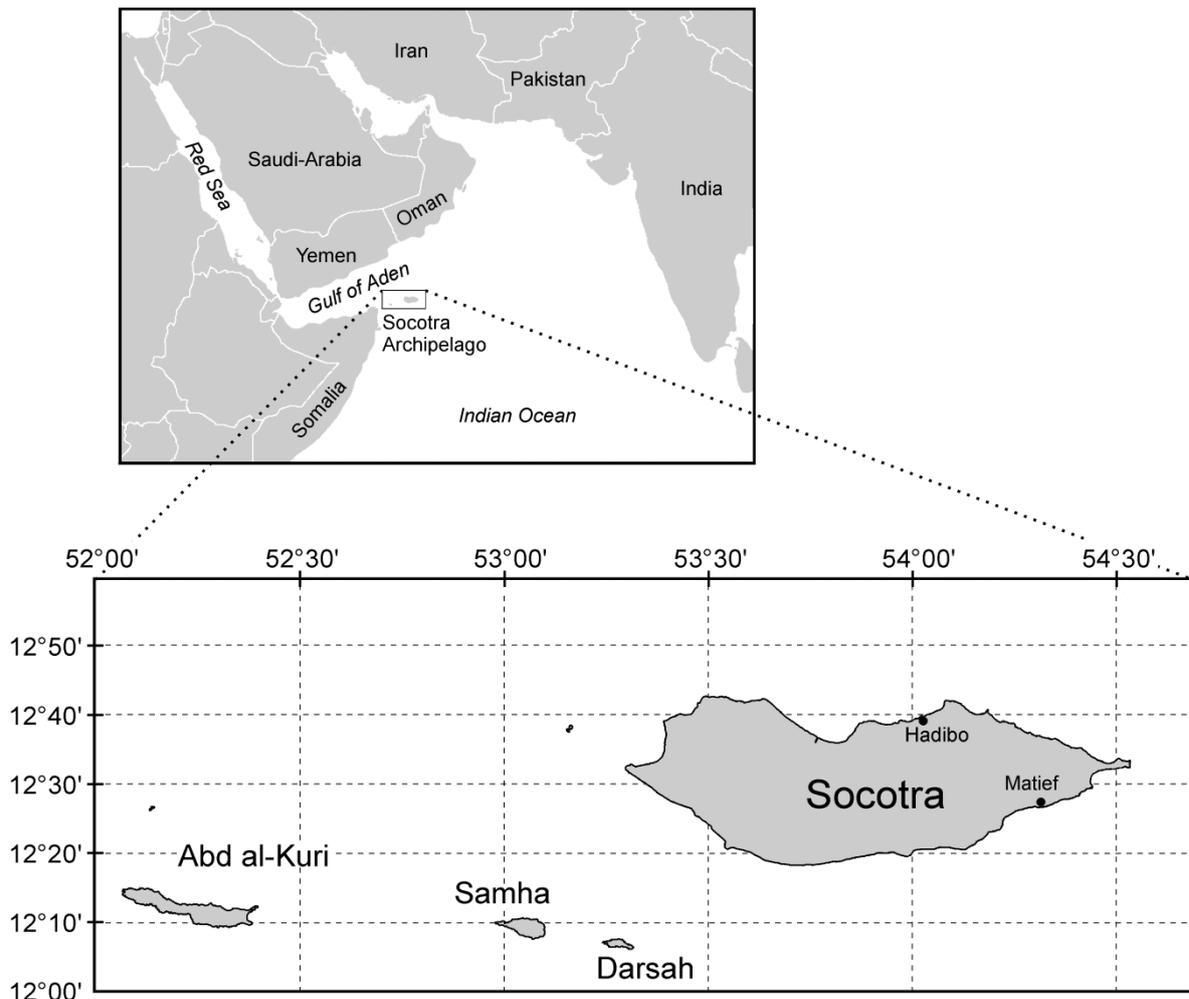
Ten polymorphic microsatellite loci were identified and characterized from 22 individuals of *Terapon jarbua* (Forsskål, 1775) from Socotra Island (Gulf of Aden, Yemen). Microsatellite polymorphism was tested, revealing 4 to 19 alleles per locus. The observed heterozygosity values ranged from 0.318 to 0.909. Nine loci out of ten conformed to Hardy-Weinberg proportions. They did not show evidence for null alleles and gametic disequilibrium. These loci will be used in an ongoing study of the population structure of this species; associated with a study assessing habitat connectivity based on otolith microchemistry of *T. jarbua*. Results are expected to inform estuarine conservation efforts on Socotra Island and in the Gulf of Aden region.

**Keywords:** *Terapon jarbua*, microsatellites, population genetics, Socotra Island

*Terapon jarbua* (Terapontidae, Perciformes) inhabits marine and brackish waters of the Indo-Pacific, from the Red Sea and east coast of Africa to Samoa. Its juveniles have been observed to thrive even in coastal freshwater courses. The type locality of the species is Jeddah, Saudi Arabia, and the type series is deposited in the Zoological Museum of Copenhagen (Klausewitz and Nielsen, 1965; Nielsen, 1974). Although advances have been made in the taxonomy and biology of the Terapontidae (Miu, 1990; Vari, 1978; Whitfield and Blaber, 1978), no in-depth studies of the reproductive ecology, life history strategy and population structure of *T. jarbua* have been conducted as of yet. The microsatellite markers presented herein are therefore the first developed for this species, and will be especially supportive to further genetic studies of the species.

DNA libraries for *Terapon jarbua* enriched for microsatellite sequences containing AAC, ATG, CATC and TAGA repeat motifs were constructed by Genetic Identification Services following the method described by Jones et al. (2002). Resulting recombinant clones were selected at random and sequenced on an Applied Biosystems™ 377 DNA Sequencer, using Amersham's DYEnamic™ ET Terminator Cycle Sequencing Kit (Amersham Biosciences P/N US81050). Initial polymerase chain reaction (PCR) primers were designed for flanking regions of microsatellite containing sequences using DESIGNER PCR v1.03 (Research Genetics Inc.).

Genomic DNA was extracted from muscle tissue, preserved in 95% ethanol of 22 individuals collected in March 2007 by seine net at Khor Matief (12° 26' 48.5'' N and 54° 18' 17.6'' E) on Socotra Island (Fig. 3.1) (khor = estuary). Extractions were performed using AcroPrep™ 96 well Filter Plates (1mL) with 1µm Glass Fiber media (PALL® 5051), following the extraction protocol for DNA barcoding by Ivanova et al. (2006). PCRs conducted on a GeneAmp PCR system 9700 (Applied Biosystems™) were optimized for each primer individually on four randomly selected samples. After optimization, PCR reactions were multiplexed in a total reaction volume of 10µL, using 5µL of Master-mix, 1µL of Solution Q both from the Qiagen Multiplex PCR kit, 1µL of multiplexed primer-mix (Table 3.1) containing specific primers and the labelled universal primers 6Fam-TAGTCGACGACCGTTA, Yakima Yellow YY-TCGGATAGCTAGTCGT, and Dargonfly Orange DO-CTGGCCGTCGTTTTAC (Chang et al. 2004) in order to avoid the expenses of using specific fluorescent primers, 1µL of template DNA (30-50 ng.µL<sup>-1</sup>) and 2µL of water. Touchdown PCR conditions consisted of an initial denaturing step at 95°C (15') followed by 11 cycles at 94°C (30''), 63-53°C (1'30'') and 72°C (1'), followed by 25 cycles at 94°C (30''), 53°C (1'30'') and 72°C (1'). A final elongation step at 60°C (30 min) ended the PCR. 3µL of PCR products were added to 12µL of formamide and 0.2µL of a 50-500bp size standard (GeneScan-500 LIZ™) to visualize microsatellite alleles using an ABI 3130 Genetic Analyzer (Applied Biosystems™). Alleles were then scored using GeneMapper® Software v4.0 (Applied Biosystems™).



**Figure 3.1: Map of Socotra Archipelago and sampling site location (Matief)**

The number of alleles and the observed and expected heterozygosity values were calculated using GENETIX v4 (Belkhir, 2004); deviation from the Hardy–Weinberg proportions (Fisher’s exact test) and gametic disequilibrium (Fisher’s exact test) among loci were tested using GENEPOP v4 (Raymond and Rousset, 1995; Rousset, 2008). Both tests were corrected for multiple simultaneous tests by calculating the q-value of each test which measures the minimum *false discovery rate (FDR)* that is incurred when calling that test significant. The bootstrap method was chosen as recommended by the authors for a limited number of p-values (Storey 2002). The q-values were calculated using the R package QVALUE ([www.r-project.org](http://www.r-project.org), Ihaka and Gentleman, 1996; Storey, 2002, 2003; Storey and Tibshirani, 2003; Storey et al., 2004). This correction was preferred over the commonly used sequential Bonferroni correction (Rice, 1989) following Moran (2003). Null allele frequencies were calculated based on Brookfield (1996) using the program MICRO-CHECKER (Van Oosterhout et al., 2004).

Ten out of 12 loci were reliably amplified and found to be polymorphic for *T. jarbua* (Table 3.2). The number of alleles per locus ranged from 4 to 19, with observed and expected heterozygosity values varying respectively from 0.318 to 0.909, and from 0.328 to 0.941. Exact

tests after correction indicated that one locus (B107) deviated significantly from Hardy-Weinberg proportions ( $q$ -value  $< 0.01$ ). Exact test for gametic disequilibrium yielded five weakly significant  $p$ -values ( $p$ -value  $< 0.05$ ) out of 45 pair wise comparisons; none of which were ultimately found to be significant following the FDR correction ( $q$ -value  $> 0.05$ ). No locus showed evidence for a null allele. Therefore, nine of the ten markers presented in this study can be applied in studying the genetic structure of *T. jarbua* populations. Such studies are expected to be instrumental in future estuary conservation and management efforts (1) in Yemen including the Socotra Archipelago, representing a UNESCO World Heritage (2008), which is a treasure of marine biodiversity of regional and global importance (Zajonz and Krupp, 2006), and (2) in the wider Indian Ocean.

**Table 3.1: Multiplex primer-mix**

<b>Multiplex PCR 1</b>	<b>Multiplex PCR 2</b>
5 $\mu$ L R C102 primer, 100nM	5 $\mu$ L R A4 primer, 100nM
5 $\mu$ L R C108 primer, 100nM	5 $\mu$ L R B107 primer, 100nM
5 $\mu$ L R C3 primer, 100nM	5 $\mu$ L R D108 primer, 100nM
1 $\mu$ L F C102 primer + univ. ext., 10nM	1 $\mu$ L F A4 primer + univ. ext., 10nM
1 $\mu$ L F C108 primer + univ. ext., 10nM	1 $\mu$ L F B107 primer + univ. ext., 10nM
1 $\mu$ L F C3 primer + univ. ext., 10nM	1 $\mu$ L F D108 primer + univ. ext., 10nM
5 $\mu$ L 6FAM-univ. primer, 100nM	5 $\mu$ L 6FAM-univ. primer, 100nM
5 $\mu$ L YY-univ. primer, 100nM	5 $\mu$ L YY-univ. primer, 100nM
5 $\mu$ L DO-univ. primer, 100nM	5 $\mu$ L DO-univ. primer, 100nM
117 $\mu$ L H <sub>2</sub> O	117 $\mu$ L H <sub>2</sub> O
150 $\mu$ L	150 $\mu$ L
<b>Multiplex PCR 3</b>	<b>Multiplex PCR 4</b>
5 $\mu$ L R B103 primer, 100nM	5 $\mu$ L R B106 primer, 100nM
5 $\mu$ L R C103 primer, 100nM	5 $\mu$ L R C105 primer, 100nM
5 $\mu$ L R D102 primer, 100nM	5 $\mu$ L R D3 primer, 100nM
1 $\mu$ L F B103 primer + univ. ext., 10nM	1 $\mu$ L F B106 primer + univ. ext., 10nM
1 $\mu$ L F C103 primer + univ. ext., 10nM	1 $\mu$ L F C105 primer + univ. ext., 10nM
1 $\mu$ L F D102 primer + univ. ext., 10nM	1 $\mu$ L F D3 primer + univ. ext., 10nM
5 $\mu$ L 6FAM-univ. primer, 100nM	5 $\mu$ L 6FAM-univ. primer, 100nM
5 $\mu$ L YY-univ. primer, 100nM	-
5 $\mu$ L DO-univ. primer, 100nM	7,5 $\mu$ L DO-univ. primer, 100nM
117 $\mu$ L H <sub>2</sub> O	119,5 $\mu$ L H <sub>2</sub> O
150 $\mu$ L (Total volume)	150 $\mu$ L (Total volume)

Primer and universal extension association is shown in Table 3.2

**Table 3.2: Primer sequences for 10 microsatellite loci and allele statistics in one population (N = 22) of *T. jarbua***

Loci	EMBL #	Repeat motif	5' Universal Extension	Primers 5' → 3'	<i>i</i>	A	R	$H_E$	$H_O$	$P_{HW}$	$Q_{HW}$
C102	FR719958	(CTAT) <sub>13</sub> (CCAT) <sub>28</sub> (CTAT) <sub>2</sub>	F: CTGGCCGTCGTTTTACGTCTCCCTCCCTCATGTCTG R: TTGCCACAGTGGACCTGTAG	1 19 171-257	0.938	0.909	0.0662	0.0513			
C108	FR719959	(ATCC) <sub>9</sub> ATTT(ATCC) <sub>2</sub>	F: TCGGATAGCTAGTCGTCCATCCATTCATCCATCTAC R: GCTTTGGAGTATTTTGCAGTT	1 7 274-336	0.763	0.727	0.2318	0.0773			
C3	FR719960	(CATC) <sub>7</sub>	F: TAGTCGACGACCGTTACATAATGAGCGAGGTCAGAT R: ATCACGGAGGTTCTAAGAGTC	1 6 278-305	0.791	0.727	0.0770	0.0513			
A4	FR719961	(AAC) <sub>14</sub>	F: TCGGATAGCTAGTCGTACCTGCCTACTACAGCCTCAG R: CACTCCACTTGCCCATTTT	2 5 262-271	0.711	0.636	0.2146	0.0773			
B107	FR719962	(CAT)CAA(CAT) <sub>7</sub>	F: CTGGCCGTCGTTTTACCCAAGTTCCTGATGCTAAAAG R: AGACGATGATGGGATTATTTG	2 10 205-231	0.868	0.773	0.003*	0.0008*			
B103	FR719963	(CAT) <sub>2</sub> CTT(CAT) <sub>9</sub> CAC(CAT)	F: TCGGATAGCTAGTCGTGGGCTGTAACAGTATGCAATG R: ATGCAGCACCTTCAGAGTTTA	3 4 215-227	0.669	0.727	0.5839	0.1557			
C103	FR719964	(TCCA) <sub>8</sub>	F: CTGGCCGTCGTTTTACCTTTCAATAGCCAGGACTACC R: TCTTCCACACTGAGACTGCT	3 4 183-198	0.665	0.545	0.1209	0.0645			
B106	FR719965	(CAT) <sub>2</sub> CA(CAT) <sub>4</sub> CAC(CAT)	F: CTGGCCGTCGTTTTACAGAGGAGGACCACATAAACAC R: TTCCACCAGATGAGAGGAG	4 11 112-159	0.859	0.727	0.0540	0.0513			
C105	FR719966	(ATCC) <sub>5</sub> CTCC(ATCC) <sub>12</sub>	F: CTGGCCGTCGTTTTACAGCTTTGTGAGGCTAATACCAG R: AAGTCTTCTTCAACCCTGTGAG	4 6 242-314	0.328	0.318	0.5475	0.1557			
D3	FR719967	(TCTA) <sub>10</sub>	F: TAGTCGACGACCGTTACAGTCCAGTAATGTCGTTTGT R: AGTGTTAGACAGGAGCACATG	4 19 283-349	0.941	0.909	0.2256	0.0773			

*i*, multiplex PCR index (Table 3.1); A, allele nb; R, size range;  $H_E$ , expected heterozygosity;  $H_O$ , observed heterozygosity;  $P_{HW}$ , *p*-value of HW exact test;  $Q_{HW}$ , *q*-value of HW exact test; \*, Significant deviation from HWE.

### **Acknowledgments**

The present study was mainly funded by the Total Foundation, Paris. It was partially conducted at the Socotra Field Research Station and the Molecular Laboratory of the Biodiversity and Climate Research Centre (BiK-F) based on financial support of the research funding programme “LOEWE – Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz” of Hesse's Ministry of Higher Education, Research, and the Arts. Additional mobility funds were provided by scholarships from the GRADE - Goethe Graduate Academy of the Goethe University Frankfurt a.M. and the International Doctoral College of the European University of Brittany (UEB). A European Community fund (CPER-FEDER project) allowed the LEMAR laboratory to acquire the high performance DNA sequencer used in this study. We would like to express our gratitude to the Ministry of Water and Environment and the Environment Protection Authority of Yemen for granting research and sample export permits. The Socotra Conservation and Development Program (SCDP-UNDP) is thanked for providing indispensable support during the field work. We wish to express our gratitude to Fouad Naseeb and Motea Sheikh Aideed for their efficient assistance in the field, to Dr. Le Maréchal for providing us the universal primer sequences and to Leila Meistertzheim for her useful comments on the manuscript. Friedhelm Krupp is cordially acknowledged for his support to the Ph.D. project of the first author.

# Chapter

# 4

**Complex genetic structure of *Terapon jarbua* (Forsskål, 1775) nurseries in temporarily open closed estuaries from the wider Gulf of Aden**

---



## Summary

**Context:** Few studies were led on fish genetic structure in the North-Western Indian Ocean, an area under strong climatic influence, characterized by the alternating monsoon seasons driven by the Inter-Tropical Convergence Zone (ITCZ). In this region, the marine and estuarine inshore communities of Socotra are important “stepping stones” connecting populations of various taxonomic groups from various parts of the four biogeographic units with each other, allowing distinct faunal communities to overlap, and thus creating a biogeographically complex picture. There is a need to fill an important gap in available information about phylogeography and genetic structure of marine and estuarine fishes in the region, which could contribute to the first stage for future conservation plans around Socotra Island.

**Aim:** The aim of this study is to explore the phylogeography over both the Indo-West Pacific and the North-Western Indian Ocean scales and the genetic structure over the wider Gulf of Aden including Socotra Island of *Terapon jarbua*, by considering several genetic markers. The objectives are 1) to analyse the polymorphism of the Cytochrome *c* Oxydase sub-unit 1 (CO1) and 2) to genotype nine microsatellites as their high variability allowed to explore a more recent population history, and a possible genetic structure over reduced spatial scales.

**Materials and methods:** *T. jarbua* DNA were extracted from muscle tissues following the protocol developed by Ivanova et al. (2006).

1) High Resolution Melting Analysis, a diagnosis tool of genetic polymorphism: HRMA is a close-tube PCR allowing real-time visualisation of DNA product amplification. This method was firstly developed for clinical and diagnostic studies (Malewski et al., 2010). Recently HRMA has been used in numerous other applications such as the scanning of SNPs, the discovery of mutations, the analysis of DNA methylation, the DNA cartography, the identification of species or the study of viral populations. In front of this success, scientists started to be interested in the use of HRMA to study marine populations because of its relatively low cost, its ease of setting up and implementing and its short manipulation time compare to other methods available (SSCP, mass sequencing) (Larsen et al., 2007; Metzker, 2010). This new tool was used in the present study to determine CO1 variants in 229 individuals from 11 locations across Indo-West Pacific, and two out-group locations in India and China. Each of these variants was discriminated by sequencing at least one individual per variants (Meistertzheim et al., 2012). Relationships among haplotypes were estimated by a statistical parsimony procedure (Crandall and Templeton, 1994; Templeton et al., 1992) and genetic differentiation statistics based on haplotype frequencies

(Duran et al., 2004; Raymond and Rousset, 1995) were calculated to test the null hypothesis of random haplotype distribution among sampling locations. Pairwise genetic distances (Tamura and Nei, 1993) based on nucleotide frequencies were also calculated. MDS at both large and reduced scales were used to graphically represent genetic differentiation between locations. Analyses of molecular variance (AMOVA) (Excoffier et al., 1992) were performed to quantify the level of genetic differentiation among and within previously identified MDS groups.

2) Microsatellite genotyping: Primers developed in the previous chapter have been used to amplify nine microsatellite loci from 288 specimens of *T. jarbua* caught from 10 locations on Socotra Island and Yemen mainland. Following touchdown PCR's, microsatellite alleles were visualized on an ABI 3130 Genetic Analyzer (Applied Biosystems™) and scored using GeneMapper® Software v4.0 (Applied Biosystems™). Descriptive,  $F$  statistics (Weir and Cockerham, 1984) and genetic distances (Cavalli-Sforza and Edwards, 1967) were calculated in order to detect any genetic differentiation between locations. An MDS was performed to assess whether any indications for group structure could be observed. Finally, isolation by distance was tested using a Mantel permutation procedure (Mantel, 1967).

### **Results and conclusion:**

High levels of haplotype diversity and genetic structure ( $\Phi_{ST} = 0.882$ ,  $p < 0.01$ ) were revealed, suggesting a restricted gene flow between the North-Western Indian Ocean, West India (Indian Ocean) and the South Chinese Sea (Pacific Ocean) imposed by the well known biogeographical barrier between the Arabian Sea and the Indian Ocean and the Indo-Pacific Barrier between the Indian and Pacific Ocean. By using such molecular data from a large part of this species distribution, we suggest that *T. jarbua* might in fact be a species complex

Over the Socotra – Yemen area, this study detected a significant genetic differentiation between estuaries, considering the variability of the microsatellites ( $F_{ST} = 0.035$ ,  $p < 0.01$ ). Geographical distance was not a structuring factor for *T. jarbua* populations in this region. This spatial structure might be the result of stochastic environmental variables (i.e.: currents, opening of estuaries, mortality) on estuary recruitment, post-larvae settlement and juvenile survival. Thus some nurseries might be randomly dominated by particular subpopulations while others might be colonized by possible larval pool stemming from different subpopulations.

**Next chapter:** Combining microsatellite with markers such as otolith elemental fingerprints would lead to complementary information on population connectivity. Thus, the last chapter will reconstruct migratory pattern and geochemically define nursery and natal origins of *T. jarbua* in an attempt to correlate this results with potential genetic structure.

## Complex genetic structure of *Terapon jarbua* (Forsskål, 1775) nurseries in temporarily open closed estuaries from the wider Gulf of Aden

E. Lavergne<sup>1, 2, 3</sup>, I. Calves<sup>3</sup>, A. L. Meistertzheim<sup>4</sup>, G. Charrier<sup>5</sup>, U. Zajonz<sup>2, 1</sup> and J. Laroche<sup>3</sup>

<sup>1</sup> Senckenberg Forschungsinstitut und Naturmuseum, Sektion Ichthyologie – Senckenberganlage 25, 60325 Frankfurt am Main, Deutschland

<sup>2</sup> Biodiversität und Klima Forschungszentrum (BiK-F) – Senckenberganlage 25, 60325 Frankfurt am Main, Deutschland

<sup>3</sup> Université de Bretagne Occidentale, UMR 6539, CNRS/IRD/UBO, Laboratoire des Sciences de l'Environnement Marin LEMAR, Institut Universitaire Européen de la Mer, Rue Dumont d'Urville, 29280 Plouzané, France

<sup>4</sup> Centre de Formation et de Recherche sur l'Environnement Méditerranéen (CEFREM), UMR 5110, CNRS/UPVD, Université de Perpignan, France

<sup>5</sup> Department of Marine Ecology, Tjärnö University of Gothenburg, SE-452 96 Strömstad Sweden

**Corresponding author:** E. Lavergne, Tel +33 2 98 49 86 27

Email address: edouard.lavergne@gmail.com

To be submitted

### Abstract

The population structure of the Indo-West Pacific grunter *Terapon jarbua* is described by analysing sequence variation in a fragment of the mitochondrial gene Cytochrome *c* Oxidase subunit I in 229 individuals from 11 locations across the Indo-West Pacific, and two out-group locations in India and China. High levels of haplotype diversity and genetic structure ( $\Phi_{ST} = 0.882$ ,  $p < 0.01$ ) revealed a restricted gene flow between the North-Western Indian Ocean, West India and the South Chinese Sea (Pacific Ocean) imposed by the well known biogeographical barrier between the Arabian Sea and the Indian Ocean and the Indo-Pacific Barrier between the Indian and Pacific Ocean. According to the molecular data collected from a large part of the species distribution, we suggest that *T. jarbua* might in fact be a species complex with mtDNA introgression by hybridization with an other species.

The use of nine microsatellites in 288 individuals from 10 locations across the Wider Gulf of Aden including Socotra Island underlined a significant genetic differentiation between nurseries ( $F_{ST} = 0,035$ ,  $p < 0.01$ ). This spatial structure might be the result of stochastic environmental variables (i.e.: currents, opening of estuaries, mortality) on estuary recruitment, post-larvae

settlement and juvenile survival. Thus some nurseries might be randomly dominated by particular subpopulations while others might be colonized by possible larval pool stemming from different subpopulations.

**Keywords:** Grunter, *Terapon jarbua*, Socotra, Yemen, temporarily open closed estuary, nursery, population genetics

## Introduction

In the marine environment, larval dispersal and migration minimize fish population structure (Bradbury et al., 2008; Hastings and Botsford, 2006; Sinclair, 1988). Although marine species are often characterized by a large gene flow between populations, weak genetic structure, and large genetic neighbourhoods (Roman and Palumbi, 2004), biotic factors such as life history, behaviour or demography and abiotic factors such as currents, climate or environmental stress can shape fish genetic structure on limited geographical scales up to few hundred kilometres (Bradbury et al., 2008; Nielsen et al., 2004; Olsen et al. 2008).

Genetic studies have become in the last 30 years an essential tool for the conservation of estuarine, coastal and marine populations, providing estimations of their genetic diversity and possibly of their ability to survive in a changing environment (Schmitt and Hewitt, 2004; Visram et al., 2010). Several investigations on the phylogeography and genetic structure of marine organisms have been conducted over the Indo-Pacific (Gaither et al., 2010; Gill and Kemp, 2002; Gill, 2004; Harold et al., 2008; He et al., 2011; Winters et al., 2010). However, only few population genetic studies have been performed on fish from the North-Western Indian Ocean.

The Socotra Archipelago is characterized by alternating monsoon seasons driven by the Inter-Tropical Convergence Zone (ITCZ): the weak and wet winter or north-east monsoon (October – February) and the forceful and dry summer or south-west monsoon (Currie et al., 1973; Fleitmann et al., 2004; Fratantoni et al., 2006; Glynn, 1993; Kemp, 1998; Klaus and Turner, 2004; Scholte and de Geest, 2010). The particular geography and climate of Socotra Island is responsible of the presence of rivers (i.e.: wadi) and temporarily open/closed estuaries (TOCE or “Khor”), which are often separated from the sea by gravelly or sandy berms. These last systems are only connected to the sea after flush floods during the rainy seasons or by storm surges. Thus, in Socotra the connectivity between the brackish waters and the marine environment could be temporally limited.

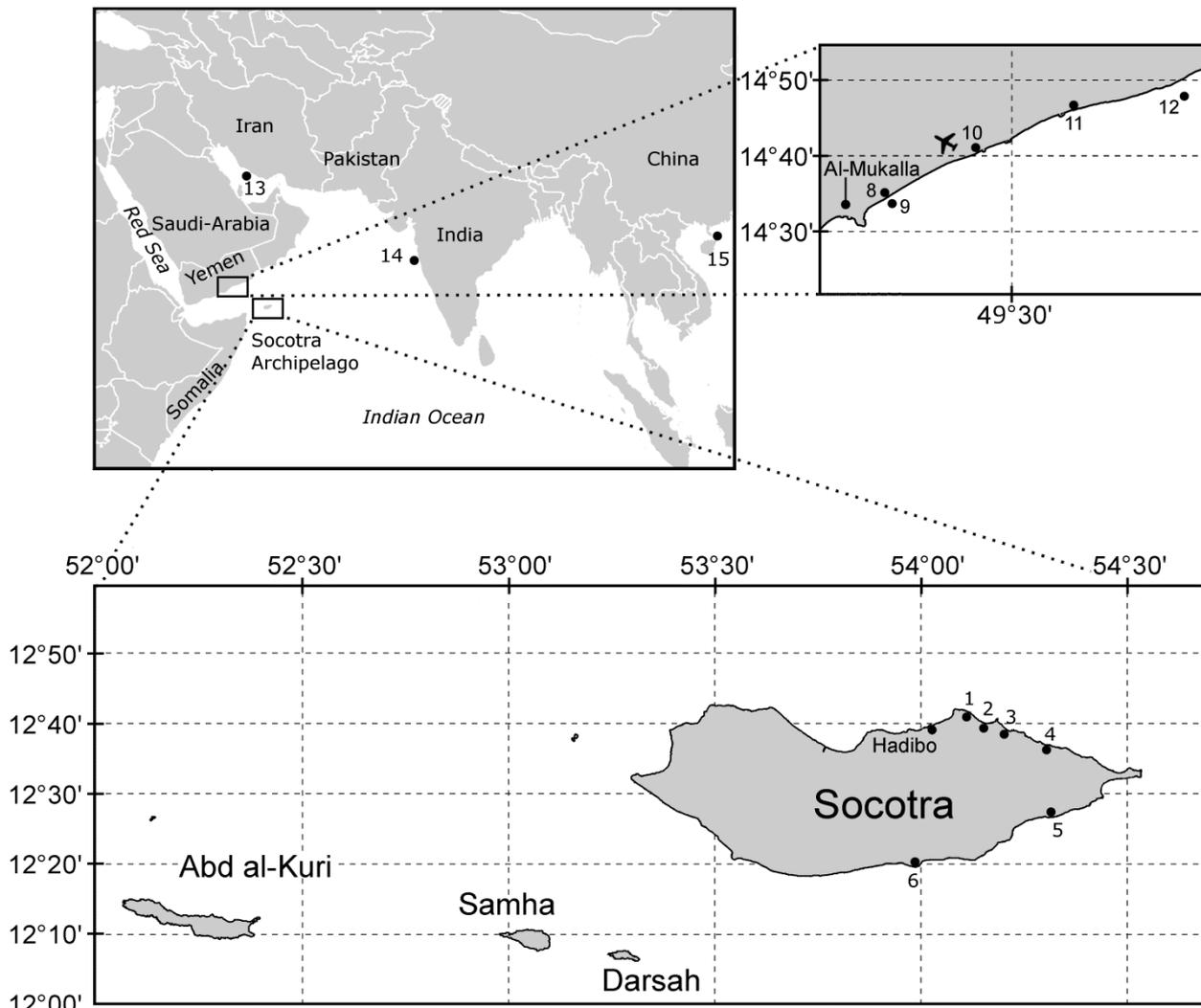
The island of Socotra lies in the north-western corner of the Indian Ocean, at the junction between the Gulf of Aden and the Arabian Sea at 12°30'N and 54°00'E, close to the boundaries of four major biogeographic units of the circum-Arabian seas: the Eritrean, South Arabian and

Persian sections of the Arabian subprovince and the Western Indian Ocean subprovince (Kemp, 1998; Zajonz et al., 2000). In this context, the marine inshore communities of Socotra are important “stepping stones” connecting populations of various taxonomic groups from diverse parts of the four biogeographic units, allowing distinct faunal communities to overlap, and thus creating a biogeographically complex assemblage (Zajonz et al., 2000, Chapter 1). There is a need to fill an important lack of information about the phylogeography and genetic structure of fishes in the region, as a first stage for future conservation plans around Socotra Island.

Considering the mitochondrial control region D-Loop of the blue barred parrotfish, *Scarus ghobban* Forsskål, 1775, Visram et al. (2010) observed a significant but weak genetic differentiation among populations along with some isolation by distance from the coasts of Kenya to Mauritius, which are separated by the Equatorial currents. Dorenbosch et al. (2006), using amplified fragment length polymorphism (AFLP), observed a significant but low genetic differentiation among Dory snapper, *Lutjanus fulviflamma* (Forsskål, 1775) populations from the coasts of Kenya to the Comoros Archipelago, suggesting a genetic connexion over large distances in the region.

The grunter *Terapon jarbua* (Forsskål, 1775) (Terapontidae, Perciformes), locally known as “Dirhar” in Yemen mainland and “Habraham” on Socotra Island, inhabits marine and brackish waters of the Indo-West Pacific from the Red Sea and east coast of Africa to Samoa (Klausewitz and Nielsen, 1965; Nielsen, 1974; Vari, 1978). Juveniles have been observed to thrive even in coastal freshwater courses. More recently, Golani and Appelbaum-Golani (2010) reported the species as a Lessepsian migrant to the Eastern Mediterranean. The type locality of the species is Jeddah, Saudi Arabia, and the type series is deposited in the Zoological Museum of Copenhagen (Klausewitz and Nielsen, 1965; Nielsen, 1974). Wallace et al. (1984) observed that the reproduction, spawning and early larval life of *T. jarbua* is limited to the marine environment, but estuarine recruitment seems to take place at an early stage. Miu et al. (1990) suggested that *T. jarbua* is a fractional spawner according to multimodal egg size frequency distribution in ovary at any gonad stage. Spawning in several batches is a common reproductive behaviour among tropical and subtropical fish, which seems to avoid overcrowding of larvae and reduce food competition among offspring. The wide distribution of the species beyond the studied region and its ability to cope with contrasted environments (salinity: 0-39 ‰, temperatures: up to 36°C) indicate that this species can be considered as an excellent sentinel species for the estuaries of the studied region. Although advances have been made in the taxonomy and biology of the Terapontidae (Miu et al., 1990; Vari, 1978; Whitfield and Blaber, 1978), the genetic structure of *T. jarbua* remains unknown.

In this study, the genetic structure of *T. jarbua* in the wider Gulf of Aden including Socotra Island, have been explored by considering several genetic markers. Firstly, the polymorphism of the Cytochrome *c* Oxidase sub-unit 1 (CO1) was analysed to infer the historical relationships between populations (Avise, 2004; He et al., 2011) i.e.: the *T. jarbua* phylogeography. Secondly, nine microsatellites were analysed to explore the more recent history of *T. jarbua* populations, and a possible genetic structure over reduced spatial scales.



**Figure 4.1: Map of sampling locations**

1 – Khor Delisha, 2 – Khor Dubena, 3 – Khor Quariya, 4 – Arhen, 5 – Khor Matief, 6 – Khor Bidholeh,  
8 – Khor Rukup, 9 – Rukup (Sea 40 m), 10 – Khor Sahier, 11 – Khor Dufega, 12 – Dufega Sea, 13 – Iran,  
14 – India and 15 – China.

## Materials and methods

### *Sampling and DNA extraction*

A total of 288 specimens of *Terapon jarbua* were sampled using a seine net at ten locations (eight TOCE's, one freshwater stream and one at sea) in the wider Gulf of Aden region including Socotra Island and the Hadramout coast of Yemen (Fig. 4.1, Table 4.1) from 2007 to 2008. In

addition, the data set was completed with already published sequences from Iran, India and China. All individuals were photographed, measured and weighted (Chapter 2); muscle tissues were sampled and placed in 95% ethanol. Muscle tissues of seven additional frozen specimens collected by fishermen in coastal water 25 miles off Mogadiscio (Somalia) were also preserved in 95% ethanol. Total genomic DNA was extracted from tissue samples using AcroPrep™ 96 well Filter Plates (1 mL) with 1 µm Glass Fiber media (PALL® 5051), following the extraction protocol for DNA barcoding by Ivanova et al. (2006).

**Table 4.1: Sampling locations**

Locations	Coordinates (Lat., Long.)	
1-Khor Delisha	12°41'11.3''N, 54°07'47.8''E	Shallow khor isolated by a sand berm, with a very low water level during the dry period. Very eutrophicated, many <i>Chara</i> sp. and filamentous algae. A “bridge” should allow water to circulate but disintegrating construction material (rocks) reduces significantly the water flow.
2-Khor Dubena	12°40'16.3''N, 54°09'01.6''E	Shallow khor periodically isolated by a sand berm. Continuous slow flow of very clear fresh to brackish water crossing a date palm plantation.
3-Khor Quariya	12°38'31.8''N, 54°13'29.1''E	Large khor connected to the sea at the time of the surveys, only rarely isolated by a sand berm. Stagnant to very slow flowing water from the hinterland.
4-Arhen	12°36'44.0''N, 54°18'16.0''E	Very small freshwater stream running from karst caves in the coastal escarpment.
5-Khor Matief	12°26'48.5''N, 54°18'17.6''E	Large khor isolated by a gravelly berm resting on a sandy bottom, which may imply slight interstitial water exchange when not connected to the sea. Opened during the monsoon storms and associated floodwaters.
6-Khor Bidholeh	12°19'45.8''N, 54°00'29.5''E	Khor opened to the sea with highly limited freshwater input, used by local fishermen as a fish landing site.
8-Khor Rukup	14°34'34.5''N, 49°13'43.6''E	Khor periodically isolated by a sand berm. The wadi is crossed up stream by a large road.
9- Rukup (Sea)	14°33'20.3''N, 49°14'12.8''E	Located in front of Khor Rukup (40 m depth).
10-Khor Sahier	14°39'55.4''N, 49°24'55.6''E	Khor periodically isolated by a sand berm. The wadi is crossed up stream by a large road.
11-Khor Dufega	14°45'45.4''N, 49°37'51.2''E	Khor periodically isolated by a sand berm. The wadi is crossed up stream by a large road.
13-Iran	27°23'60.0''N, 52°21'36.0''E	No information
14-India	19°01'12.0''N, 72°27'36.0''E	No information
15-China	≈ 21°N, 110°35'60''E	Fishes were caught at different sites around Zhanjiang (China), however all specimens were collected within a 50-75 km radius area.

This study is part of a larger survey including estuarine fish community analysis (Chapter 1), and trace element analysis of *T. jarbua* otoliths (Chapter 5). As we wished to be consistent with location numbering between studies and because all locations of the survey were not involved in the present study, the locations 7 and 12 were not presented here.

### **Protocol for High Resolution Melting Analysis (HRMA) of CO1**

*Principals.* HRMA is a close-tube PCR (Polymerase Chain Reaction) allowing real-time visualisation of DNA product amplification by monitoring the release of an intercalating DNA dye from a denaturated DNA double helix by increasing temperature (Malewski et al., 2010).

HRMA has already been used in detecting heterozygosity and DNA sequence variations, and in identifying organisms such as fishes (Dalmaso et al., 2007).

*PCR design and optimization.* A fragment of the mitochondrial DNA (mtDNA) COI gene of 213 individuals of *T. jarbua* was amplified using the primers Fish-F2 and Fish-R2 described by Ward et al. (2005). Real time PCR reactions were carried out in 96-well plates on a Light Cycler<sup>TM</sup> 480 Instruments (Roche, USA). The reactions were performed in a 15  $\mu$ L volume containing the High Resolution Melting master mix containing the Resolight<sup>®</sup> set of fluorescent dyes (Roche, USA), 3 mM MgCl<sub>2</sub>, 0.5  $\mu$ M of each primer and 15 ng of DNA. Reaction solutions were overlaid with mineral oil to prevent evaporation and ensure melting profile uniformity. The amplification protocol consisted of an initial pre incubation step at 95°C (10'') followed by 40 cycles using the following conditions: a denaturing step at 95°C (15'' with a ramp rate of 4.4°C/second), a touchdown annealing step at 65-53°C (15'' with a ramp rate of 2.2°C/second), and an extension step at 72°C (20'' with a ramp rate of 4.4°C/second). The HRM Genotyping method included in the LightCycler 480 v.1.5.0 Software (Roche, USA) was used to analyse the PCR products based on their melting curve. Prior to obtain HRM curves, the PCR products were incubated at 95°C (1''), followed by a hybridisation step at 40°C (1'). Melting curves were then generated by ramping from 65 to 95°C at 0.02°C/second, taking 25 acquisitions per degree centigrade. HRM curves were plotted using the automated grouping option in the LightCycler 480 v.1.5.0 software (Meiztertzheim et al., unpublished).

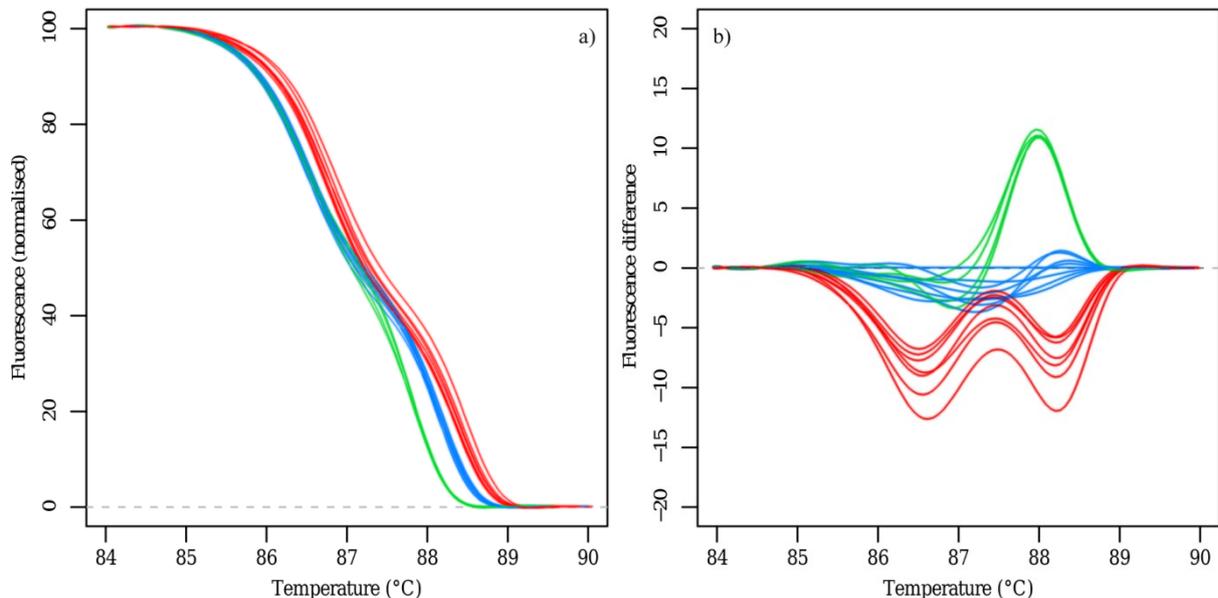
*Identification of variants.* The Gene Scanning module of the LightCycler 480 v.1.5.0 Software (Roche, USA) was designed to improve the discrimination ability between variants. For this purpose, melting curve data were manually adjusted and fluorescence normalized conditions were established and adjusted, threshold at 0 and sensitivity at 0.26. The clustering obtained by HRM was finally compared with the sequences of PCR fragments. Fourty eight variants among the 213 individuals were identified (Fig. 4.2).

**Table 4.2: Multiplex Primer-mix**

Multiplex PCR 1	Multiplex PCR 2	Multiplex PCR 3
5 $\mu$ L R C102, 100nM	5 $\mu$ L R D3, 100nM	5 $\mu$ L R A4, 100nM
5 $\mu$ L R C108, 100nM	5 $\mu$ L R B103, 100nM	5 $\mu$ L R B106, 100nM
5 $\mu$ L R C3, 100nM	5 $\mu$ L R C103, 100nM	5 $\mu$ L R C105, 100nM
1 $\mu$ L F C102 + univ. ext., 10nM	1 $\mu$ L F D3 + univ. ext., 10nM	1 $\mu$ L F A4 + univ. ext., 10nM
1 $\mu$ L F C108 + univ. ext., 10nM	1 $\mu$ L F B103 + univ. ext., 10nM	1 $\mu$ L F B106 + univ. ext., 10nM
1 $\mu$ L F C3 + univ. ext., 10nM	1 $\mu$ L F C103 + univ. ext., 10nM	1 $\mu$ L F C105 + univ. ext., 10nM
5 $\mu$ L 6FAM-univ. primer, 100nM	5 $\mu$ L 6FAM-univ. primer, 100nM	-
5 $\mu$ L YY-univ. primer, 100nM	5 $\mu$ L YY-univ. primer, 100nM	5 $\mu$ L YY-univ. primer, 100nM
5 $\mu$ L DO-univ. primer, 100nM	5 $\mu$ L DO-univ. primer, 100nM	7.5 $\mu$ L DO-univ. primer, 100nM
117 $\mu$ L H <sub>2</sub> O	117 $\mu$ L H <sub>2</sub> O	119.5 $\mu$ L H <sub>2</sub> O
150 $\mu$ L (Total volume)	150 $\mu$ L (Total volume)	150 $\mu$ L (Total volume)

Primers and universal extension associations are shown in Lavergne et al. (2011), Table 3.2.

**DNA sequencing.** One sample of each 48 variants was then sequenced. DNA fragments amplified by real time PCR were cleaned using a PCR $\mu$ 96 Filter Plate (Millipore) according to the manufacturer's protocol, eluted in 20  $\mu$ l of milliQ water. Purified PCR products were sequenced in both directions using the BigDye V3.1 sequencing reagent (Applied Biosystem™) and Ward's primers previously used for the real time PCR assay. The initial phase consisted of a denaturing step at 96°C (2'), followed by 40 cycles at 96°C (30''), 50°C (30'') and 60°C (4'). Sequences were then generated on an ABI 3730 automated sequencer (Applied Biosystems™).



**Figure 4.2: HRM profiles showing three CO1 variants of *T. jarbua***

a) Normalized melting profiles and b) Fluorescence difference plot for three randomly selected CO1 variants of *Terapon jarbua* (red, green and blue lines). In the fluorescence difference plot, the difference is based on one chosen melting curve set as standard and each melting profile minus the standard was plotted against temperature.

### ***Microsatellite analysis protocol***

Primers of nine polymorphic microsatellite loci previously isolated and characterized for *T. jarbua* were used in the study (Lavergne et al., 2011). PCRs were conducted on a GeneAmp PCR system 9700 (Applied Biosystems™) and were optimized for each primer pair on four randomly selected samples. PCR reactions were multiplexed in a total reaction volume of 10  $\mu$ L, using 5  $\mu$ L of Master-mix, 1  $\mu$ L of Solution Q both from the Qiagen™ Multiplex PCR kit, 1  $\mu$ L of multiplexed primer-mix (Table 4.2) containing specific primers and the labelled universal primers 6Fam-TAGTCGACGACCGTTA, Yakima Yellow YY-TCGGATAGCTAGTCGT, and Dargonfly Orange DO-CTGGCCGTCGTTTTAC (Chang et al., 2004) in order to avoid the expenses of using specific fluorescent primers, 1  $\mu$ L of template DNA and 2  $\mu$ L of milliQ water. Touchdown PCR conditions consisted of an initial denaturing step at 95°C (15') followed by 11 cycles at 94°C (30''), 63-53°C (1'30'') and 72°C (1'), followed by 25 cycles at 94°C (30''), 53°C (1'30'') and 72°C (1'). A final elongation step at 60°C (30') ended the PCR. 1  $\mu$ L of PCR

products were added to 12  $\mu\text{L}$  of formamide (Applied Biosystems™) and 0.3  $\mu\text{L}$  of a 50-500bp size standard (GeneScan-500 LIZ™), the mix was heated at 95°C (3') and immediately chilled on ice for a few minutes before loading and genotyping samples on an ABI 3130 Genetic Analyzer (Applied Biosystems™).

### **Data analysis**

#### *Cytochrome C Oxydase sub-unit 1*

The genetic structure of *T. jarbua* was investigated at two geographical scales 1) the wider Gulf of Aden including Socotra Island using the sequences obtained in the present study and 2) the Indo-West Pacific (IWP) using additional sequences of *T. jarbua* from the Arabian (Persian) Gulf – Iran (Accession numbers: HQ149959-HQ149961, Asgharian et al. 2011), from the West Indian Shelf – Western India (Accession numbers: FJ237549, FJ347885-FJ347887, Lakra et al. 2011) and from the Chinese Sea – China (Accession numbers: EF607573-EF607575, EF607577-EF607580, EU871691 and EU871692, Zhang 2011). A total of 48 CO1 sequences of 619-bp were reconstructed using both direction sequences and aligned with the alignment function of GENEIOUS Pro 5.3.4 (Drummond et al., 2011). One sequence was then attributed to each of the 165 remaining samples according to the variant group. Haplotype ( $h$ ) and nucleotide ( $\pi$ ) diversity values were calculated for each location using ARLEQUIN v.3.5.1.3 (Excoffier and Lischer, 2010). The most relevant substitution model was tested with jModelTest v.0.1.1 (Posada, 2008). According to the AICc criterion, the best model among those proposed by ARLEQUIN, was Tamura-Nei (1993) which takes into account unequal nucleotide frequencies and unequal mutation rates. Therefore, nucleotide diversities were estimated using Tamura and Nei (1993) with a gamma distribution. The shape parameter of the gamma distribution ( $\alpha$ ) was determined by a maximum likelihood method using PHYML (Guindon and Gascuel, 2003) in jModelTest v.0.1.1.

Relationships among haplotypes were estimated by a statistical parsimony procedure (Crandall and Templeton, 1994; Templeton et al., 1992) using TCS v.1.12 (Clement et al., 2000). A Fisher's exact test of population differentiation, based on haplotype frequencies (Duran et al., 2004; Raymond and Rousset, 1995) was performed in ARLEQUIN to test the null hypothesis of random haplotype distribution among sampling locations. The significance of individual tests was tested by comparison with simulated distribution constructed from 10,000 random permutations of the original data matrix. ARLEQUIN was also used to calculate the estimations of genetic differentiation ( $\Phi_{ST}$ ) according to the model of Tamura and Nei (1993) (with gamma correction). The significance of the genetic differentiation estimations was tested by 10,000 random permutations of the original data matrix. Corrections for multiple

simultaneous tests were performed by calculating the  $q$ -value of each test which measures the minimum *false discovery rate* ( $FDR$ ) that is incurred when calling that test significant (Storey, 2002). The  $q$ -values were calculated using the R package QVALUE (Ihaka and Gentleman, 1996; Storey, 2002, 2003; Storey and Tibshirani, 2003; Storey et al., 2004). This correction was preferred over the commonly used sequential Bonferroni correction (Rice, 1989) following Moran (2003).

Classical (metric) Multidimensional scaling analyses (MDS) also known as principal coordinates analysis (Gower, 1966) were performed using the *cmdscale* function of the R package *stats* on linearised pairwise  $\Phi_{ST}$  (as  $\Phi_{ST}/(1-\Phi_{ST})$ ) (Slatkin, 1995) to assess whether any indications for group structure could be observed at both geographical scale. Analyses of molecular variance (AMOVA) (Excoffier et al., 1992) were performed in ARLEQUIN on linearised  $\Phi_{ST}$  to quantify the level of genetic differentiation among and within groups previously identified by MDS. 16,000 permutations were executed to guarantee having less than 1% difference with exact probability in 99% of cases (Duran et al., 2004; Guo and Thompson, 1992). In addition, to verify isolation by distance the correlation between pairwise linearised  $\Phi_{ST}$  and geographic pairwise distances between locations were tested. A Mantel test was performed (Mantel, 1967) in ARLEQUIN and its significance was tested by 10,000 permutations. Geographical distances were measured as the shortest distance between two locations along the coastline.

The hypothesis of neutral evolution was tested by Tajima's  $D$  test (Tajima, 1989) and Fu's  $F_S$  test (Fu, 1997) with 10,000 permutations as implemented in ARLEQUIN. Both parameters are not only sensitive to selection processes, but also to population demographic expansions, which generally lead to large negative values. According to ARLEQUIN manual,  $D$  and  $F_S$  statistics were considered significant when the  $p$ -value was below 2%. Mismatch analyses implemented in DnaSP v.5 (Librado and Rozas, 2009) were used to determine whether the number of pairwise differences among DNA sequences from the North-Western Indian Ocean reflects expanding or stable populations (Gaither et al. 2010; Harpending, 1994). Sequences from West India and China were not included in this analysis due to the small number of available sequences. Sequences were grouped according to pairwise genetic differentiation estimations ( $\Phi_{ST}$ ) and MDS results. A rapid population expansion in the recent past usually results in a unimodal mismatch distribution, while a multimodal distribution is encountered in populations at demographic equilibrium or constituted by several units having experienced different demographic events. The Harpending's raggedness test (1994) was used to determine if the observed mismatch distribution was drawn from an expanded population (small raggedness index) or a stationary one (large raggedness index), and parameters of the sudden expansion

model ( $\theta_0$ ,  $\theta_1$  and  $\tau$ ; Rogers and Harpending, 1992) were estimated. The time (in generations) since population expansion ( $t$ ) was estimated using the equation  $\tau = 2ut$ , where  $\tau$  is the mode of the mismatch distribution and  $u$  is the mutation rate of the DNA sequence under study. The mutation rate was calculated through the relationship  $u = 2\mu k$ , where  $\mu$  is the mutation rate per nucleotide and  $k$  is the number of nucleotides of the sequence under study. According to Bowen et al. (2006), Ho (2005; 2008) and Liu et al. (2011), we assumed a mutation rate range from 1.6 to 16 % per nucleotide per Myr. This range was chosen as it encompasses the lowest and highest estimates reported for fishes. In addition, the generation time of *Terapon jarbua* was estimated at 3.5 years (Froese and Pauly, 2011).

Bayesian analyses of phylogenetic relationships were conducted using BEAST v.1.7.1 (Drummond et al., 2012; Drummond and Rambaut, 2007). Four Markov Chains were run over 10,000,000 generations with a sampling frequency of 1,000 generations based on UPGMA (Unweighted Pair Group Method with Arithmetic Mean) starting tree. All analyses were performed assuming a Tamura-Nei model (1993) with a gamma distribution. Results were visualized with Tracer v.1.5 (Rambaut and Drummond, 2007) to assess the effective sample sizes (ESS) and the convergence among Markov chains. The four runs were combined using LogCombiner v.1.7.1 with default burn-in and sample frequency. Following the removal of 10 % burn-in, the sampled posterior trees were summarized in a consensus tree using TreeAnnotator v.1.7.1 to generate a maximum clade credibility tree and calculate mean node ages, 95 % highest posterior density (HPD) intervals and posterior probabilities. The consensus tree was then drawn using FigTree v1.3.1 (Rambaut, 2009).

### *Microsatellites*

Alleles were scored using GeneMapper<sup>®</sup> Software v4.0 (Applied Biosystems<sup>™</sup>). Allele frequencies and the observed ( $H_O$ ) and expected ( $H_E$ ) heterozygosities were calculated in GENETIX v.4.05.2 (Belkhir et al. 2004).  $F_{IS}$  and  $F_{ST}$  (i.e.: index of Hardy-Weinberg disequilibrium and of genetic differentiation) were estimated according to Weir and Cockerham (1984). The significance of these  $F$  parameters was tested by 10,000 permutations of the original data matrix using GENETIX and Fisher's exact test using GENEPOP v.4.1 (Raymond and Rousset, 1995; Rousset, 2008). Corrections for multiple simultaneous tests were performed by calculating the  $q$ -value of each test. Deviation from the Hardy-Weinberg proportions and gametic disequilibrium among loci were tested using exact-tests in GENEPOP. Null allele frequencies were calculated based on Brookfield (1996) using the program MICRO-CHECKER v.2.2.3 (Van Oosterhout et al., 2004) and the EM algorithm (Dempster et al., 1977)

implemented in FreeNA (Chapuis and Estoup, 2006). To allow for the presence of null alleles, corrected  $F_{ST(ENA)}$  was computed using the program FreeNA.

Allele frequencies were then used to calculate pairwise corrected genetic distances  $D_C$  (Cavalli-Sforza and Edwards, 1967) using GENETIX. To assess whether any indications for group structure could be observed, a Classical (metric) Multidimensional scaling analyses was performed on corrected linearised  $D_C$  (as  $D_C/(1-D_C)$ ) in R. Correlation of linearised  $D_C$  over pairwise geographical distances for all pairs of populations was tested with the Mantel permutation procedure available in GENETIX (5,000 permutations).

## Results

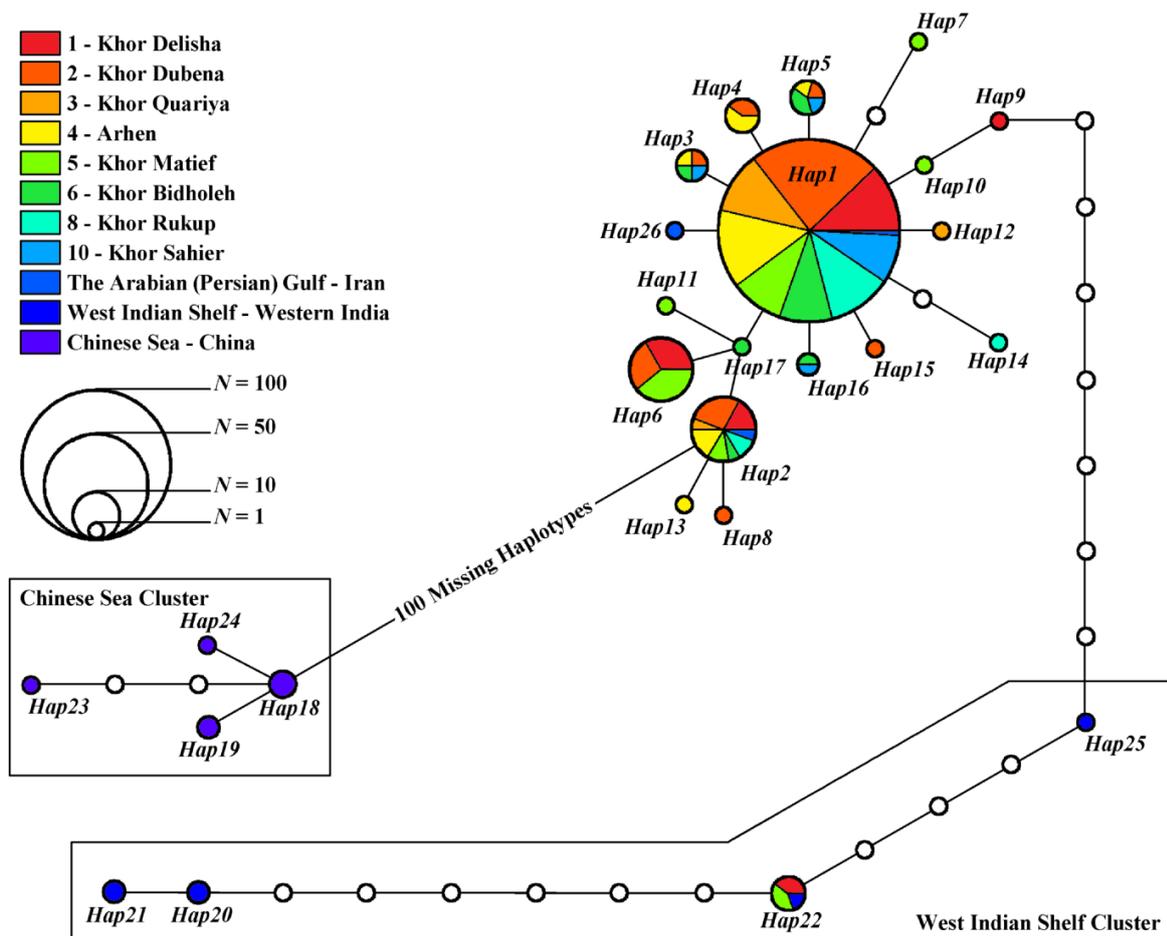
### *Cytochrome C Oxydase sub-unit 1*

#### *Genetic diversity*

CO1 sequences of 619-bp was obtained in 48 individuals of *T. jarbua* and the remaining 165 individuals from eight locations in the wider Gulf of Aden were grouped according to their respective haplotype with the HRMA. All the sequences were deposited in the GenBank Database (Accession numbers: JQ342095-JQ342112). Including CO1 sequences of *T. jarbua* from the Arabian (Persian) Gulf, the Western Indian Shelf and the Chinese Sea, 229 individuals from 11 locations were analysed. A total of 26 haplotypes was observed (18 only for the wider Gulf of Aden), with 14 represented by unique individuals. All mutations in all haplotypes except the ones from China resulted in synonymous substitutions (translation was implemented in GENEIOUS). Mutations in haplotypes from China also resulted in synonymous substitutions; however this unique protein sequence differed from the other studied region by four amino acids. No clear trend was detected between the number of haplotypes per location (from 3 to 8) (Table 4.3) and the geographical location. The most common haplotype (*Hap1*) representing 65% of all specimens was found at every location except in West India and China. Interestingly China shared no haplotypes with any other location and formed an isolated cluster in the parsimony network. The statistical parsimony procedure produced a network with no ambiguous connection (Fig. 4.3). Three clusters were detected: the North-Western Indian Ocean cluster which includes all haplotypes sequenced in this study and all haplotypes from the Arabian (Persian) Gulf, the West Indian Shelf cluster and the Chinese Sea cluster. The first cluster of the haplotype network displayed a “star-like” shape; the most frequent haplotypes being located in the central position of the network and surrounded by several low frequency haplotypes showing a small number of mutations from the common haplotype.

Numbers of sequenced individuals ( $n$ ), haplotypes ( $N_h$ ), polymorphic sites ( $N_p$ ), haplotype diversity ( $h$ ), and nucleotide diversity ( $\pi$ ) values are provided for each location in Table 4.3.

Overall, the nucleotide diversity was low and homogeneous ranging from 0.0005 to 0.0094 (gamma shape parameter = 0.572), whereas the corresponding haplotype diversity was relatively high and heterogeneous, ranging from 0.216 to 0.698. However samples from Iran, West India and China presented very high haplotype diversity values (above 0.8) that should be considered cautiously due to the small number of sequences available in GenBank for those locations (seven or less). The highest values of haplotype and nucleotide diversities for the data collected in the present study, were found in Khor Delisha ( $h = 0.605$ ,  $\pi = 0.0052$ ) and Khor Matief ( $h = 0.698$ ,  $\pi = 0.0057$ ), two estuaries of Socotra Island which remain closed most of the year. The lowest values of haplotype and nucleotide diversities were found in Khor Quariya ( $h = 0.216$ ,  $\pi = 0.0005$ ), Khor Rukup ( $h = 0.279$ ,  $\pi = 0.0009$ ) and Khor Sahier ( $h = 0.350$ ,  $\pi = 0.0006$ ), which are the largest estuaries sampled, most of the time open to the ocean, with stable environmental conditions and located close to villages of moderate to large size.



**Figure 4.3: Haplotype network of *T. jarbua* constructed with the parsimony method of Templeton et al. (1992)** Haplotypes are coloured according to their respective sampling locations (see legend in the upper left corner). The area of the haplotype circles reflects the number of specimens sharing the same haplotype (see scale below the colour legend). A unit branch length represents one mutation and each open circle along the branches represents a “missing haplotype”.

**Table 4.3: COI diversity measures for the studied population of *T. jarbua***

Locations (Fig. 4.1)	<i>n</i>	<i>N<sub>h</sub></i>	<i>N<sub>p</sub></i>	<i>H</i>	$\pi$
<b><i>Terapon jarbua</i>:</b>	<b>229</b>	<b>26</b>	<b>43</b>		
1-Khor Delisha	30	5	18	0.605 (0.086)	0.0052 (0.0030)
2-Khor Dubena	51	8	8	0.517 (0.081)	0.0016 (0.0012)
3-Khor Quariya	18	3	3	0.216 (0.124)	0.0005 (0.0006)
4-Arhen	30	6	6	0.503 (0.105)	0.0014 (0.0011)
5-Khor Matief	28	7	20	0.698 (0.073)	0.0057 (0.0033)
6-Khor Bidholeh	20	6	5	0.516 (0.132)	0.0011 (0.0010)
8-Khor Rukup	20	3	4	0.279 (0.123)	0.0009 (0.0009)
10-Khor Sahier	16	4	3	0.350 (0.148)	0.0006 (0.0007)
13-Iran	3	3	3	1.000 (0.272)	0.0033 (0.0031)
14-India	6	4	12	0.867 (0.129)	0.0094 (0.0061)
15-China	7	4	5	0.809 (0.130)	0.0026 (0.0020)

Sample size (*n*), number of haplotypes (*N<sub>h</sub>*), number of polymorphic sites (*N<sub>p</sub>*), haplotype diversity (*h*), and nucleotide diversity ( $\pi$ ). Standard deviations are reported in parentheses

### Population structure

Overall  $\Phi_{ST}$  for the Indo-West Pacific was 0.882 ( $p < 0.001$ ) with a maximum pairwise  $\Phi_{ST}$  of 0.996 between Khor Quariya and China, while the overall  $\Phi_{ST}$  within the wider Gulf of Aden was smaller 0.039 but significant ( $p < 0.01$ ) with all pairwise  $\Phi_{ST}$  values for this region smaller than 0.093 (Table 4.4). Three locations were significantly differentiated from the other locations: Khor Matief, West India and China. A fourth locality Khor Delisha presented also high pairwise  $\Phi_{ST}$  values, but none of them was significant. Fisher's exact tests of population differentiation were congruent with pairwise  $\Phi_{ST}$  values (Table 4.4). Samples from West India and China were strongly differentiated from samples from the wider Gulf of Aden and Iran, in agreement with the clusters defined in the haplotype network.

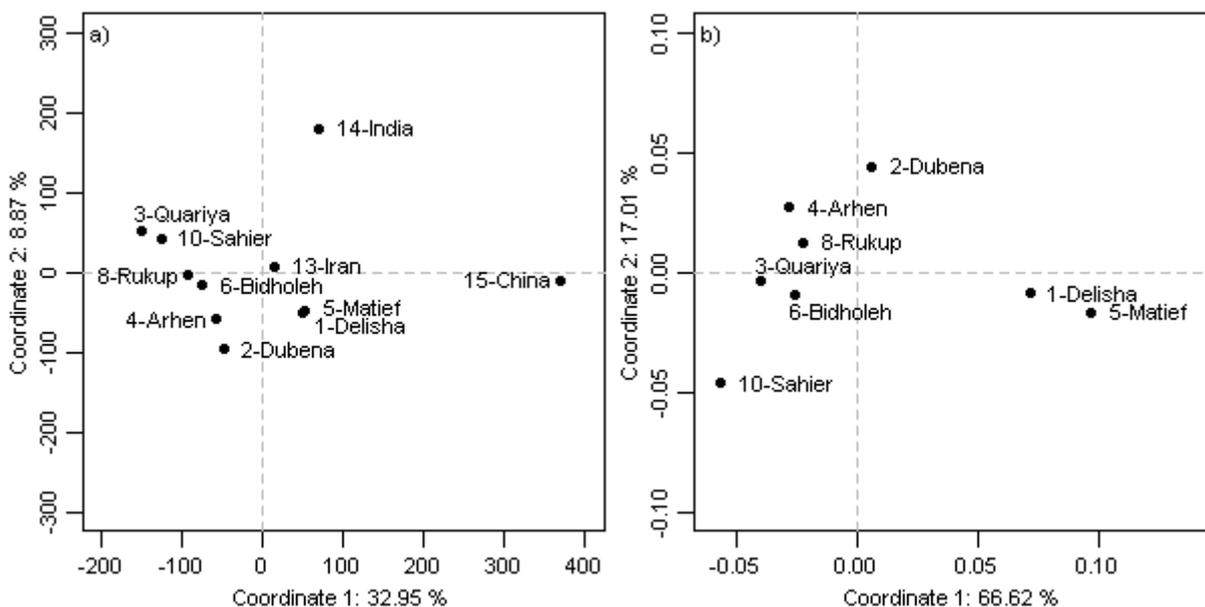
**Table 44: COI pairwise  $\Phi_{ST}$  (below diagonal) and *p*-values of the pairwise exact tests of population differentiation (above diagonal) in the Indo-West Pacific**

	1-Delisha	2-Dubena	3-Quariya	4-Arhan	5-Matief	6-Bidholeh	8-Rukup	10-Sahier	13-Iran	14-India	15-China
<b>1-Delisha</b>	-	0.324	0.077	<b>0.020</b>	0.924	<b>0.031</b>	0.077	<b>0.037</b>	0.116	<b>0.000</b>	<b>0.000</b>
<b>2-Dubena</b>	0.034	-	0.636	0.483	<b>0.042</b>	0.192	0.629	0.324	0.123	<b>0.000</b>	<b>0.000</b>
<b>3-Quariya</b>	0.059	0.018	-	0.566	<b>0.028</b>	0.602	1.000	0.461	<b>0.049</b>	<b>0.000</b>	<b>0.000</b>
<b>4-Arhan</b>	<b>0.053 *</b>	-0.002	-0.002	-	<b>0.002</b>	0.502	0.483	0.444	0.189	<b>0.000</b>	<b>0.000</b>
<b>5-Matief</b>	-0.032	<b>0.053 *</b>	<b>0.079 *</b>	<b>0.075 **</b>	-	<b>0.016</b>	<b>0.022</b>	<b>0.019</b>	0.223	<b>0.000</b>	<b>0.000</b>
<b>6-Bidholeh</b>	0.049	0.010	-0.014	-0.008	<b>0.067 *</b>	-	0.411	1.000	0.234	<b>0.001</b>	<b>0.000</b>
<b>8-Rukup</b>	0.048	0.002	-0.028	-0.014	<b>0.068 *</b>	-0.014	-	0.291	0.123	<b>0.000</b>	<b>0.000</b>
<b>10-Sahier</b>	0.074	0.052	0.001	0.027	<b>0.093 *</b>	-0.031	0.019	-	0.180	<b>0.000</b>	<b>0.000</b>
<b>13-Iran</b>	-0.134	0.005	<b>0.248 *</b>	0.033	-0.124	0.117	0.109	0.291	-	<b>0.000</b>	<b>0.000</b>
<b>14-India</b>	<b>0.833 **</b>	<b>0.935 **</b>	<b>0.929 **</b>	<b>0.927 **</b>	<b>0.819 **</b>	<b>0.921 **</b>	<b>0.925 **</b>	<b>0.923 **</b>	<b>0.792 *</b>	-	<b>0.020</b>
<b>15-China</b>	<b>0.981 **</b>	<b>0.993 **</b>	<b>0.996 **</b>	<b>0.994 **</b>	<b>0.980 **</b>	<b>0.994 **</b>	<b>0.995 **</b>	<b>0.995 **</b>	<b>0.989 **</b>	<b>0.978 **</b>	-

Significance was tested using 10,000 permutations for pairwise  $\Phi_{ST}$  (\*  $p < 0.05$ ; \*\*  $p < 0.01$ ) and with 10,000 iterations for pairwise exact tests. All significant *p*-values for both tests remained significant after correction and are shown in bold (permutation test *q*-values threshold = 0.0183 and exact test *q*-values threshold = 0.0169)

The first MDS analysis (Fig. 4.4a) on the whole mtDNA data set confirmed the clear isolation of the three previously identified clusters: 1/ Socotra, Yemen, Iran 2/ India 3/ China. The analysis of the geographical distribution of genetic variability with an AMOVA, showed that grouping the samples according to these three clusters accounted for 98.3% of the total genetic variance in *T. jarbua* ( $F_{CT} = 0.983$ ,  $p = 0.037$ ), confirming the strong genetic structure over the Indo-West Pacific.

The second MDS analysis (Fig. 4.4b) performed only on samples from the wider Gulf of Aden stressed some genetic heterogeneity within this region, with three samples different from the rest: two populations of Socotra (Khors Delisha and Matief which clustered together) and one population of Yemen mainland (Khor Sahier). The distribution of the genetic variability assessed by AMOVA, showed that grouping the samples according to the MDS groups accounted for 9.59% of the total genetic variance in *T. jarbua* at the scale of the wider Gulf of Aden ( $F_{CT} = 0.095$ ,  $p = 0.005$ ), confirming a small but significant genetic structure over this region. The Mantel's test revealed a lack of correlation between geographic distances and pairwise linearised  $\Phi_{ST}$  values ( $r = -0.095$ ,  $p = 0.643$ ) over the wider Gulf of Aden.



**Figure 4.4: Multidimensional scaling analyses on CO1 data set**

(a) MDS plot of linearised pairwise  $\Phi_{ST}$  (as  $\Phi_{ST}/(1-\Phi_{ST})$ ) for the IWP. Dimension 1 explains 32.95% while dimension 2 explains 8.87% of the total variance. (b) MDS plot of linearised pairwise  $\Phi_{ST}$  (as  $\Phi_{ST}/(1-\Phi_{ST})$ ) for the wider Gulf of Aden. Dimension 1 explains 66.62% while dimension 2 explains 17.01% of the total variance.

### Demography

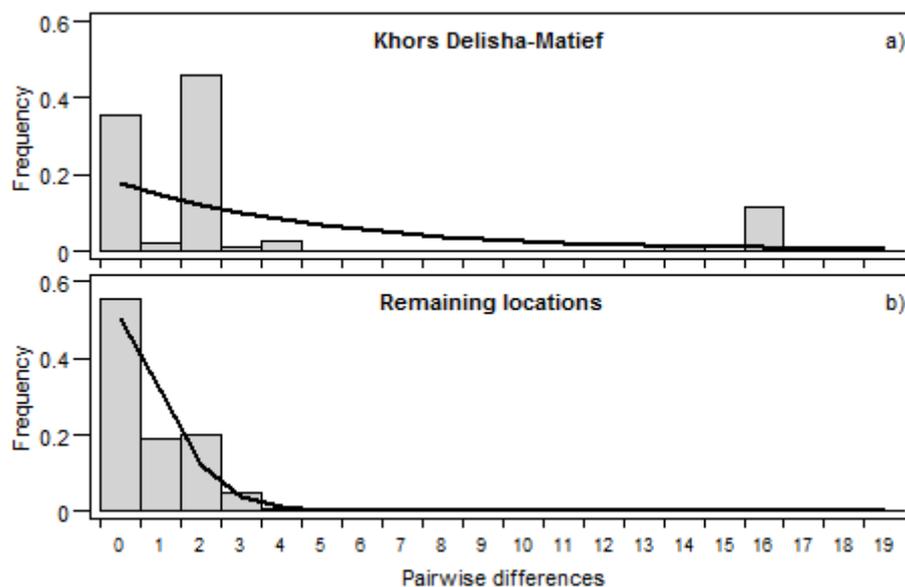
The  $D$  and  $F_S$  tests for the population Khors Delisha-Matief (1-5) were respectively negative and positive but both non-significant (Table 4.5) and the mismatch distribution (Fig. 4.5a) was bimodal and did not match with the expected distribution under a sudden expansion model

( $R = 0.528$ ,  $p = 0.013$ ). This result might indicate that the population Khors Delisha-Matief is at demographic equilibrium or constituted by several population units with different demographic histories. For the remaining estuaries of the North-Western Indian Ocean grouped together,  $D$  and  $F_S$  parameters were negative and highly significant (Table 4.5) and the mismatch distribution (Fig. 4.5b) appeared to be unimodal and matched with the expected distributions under a sudden expansion model ( $R = 0.157$ ,  $p = 0.999$ ). Based on  $\tau = 0.331$ , a divergence rate range of 1.6 to 16 % per nucleotide per Myr and a generation time of 3.5 years, the timing of expansion of this North-Western Indian Ocean population of *T. jarbua* is estimated back to the end of the Pleistocene, beginning of the Holocene, between 3 and 30 kyr.

**Table 4.5: Estimated parameters from mismatch distribution analysis of *T. jarbua***

	North-Western Indian Ocean	
	1-5	2-3-4-6-8-10-Iran
$n$	58	158
$h$	0.643	0.444
$\pi$	0.005	0.001
Tajima's $D$	-0.970	<b>-1.798</b>
$D p$ -value	0.158	<b>0.009</b>
Fu's $F_S$	1.522	<b>-10.433</b>
$F_S p$ -value	0.744	<b>0.000</b>
$R$ index	<b>0.528</b>	0.157
$R p$ -value	<b>0.013</b>	0.999
$\tau$	0.000	0.331
$\theta_0$	4.713	0.423
$\theta_1$	1000	1000

Bold values are significant

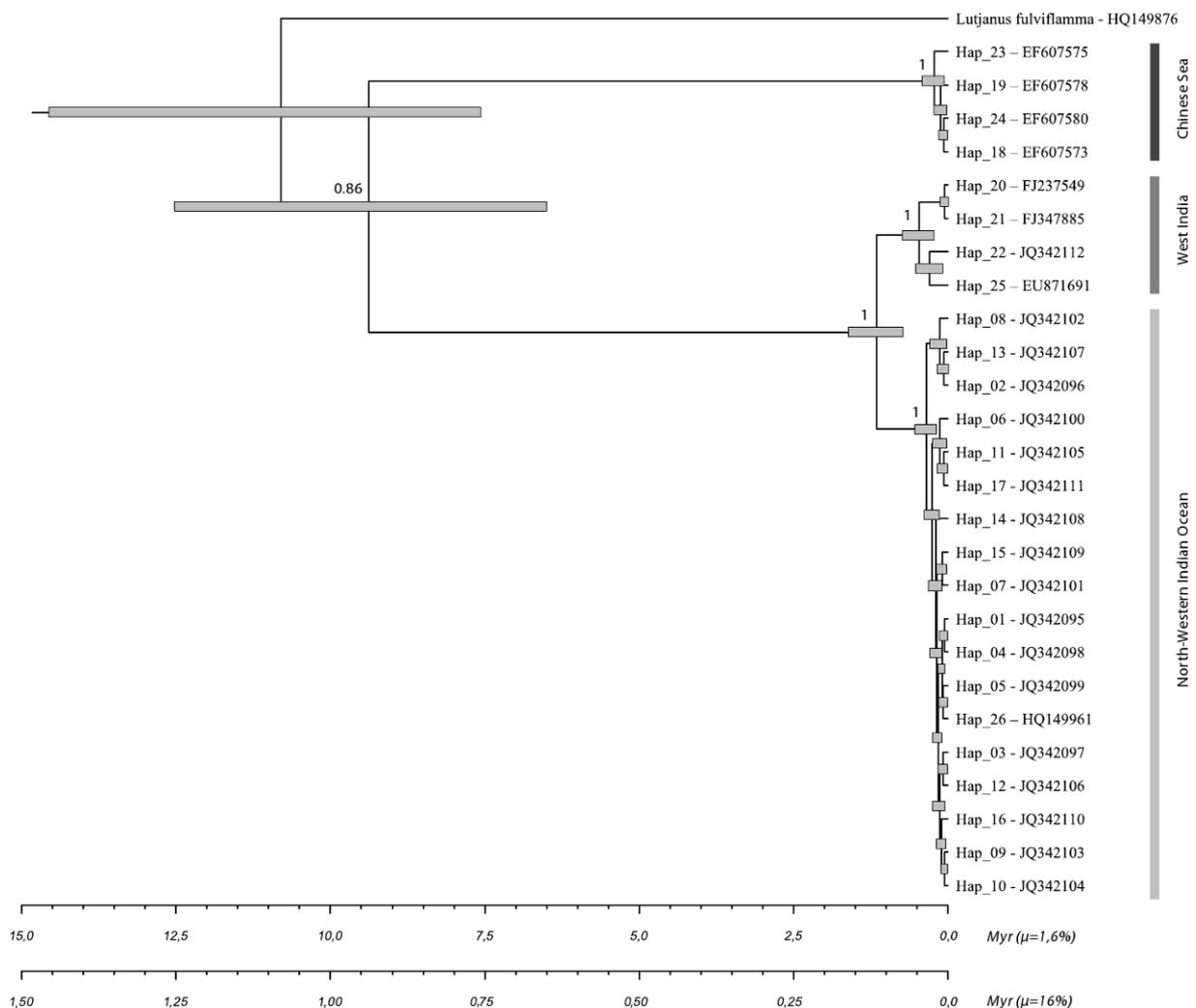


**Figure 4.5: Observed mismatch distributions (bars) and expected mismatch distributions under sudden expansion model (solid line) of CO1 for a) Khors Delisha-Matief population and b) the population formed by the remaining locations from the North-Western Indian Ocean**

Overall, the three clusters do not share haplotypes except for *hap22* between India and two locations on Socotra (Khors Delisha and Matief) (Fig. 4.3 and 4.5a). With no intermediate haplotype present on Socotra and assuming sampling effort was sufficient, the more likely hypothesis for the presence of *hap22* on Socotra might be a secondary contact through artificial gene flow by commercial ship water ballast. Indeed Socotra Island is regularly supplied by vessels chartered from different locations including India.

*Phylogenetic relationship*

The phylogenetic tree obtained by Bayesian analysis with the Tamura-Nei model (1993) and using the complete data set of CO1 haplotypes revealed three distinct clusters (North-Western Indian Ocean, West Indian Shelf and Chinese Sea) with high posterior probabilities. This result supports the parsimony haplotype network (Fig. 4.3), which shows that the clusters Socotra, Yemen, Iran and India vs. China are separated from each other by 100 mutational steps and the clusters Socotra, Yemen, Iran vs. India by 14 (Fig. 4.3). Under the slowest CO1 divergence rate hypothesis (1.6 % per Myr), the earliest evolutionary separation isolating *Terapon jarbua* populations of China (Pacific Ocean) from the remaining populations of the Indian Ocean occurred about 9.4 Myr ago, in the late Miocene, while under a ten time faster divergence rate (16 % per Myr) the earliest evolutionary separation occurred at least 940 kyr ago. Divergence between India and the North-Western Indian Ocean is more recent around 1.2 Myr for the slowest rate and 120 kyr for the fastest rate (Fig. 4.6).



**Figure 4.6: Maximum clade credibility trees and chronograms showing the timing of evolution obtained for *Terapon jarbua* under two hypothetical mutation rates.** This Bayesian tree for mtDNA CO1 haplotypes was constructed under the Tamura-Nei model (1993) with gamma distribution and invariant sites and rooted to *Lutjanus fulviflamma* using BEAST v.1.7.1. Horizontal gray bars around mean node ages indicate the 95 % HPD intervals (Myr). Numbers above branches show posterior probabilities for the five first nodes.

## ***Microsatellites***

### *Genetic diversity*

In the present study, 288 fish collected in ten locations were genotyped. A similar level of polymorphism was observed across samples with a mean number of alleles of 14.29 ranging from 7.3 to 30.8 alleles per locus and from 12.1 to 14.9 (12.4 to 15.8 without locus A4) alleles per location. The total number of alleles per locus ranged from 13 (C3) to 74 (C102). A total of 44 private alleles were present, ranging from one to 11 per locus and from one to six per location. Although the seven additional specimens from Somalia were not included in the genetic differentiation analysis due to the small sample size, two specimens presented respectively three and one private alleles, suggesting a possible separation from other locations.

The mean observed heterozygosity ( $H_O$ ) per locus varied between 0.43 (A4) and 1.00 (C108 and D3) while the mean expected heterozygosity ( $H_E$ ) ranged from 0.48 (C105) to 0.98 (C102). Significant departures from HWE proportions were observed for some loci and samples (Table 4.6). Although A4 presented the highest values of  $F_{IS}$  (range: 0.111-0.499) and contributed most to heterozygote deficiency, once this locus was removed from the multilocus estimates, four out of the six significant  $F_{IS}$  estimates remained significant for the populations of Khors Quaryia, Matief, Rukup and Dufega (maximum multilocus  $F_{IS}$ : 0.139). In particular, the Rukup population displayed a heterozygote deficit for seven out of nine loci (Table 4.6).

Results from MICRO-CHECKER stressed that most of the observed heterozygote deficits were likely due to the presence of null alleles. Null alleles were present at high frequency for the locus A4 at almost all locations, ranging from 0.041 to 0.229. For this reason, this locus was excluded for further analysis, thus reducing multilocus heterozygote deficiency. Genotype data for the eight loci were tested for gametic disequilibrium, but no significant disequilibrium was detected whatever the considered pair of loci or location.

### *Genetic structure*

Although null allele frequencies across some loci and locations were low, they remained significant even after the removal of the locus A4 from the analysis. Thus  $F_{ST}$  were estimated based on the data set corrected for null alleles  $F_{ST(ENA)}$ , according to the method implemented in FreeNA (Table 4.7). Values of uncorrected  $F_{ST}$  were in the range 0.004-0.094 (overall 0.035), while  $F_{ST(ENA)}$  were in the range 0.004-0.097 (overall 0.035).  $F_{ST(ENA)}$  values did not differ strongly from original  $F_{ST}$  estimates:  $F_{ST(ENA)}$  was lower than  $F_{ST}$  for four loci with the greatest change of -1.07 % of original value for locus B106 and was higher than  $F_{ST}$  for the four other loci with the greatest change of +4.23 % of original value for locus C3. Therefore  $F_{ST}$  values did

not appear to have been over estimated compared to  $F_{ST(ENA)}$  values due to the presence of null alleles, contrary to what was Chapuis and Estoup (2006) have assumed.

**Table 4.6: Number of alleles ( $N_A$ ), observed ( $H_O$ ) and unbiased expected ( $H_E$ ) heterozygosity and  $F_{IS}$  for each location and each locus**

		Loci									All loci	All -A4
		C3	C108	C102	D3	B103	C103	A4	B106	C105		
1-Delisha	$N_A$	9	13	35	22	10	14	8	15	8	14.9	15.8
	$H_O$	0.700	0.862	0.933	0.862	0.857	0.621	0.483	0.897	0.586	0.756	0.790
	$H_E$	0.786	0.822	0.975	0.931	0.872	0.853	0.829	0.881	0.667	0.846	0.848
	$F_{IS}$	0.112	-0.049	<b>0.043*</b>	<b>0.075*</b>	0.017	<b>0.276**</b>	<b>0.422**</b>	-0.017	0.123	<b>0.109**</b>	0.070
2-Dubena	$N_A$	8	14	35	26	9	9	8	14	10	14.8	15.6
	$H_O$	0.867	0.900	0.833	0.833	0.867	0.733	0.467	0.967	0.867	0.815	0.858
	$H_E$	0.754	0.854	0.977	0.914	0.804	0.757	0.832	0.851	0.709	0.828	0.827
	$F_{IS}$	-0.152	-0.055	<b>0.150**</b>	<b>0.089*</b>	-0.079	0.031	<b>0.443**</b>	-0.139	-0.227	0.016	-0.038
3-Quariya	$N_A$	6	11	27	23	8	8	4	14	11	12.4	13.5
	$H_O$	0.533	0.767	0.833	0.897	0.667	0.793	0.600	0.800	0.567	0.717	0.732
	$H_E$	0.728	0.843	0.971	0.938	0.844	0.779	0.674	0.892	0.548	0.802	0.818
	$F_{IS}$	<b>0.270**</b>	0.092	<b>0.144**</b>	0.045	<b>0.213**</b>	-0.018	0.111	<b>0.104*</b>	-0.036	<b>0.107**</b>	<b>0.106**</b>
4-Arhen	$N_A$	11	13	34	26	8	9	9	14	9	14.8	15.5
	$H_O$	0.800	0.900	0.800	1.000	0.833	0.733	0.700	0.833	0.767	0.819	0.833
	$H_E$	0.855	0.887	0.962	0.944	0.699	0.779	0.792	0.898	0.673	0.832	0.837
	$F_{IS}$	0.066	-0.015	<b>0.171**</b>	-0.060	-0.196	0.060	0.118	0.073	-0.142	0.017	0.005
5-Matief	$N_A$	8	12	31	27	10	10	7	15	12	14.7	15.4
	$H_O$	0.688	0.781	0.875	0.938	0.750	0.563	0.531	0.813	0.469	0.712	0.734
	$H_E$	0.762	0.804	0.963	0.954	0.836	0.775	0.734	0.856	0.48	0.796	0.804
	$F_{IS}$	0.100	0.028	<b>0.093**</b>	0.018	<b>0.104*</b>	<b>0.277**</b>	<b>0.280**</b>	0.051	0.024	<b>0.107**</b>	<b>0.088*</b>
6-Bidholeh	$N_A$	8	16	29	22	5	8	6	15	6	12.8	13.6
	$H_O$	0.767	1.000	0.828	0.967	0.767	0.733	0.467	0.933	0.900	0.818	0.862
	$H_E$	0.799	0.898	0.975	0.938	0.668	0.712	0.709	0.850	0.683	0.803	0.815
	$F_{IS}$	0.041	-0.116	<b>0.153**</b>	-0.031	-0.151	-0.031	<b>0.345**</b>	-0.100	-0.326	-0.018	-0.058
8-Rukup	$N_A$	7	9	30	22	10	9	8	14	7	12.9	13.5
	$H_O$	0.533	0.633	0.867	0.867	0.667	0.767	0.533	0.700	0.500	0.674	0.692
	$H_E$	0.731	0.815	0.967	0.944	0.807	0.792	0.789	0.836	0.497	0.797	0.798
	$F_{IS}$	<b>0.274**</b>	<b>0.226**</b>	<b>0.105**</b>	<b>0.083*</b>	<b>0.176*</b>	0.032	<b>0.328**</b>	<b>0.165**</b>	-0.006	<b>0.157**</b>	<b>0.136**</b>
9-Rukup (Sea)	$N_A$	5	11	30	22	8	8	10	17	7	13.1	13.5
	$H_O$	0.767	0.867	0.867	0.867	0.733	0.667	0.733	0.900	0.633	0.782	0.788
	$H_E$	0.707	0.842	0.972	0.935	0.732	0.763	0.814	0.905	0.561	0.803	0.802
	$F_{IS}$	-0.085	-0.030	<b>0.110**</b>	<b>0.074*</b>	-0.002	0.128	0.100	0.006	-0.133	0.028	0.019
10-Sahier	$N_A$	6	12	22	18	11	6	10	14	10	12.1	12.4
	$H_O$	0.765	0.882	0.941	0.833	0.667	0.556	0.444	0.889	0.722	0.744	0.782
	$H_E$	0.770	0.838	0.966	0.949	0.894	0.764	0.875	0.870	0.773	0.855	0.853
	$F_{IS}$	0.007	-0.055	0.027	<b>0.125*</b>	<b>0.260**</b>	<b>0.278**</b>	<b>0.499**</b>	-0.023	0.068	<b>0.133**</b>	0.086
11-Dufega	$N_A$	5	12	35	16	11	9	11	15	8	13.6	13.9
	$H_O$	0.593	0.815	0.923	0.679	0.536	0.714	0.429	0.786	0.500	0.664	0.693
	$H_E$	0.688	0.781	0.982	0.923	0.849	0.756	0.832	0.881	0.565	0.806	0.803
	$F_{IS}$	0.141	-0.044	<b>0.061**</b>	<b>0.269**</b>	<b>0.374**</b>	0.056	<b>0.489**</b>	<b>0.110*</b>	0.117	<b>0.180**</b>	<b>0.139**</b>

$F_{IS}$  was estimated according to Weir and Cockerham (1984) and was tested using the Markov chain method with 10,000 iterations ( $*p < 0.05$ ,  $**p < 0.01$ ). All significant  $p$ -values remained significant after correction and are shown in bold.

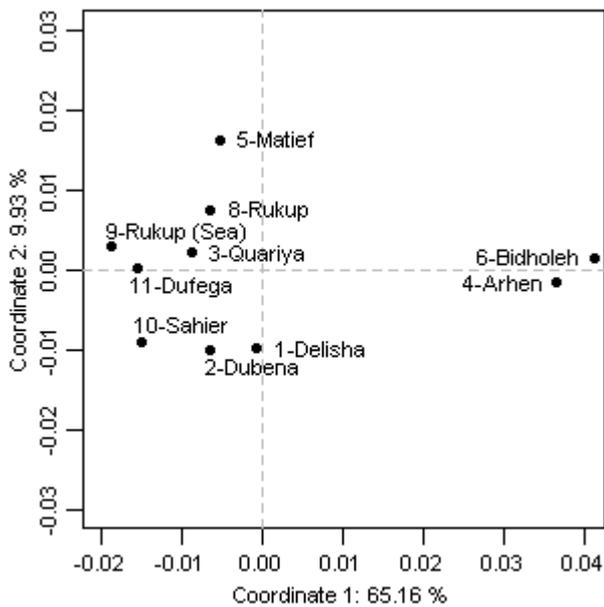
**Table 4.7: Microsatellite pairwise  $F_{ST}$  and  $F_{ST(ENA)}$  (below diagonal) and  $p$ -values of the pairwise exact tests of population differentiation (above diagonal) in the wider Gulf of Aden**

	<i>N</i>	1	2	3	4	5	6	8	9	10	11
1-Delisha	30	-	0.374	<b>0.015</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.005</b>	<b>0.000</b>	0.379	0.171
2-Dubena	30	0.004 0.005	-	<b>0.005</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.166	<b>0.046</b>
3-Quariya	30	0.004 0.005	<b>0.009 *</b> 0.009	-	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.004</b>	<b>0.000</b>	<b>0.007</b>	0.409
4-Arhan	30	<b>0.042 **</b> 0.042	<b>0.064 **</b> 0.064	<b>0.077 **</b> 0.075	-	<b>0.000</b>	0.780	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
5-Matief	32	<b>0.013 **</b> 0.013	<b>0.022 **</b> 0.023	0.005 0.006	<b>0.082 **</b> 0.081	-	<b>0.000</b>	0.231	<b>0.003</b>	<b>0.005</b>	<b>0.046</b>
6-Bidholeh	30	<b>0.052 **</b> 0.051	<b>0.076 **</b> 0.076	<b>0.085 **</b> 0.085	-0.003 -0.003	<b>0.094 **</b> 0.093	-	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
8-Rukup	30	<b>0.014 **</b> 0.015	<b>0.027 **</b> 0.027	0.006 0.007	<b>0.082 **</b> 0.080	-0.001 -0.001	<b>0.090 **</b> 0.090	-	0.106	0.054	0.270
9-Rukup (Sea)	30	<b>0.020 **</b> 0.022	<b>0.020 **</b> 0.021	<b>0.007 *</b> 0.009	<b>0.096 **</b> 0.096	0.006 0.007	<b>0.104 **</b> 0.104	0.003 0.003	-	<b>0.008</b>	0.510
10-Sahier	18	0.000 0.001	0.004 0.006	0.003 0.004	<b>0.059 **</b> 0.058	0.005 0.006	<b>0.071 **</b> 0.070	0.003 0.005	0.008 0.010	-	0.219
11-Dufega	28	0.003 0.004	<b>0.009 *</b> 0.009	-0.004 -0.002	<b>0.084 **</b> 0.082	0.000 0.001	<b>0.095 **</b> 0.094	0.004 0.005	0.007 0.009	0.001 0.000	-

Significance was tested using 10,000 permutations for pairwise  $F_{ST}$  (\*  $p < 0.05$ ; \*\*  $p < 0.01$ ) and with 10,000 iterations per batch for pairwise exact tests. All significant  $p$ -values for both tests remained significant after correction and are shown in bold (permutation test  $q$ -values threshold = 0.0118 and exact test  $q$ -values threshold = 0.0035).

Out of 45 pairwise population comparisons, 25  $F_{ST}$  estimates (55.56 %) and 33 exact tests of genic differentiation (73.33 %) were significant, reflecting the greater power of exact tests to detect significant population structuring (Table 4.7) (Balloux and Lugon-Moulin 2002). Pairwise  $F_{ST}$  values showed a clear differentiation between two groupings represented for the first one by Ahren and Khor Bidholeh and for the second one by the other locations. Smaller but significant differentiations within this second cluster appeared between the groups Khor Delisha – Khor Dubena vs. Khor Matief – Rukup (Sea) (Table 4.7).

The MDS analysis (Fig. 4.7), as for the pairwise  $F_{ST}$  comparisons, highlighted also the differentiation of the Ahren – Khor Bidholeh group from the other locations, and the relative isolation of the Khors Delisha – Khor Dubena group, these two groups being localized on Socotra. In the upper left quarter of the MDS (Fig. 4.7) a mixture of localities from Socotra (Khors Quariya and Matief) and Yemen (Khors Rukup and Dufega) was observed, all these samples showing a significant heterozygote deficiency. Finally, the Mandel test revealed a lack of correlation between geographic distances and pairwise linearised  $D_C$  values ( $r = 0.137$ ,  $p = 0.151$ ) at the North-Western Indian Ocean scale.



**Figure 4.7: Multidimensional scaling analyses on microsatellite data set**

MDS plot of linearised pairwise  $D_C$  (as  $D_C/(1-D_C)$ ) for the wider Gulf of Aden. The first dimension explains 65.16 % while the second explains 9.93 % of the total variance.

## Discussion

### *Phylogeography of T. jarbua*

Mitochondrial markers are particularly appropriate to identify species and infer historical processes that might be responsible for the contemporary geographic distribution of marine and freshwater species throughout the world (Baker et al., 2004; Borkenhagen et al., 2011; Lakra et al., 2011; Zhang, 2011), but they are also useful markers to investigate intra-specific phylogeography (Avice et al., 1987; Duran et al., 2004; He et al., 2011). In this study on *T. jarbua*, the analysis of mtDNA sequences from Socotra Island to China revealed three highly diverging clusters: the North-Western Indian Ocean region, the Western Indian shelf and the Chinese Sea. Although most of the nucleotide differences between North-Western Indian Ocean and Chinese sequences were synonymous, the number of nucleotide differences was large (100 out of 619 nucleotides). Sequences from China and India were obtained from GenBank where fish misidentification can be an important source of errors, and thus, conclusion from these data should be taken with caution. However, *Terapon jarbua* has a characteristic color pattern with horizontal downwardly curved black bands which is easily identifiable, even at a post-larval stage. A GenBank blast search on the CO1 sequences from China returns a mix of sequences of *Terapon jarbua* and *Terapon theraps* Cuvier, 1829 (Accession numbers: EU871698, EU871699, JF494667.1, JF494668.1, JF340158.1) with at least 99 % identification. If misidentification is not the issue, the blast result indicated that *T. jarbua* from the South Chinese Sea is more closely related to *T. theraps* also from the South Chinese Sea than to *T. jarbua* from West India of the North-Western Indian Ocean. Large intraspecific CO1 sequence divergence among populations of inshore fish species from opposite sides of the Indian Ocean and among *T. jarbua* from South Chinese Sea was also observed by Zemplak et al. (2009) and Zhang et al. (2012) respectively. A

recent introgression of mtDNA due to interspecific hybridization between *T. jarbua* from and *T. theraps* in the South Chinese Sea might led to the observed pattern. Indeed, Avise and Saunders (1984), proposed that hybridization among species of sunfish (*lepomis*) was not a random event, females of the rarest species were likely to hybridize with males of the dominant species due to the rarity of available males thus allowing mtDNA introgression. It will be of interest to investigate levels of introgression at bi-parentally inherited nuclear markers such as the RAG gene in complement to maternally inherited mtDNA in order to supported or reject this hypothesis (Bachtrog et al., 2006; Scribner et al., 2000).

The strong genetic structure from the Gulf of Aden to the Chinese Sea might be explained by the presence of marked biogeographical barriers such as the one between the Arabian Sea and the Indian Ocean (Kemp, 1998), and the Indo-Pacific Barrier (IPB) between the South Chinese Sea and the Indian Ocean (Gaither et al., 2010). This marked population differentiation along the distribution range of *T. jarbua* and based on CO1 marker may suggest in fact that this species might belong to more than one taxon (Gill and Kemp, 2002; Golani and Appelbaum-Golani, 2010; Marshall et al., 2011). The Indo-West Pacific speciation process probably occurred in the Pliocene–Early Pleistocene driven by sea-level changes isolating populations between major oceans (Pillans et al., 1998; Voris, 2000). Such pattern has been recorded in several taxa such as the crown-of-thorns starfish *Acanthaster planci* (Linnaeus, 1758) (Vogler et al., 2008), the reef fish *Myripristis berndti* Jordan and Evermann, 1903 (Craig et al., 2007), the reef fish *Chlorurus sordidus* (Forsskål, 1775) (Bay et al., 2004) or the mudcrab *Scylla serrata* (Forsskål, 1775) (Gopurenko et al., 1999).

In addition, the North-Western Indian Ocean cluster presents a “star-like” shape haplotype network with abundant low frequency haplotypes often considered as a consequence of a recent population expansion following sea-level rises after local extinctions during the Pleistocene glaciations (Craig et al., 2007; Fratini and Vannini, 2002; Grant and Waples, 2000; Pulch et al., *in prep.*). Estuaries, one of the main shallow habitats, harbour organisms which were displaced during glaciation periods resulting in demographic bottleneck events (Fauvelot et al., 2003). This was confirmed by the presence of moderately high haplotype diversity and low nucleotide diversity (e.g.: Charrier et al. 2006) and the results of Tajima’s *D* test and Fu’s *F<sub>s</sub>* test. Interestingly, a relatively strong isolation of Khors Matief and Delisha which are grouped together, from the other locations was observed within the North-Western Indian Ocean cluster, in particular within Socotra Island. Furthermore, Khors Matief and Delisha showed the highest values of haplotype and nucleotide diversities over the data set and were relatively closed to the Iranian population on the MDS analysis, thus suggesting that the juvenile recruitment process in these locations could result from larvae of a broader geographic origin compared to the other

locations. Although this cluster could not be explained geographically, it underlines the particular status of Socotra Island as a major spot of fish biodiversity in the North West Indian Ocean.

### **Genetic structure of *T. jarbua* populations**

Recent population history of *T. jarbua*, particularly during the post-glacial period, was investigated using microsatellites considered as neutral markers as they are non coding sequences (Grant and Waples, 2000). The present survey reveals significant deficits in heterozygotes for particular microsatellite loci. Heterozygote deficiency is very common in microsatellites and has been reported in marine organisms and notably in fishes (e.g.: Hoarau et al., 2002; Hoareau et al., 2007; Karlsson and Mork, 2005; O'Connell and Wright, 1997; Waldman and McKinnon, 1993). Some locations showed significant multilocus heterozygote deficiency (Table 4.6). However, this disequilibrium was mainly due to the A4 locus, and it decreased after removing this locus from the analysis. Several factors can be responsible for the remaining deficit, such as null alleles, genotyping errors, selection processes or Wahlund effects. Null alleles which arise when mutations occur on primer sequences and prevent amplification, fail to explain this deficit as  $F_{ST}$  and  $F_{ST(ENA)}$  did not show any differences. Moreover genotyping errors were not suggested as a major source of deficit in heterozygote when tested with MICRO-CHECKER.

*Terapon jarbua* is a marine spawner and has a larval stage of 25 days (Chapter 5). Post-larvae colonize the estuaries where they are recruited at the juvenile stage. In this work, genotyped fishes were mainly belonging to the 0+ cohort. Therefore significant heterozygote deficit observed in the two estuaries in Socotra (Khors Quariya and Matief) and in Yemen (Khors Rukup and Dufega), even after removal of the A4 locus, could be due to a Wahlund effect: these estuaries may harbor a mixture of juveniles stemming from genetically differentiated (sub)-populations (Hartl and Borot, 1994).

Over the Socotra – Yemen area, this study detected a significant genetic differentiation between estuaries, considering the variability at the microsatellites ( $F_{ST} = 0,035$ ,  $p < 0.01$ ). Geographical distance was not a major structuring factor for *T. jarbua* populations in this region, a genetic proximity being sometimes observed among very close estuaries (Khors Delisha and Dubena) as well as between estuaries located in the north and the south of Socotra (Arhen and Khor Bidholeh). Considering the high larval mortality at sea and the particular opening rhythm of the TOCEs, we suggest 1) that each estuarine system displays its own capacity to be an efficient nursery area for *T. jarbua*, where different stochastic demographic bottlenecks might occur and 2) that this capacity could be temporarily variable.

The strict link between juvenile *T. jarbua* and TOCE's, and the possible demographic bottlenecks in such systems might be the major structuring factors of the genetic variability over the Socotra – Yemen area. The colonization pattern of estuaries by pelagic larval flows is probably very contrasted considering the spatial and temporal scales over the zone, thus increasing the local differentiation among estuaries. These patterns have been previously described for *Austrocochlea constricta* (Lamarck and De Monet, 1822), a trochid snail dispersing planktonic larvae and showing increased subdivision and disruption of isolation by distance at small scale (2-20 km) (Johnson and Black, 2006). On the other hand, in the present study, we suggest that possible mixture of larval flows in estuaries stemming from different subpopulations, could conduct to a reduced genetic differentiation between several locations over the zone (in Socotra: Khors Quariya and Matief and in Yemen: Khors Rukup and Dufega).

Random demographic events are probably not the only factors that might be involved in such atypical genetic differentiation, which fit with a model of a metapopulation composed of open subpopulations (i.e.: multiple sources – larval pool). The north-east monsoon current flows westward through the Arabian Sea and then southward along the African coast after crossing Socotra Island from November to March and is reversed from April to October (Kemp 1998). Thus, both seasonal currents can lead to homogenization of the *T. jarbua* populations in the region. However the short larval stage duration of 25 days might reduce homogenization over broad geographical distances. According to Planes and Lenfant (2002), the variation in reproductive success can also lead to temporal differences in allelic frequencies that can interfere with spatial genetic variation and thus, the present genetic structure analysis must be interpreted with caution as sampling was not performed the same year for Arhen (i.e.: Chaotic genetic patchiness; Larson and Julian 1999).

In addition, *T. jarbua* living in TOCE's on Socotra are subject to extreme temperature (i.e.: up to 36 °C) and salinity (i.e.: up to 39 ‰). As a consequence, a significant increase in the sea surface temperature in the region coupled with human induced freshwater flow reduction might contribute to the potential dry out or long term disconnection of TOCE's from the ocean and conduct to a severe reduction of *T. jarbua* abundance by crossing the species physiological limits (Chien et al. 1999). Therefore, anthropogenic activities may lead to a general decrease of the genetic diversity of the species over the region by 1) reducing the number of suitable nursery habitats in the North-Western Indian Ocean and 2) affecting the environmental diversity linked to these nurseries. The present study emphasizes: 1) the major role of estuarine habitats in Socotra and of their seasonal opening rhythms on the life cycle of marine fish populations and 2) the urgent need for a Temporarily Open / Closed Estuarine conservation program in the region.

## **Acknowledgments**

The present study was mainly funded by the Total Foundation, Paris. It was partially conducted at the Socotra Field Research Station of the Biodiversity and Climate Research Centre (BiK-F), Frankfurt a.M., based on financial support of the research-funding programme “LOEWE – Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz” of Hesse's Ministry of Higher Education, Research, and the Arts. Additional mobility funds were provided by scholarships from the GRADE - Goethe Graduate Academy of the Goethe University Frankfurt a.M. and the International Doctoral College of the European University of Brittany (UEB). His Excellency the former Minister of Water and Environment of the Republic of Yemen, Eng. Abdul-Rahman F. Al-Eryani, and His Excellency the Chairman of the Environment Protection Authority, Eng. Mahmoud Shidiwa, are cordially acknowledged for their continued support and for granting research and sample export permits. The Socotra Conservation and Development Program (SCDP-UNDP) is thanked for providing indispensable support during the field work. We would like to thank the People of Socotra and in particular the members of the coastal communities which kindly facilitated field work and provided access to the areas in their care. We wish to express our gratitude to Fouad Naseeb and Motea Sheikh Aideed for their efficient assistance in the field, to Dr. El-Mashjary and Dr. Ali of the Hadhramout University for granting the authors access to the University wet laboratory. Friedhelm Krupp is cordially acknowledged for his support to the Ph.D. project of the first author.

# Chapter

# 5

**Early life history of *Terapon jarbua* (Forsskål, 1775) using microstructures and Laser Ablation ICP-MS elemental composition of otoliths**

---



## Summary

**Context:** The study of fish early life history strategies is essential 1) to explore the connectivity between estuarine and marine habitats, the structure and dynamics of adult fish population and 2) to set up effective conservation and fisheries management strategies (Gillanders, 2005). Most marine tropical fishes produce planktonic larvae which disperse into the ocean before being recruited in an appropriate habitat. The use of otolith microincrements as a life history event recorder provides information about the age of fish and important biological processes throughout the fish lifespan such as the metamorphosis and settlement times (Raventos and Macpherson, 2001). Moreover, advances in otolith elemental analyses allowed elucidating the early life history of several fish species (Bradbury et al., 2011; Campana, 1992; McCulloch et al., 2005, Honda et al., 2012). This approach is largely based on two key assumptions: 1) otoliths are metabolically inert with no evidence that the new material is resorbed or reworked after deposition and 2) otoliths grow continuously throughout the fish lifetime (Campana, 1999). Combining microsatellites with markers such as otolith elemental fingerprints would lead to complementary information on population connectivity.

**Aims:** The main aims of the present study are 1) to describe migration patterns between estuarine and marine habitats of juvenile *Terapon jarbua*, 2) to determine the Planktonic Larval Duration (PLD) and test whether there are differences in PLDs within the studied region, 3) to test whether otolith edge fingerprint signature allow reliable assignments to specific estuarine nurseries and 4) to verify if the population structure observed in *T. jarbua* between estuaries (Chapter 4) could be explained by sub-populations contributing more than other to the recruitment in particular estuaries.

### **Materials and methods:**

1) Planktonic Larval Duration: A total of 74 left otoliths of *T. jarbua* caught from three locations on Socotra Island and Yemen mainland, were embedded in polyester resin and sliced transversally using a low speed diamond saw to reveal otolith internal structures. Sections were grounded and polished until the nucleus becomes visible and the surface smooth. Microincrements were counted under a light microscope along the otolith growth axis from the core to the settlement marks in order to determine PLD of *T. jarbua*. Differences in PLD among the three locations were investigated using ANOVA.

2) Elemental fingerprints: A total of 80 right otoliths of *T. jarbua* caught from eight locations on Socotra Island and Yemen mainland during the pre-summer monsoon in 2007 and 2008, were

embedded in epoxy resin, sliced, grounded and polished until the surface was smooth and the core was reached. Otolith elemental composition was measured using LA-ICP-MS from the core to the edge along the otolith growth axis. Sr:Ba ratios along the otolith growth axis were used to investigate fish movements between marine and brackish water (McCulloch et al., 2005). Multivariate Analysis of Variance (MANOVA) and Linear Discriminant Function Analysis (LDFA) were used to test and visualize differences in elemental composition of the environments in which specimens were respectively born (otolith nucleus) and caught (otolith edge) to test the accuracy of the maker in assigning specimens to birth or nursery locations. In addition, Ward's hierarchical joining clustering analysis based on previously determined pairwise estimator of genetic differentiation among estuaries ( $F_{ST}$  statistics, considering microsatellite markers: Chapter 4) was then used to group estuaries according to their genetic similarity representing potential pseudo isolated sub-population. LDFA was used to test whether otolith nuclei elemental signature was effective in discriminating potential sub-populations detected by the previous population genetics approach. Assignment analyses were performed on data from 2007 only to avoid temporal variability bias.

**Results and conclusion:** Sr:Ba ratios across each transect were particularly sensitive to transitional environments, such as estuaries. *Terapon jarbua* exhibited a natal marine phase, migrating after a short planktonic larval stage into estuarine systems as post larvae or young juveniles in which they remained for at least two years. An average PLD of 25.1 days ranging from 19.5 to 31 days was estimated and no difference was observed between the assessed locations. The study highlighted that elemental fingerprints of otolith edges have great potential for discriminating nursery areas at both small (< 10 km) and large geographical scales (80 % assignment accuracy). However, elemental fingerprints of the otolith nuclei had a lower potential for discriminating unknown marine spawning grounds but pointed out the existence of several different spawning areas, thus supporting previous hypothesis on population structure and population dynamics of *T. jarbua*, i.e.: multiple sources producing more or less pronounced mixtures of larvae, leading to significant genetic differentiation between the nurseries under the influence of estuarine opening rythme and random demographic events. However, temporal variability in otolith elemental composition has been observed, limiting the use of this tool.

## Early life history of *Terapon jarbua* (Forsskål, 1775) using microstructures and Laser Ablation ICP-MS elemental composition of otoliths

E. Lavergne<sup>1,2,3</sup>, L. Sellin<sup>3</sup>, M. Labonne<sup>3</sup> and J. Laroche<sup>3</sup>

<sup>1</sup> Senckenberg Forschungsinstitut und Naturmuseum, Sektion Ichthyologie – Senckenberganlage 25, 60325 Frankfurt am Main, Deutschland

<sup>2</sup> Biodiversität und Klima Forschungszentrum (BiK-F) – Senckenberganlage 25, 60325 Frankfurt am Main, Deutschland

<sup>3</sup> Université de Bretagne Occidentale, UMR 6539, CNRS/IRD/UBO, Laboratoire des Sciences de l'Environnement Marin LEMAR, Institut Universitaire Européen de la Mer, Rue Dumont d'Urville, 29280 Plouzané, France

**Corresponding author:** E. Lavergne, Tel +33 2 98 49 86 27

Email address: edouard.lavergne@gmail.com

To be submitted

### Abstract

Early life history of *Terapon jarbua* (Forsskål, 1775) was examined using otolith microstructures and elemental composition, assignment test and linked with previous analysis of microsatellite genotypes. Eight estuaries from Socotra Island and Yemen mainland were sampled in 2007 and 2008. Laser ablation inductively coupled mass spectrometry transects across otolith growth axes of juvenile *T. jarbua* caught in estuaries were used to estimate early life migration of the species. Sr:Ba ratios across each transect were particularly sensitive to transitional environments, such as estuaries. *Terapon jarbua* exhibited a natal marine phase, migrating after a short planktonic larval stage into estuarine systems as post larvae or young juveniles in which they remained for at least two years. An average planktonic larval duration of 25.1 days was estimated and remained stable over the studied region. The study highlighted that elemental fingerprints of otolith edges have great potential for discriminating nursery areas at both small (< 10 km) and large geographical scales (80 % assignment accuracy). However, elemental fingerprints of the otolith nuclei had a lower potential for discriminating unknown marine spawning grounds but pointed out the existence of several different spawning areas, thus supporting previous hypothesis on population structure and population dynamics of *T. jarbua*. However, temporal variability in otolith elemental composition has been observed, limiting the use of this tool.

**Keywords:** Otolith, nursery, fingerprint, connectivity, Socotra Island, Gulf of Aden, Yemen.

## Introduction

The Socotra Archipelago is located in the north-western corner of the Indian Ocean at the junction between the Gulf of Aden and the Arabian Sea at 12°30'N 54°00'E (Fig. 5.1). It lies on a Palaeozoic granite block which separated from the Southern Arabian peninsula during the opening of the Gulf of Aden around 18 Mya ago (Leroy et al., 2004; Van Damme, 2009). The archipelago includes the main island of Socotra and the three smaller islands of Samha, Darsa and Abd al-Kuri. The 3,695 km<sup>2</sup> of the main island is composed of the igneous Haggier Mountains (maximum altitude 1,526 m), Paleogene karstic limestone plateaus (maximum altitude 1,000 m) and alluvial coastal plains (Scholte et al., 2011). The Archipelago lies close to boundaries among four major biogeographic units of the circum-Arabian seas: the Eritrean, South Arabian and Persian sections of the Arabian subprovince and the Western Indian Ocean subprovince (Kemp, 1998; Zajonz et al., 2000). The Archipelago is characterized by the alternating monsoon seasons in the Northern Indian Ocean driven by the Inter-Tropical Convergence Zone (ITCZ). From October to February the weaker winter or north-east monsoon dominates with a rainy period starting in October and being strongest in November/December. From April/May to September the forceful summer or south-west monsoon blows strong hot winds that generate upwelling of cold nutrient-rich waters on both the north and south coasts of Socotra, and on the south coast of Yemen mainland (Currie et al., 1973; Fleitmann et al., 2004; Fratantoni et al., 2006; Glynn, 1993; Kemp, 1998; Klaus and Turner, 2004; Scholte and De Geest, 2010). Average annual rainfall reaches 216 mm and may increase up to 800 mm in the Mountains (Banfield et al., 2011; Scholte and De Geest, 2010). The particular geography and climate of this island is responsible of the presence of wadi and temporarily open/closed estuaries (TOCE or “Khor”), which are often separated from the sea by gravelly or sandy berms and some by a road. They only get connected to the sea after flush floods during the rainy seasons or by storm surges, thus limiting the connectivity with the marine environment. Although several zoological surveys have been conducted on Socotra Island, little is known about its TOCE's and connectivity with the marine waters.

The study of fish early life history strategies is essential 1) to explore the connectivity between estuarine and marine habitats, the structure and dynamics of adult fish population and 2) to set up effective conservation and fisheries management strategies (Di Franco et al., 2012; Gillanders, 2005; Johnson et al., 2012; Robinet et al., 2008; Sponaugle, 2010). Advances in otolith analyses (i.e.: microincrements, elemental fingerprint) allowed elucidating the early life history of several fish species (Bradbury et al., 2008, 2011; Buratti and Santos, 2010; Campana, 1999; Campana, 1992; Campana and Thorrold, 2001; Elsdon et al., 2008; Honda et al., 2012; Kennedy et al., 2002; McCulloch et al., 2005; Raventos and Macpherson, 2001; Thresher, 1999).

Most tropical fishes produce planktonic larvae which disperse into the ocean before being recruited in an appropriate habitat. The use of otolith microincrements as a life history event recorder provides information about the age of fish and important biological processes throughout the fish lifespan such as the metamorphosis and settlement times (Bradbury et al., 2008; Laurel and Bradbury, 2006; Raventos and Macpherson, 2001). This is particularly true for transition habitats such as estuarine nurseries which are highly contrasted compare with marine habitats. Settlement events often result in the modification of otolith deposition processes, which can be observed on otolith transversal sections (Panfili et al., 2002).

Movements between estuarine and marine habitats have been inferred predominantly from temporal and spatial abundance estimates coupled with analysis of size-frequency distributions, various tagging methods and the examination of otolith marks (Gillanders and Kingsford, 2003). More recently, otolith natural chemical tracers (i.e.: elemental fingerprints) and isotope ratios (e.g.:  $^{87}\text{Sr}$ : $^{86}\text{Sr}$  and  $^{34}\text{S}$ : $^{32}\text{S}$ ) can be routinely quantify at high spatial resolution using in-situ Laser Ablation Inductively Coupled Plasma Mass Spectrometer (LA-ICP-MS) and LA-Multi Collector-ICP-MS respectively. Those markers have been used to identify natal origin and describe migration patterns of diadromous species (Bradbury et al., 2011; Di Franco et al., 2012; Gillanders, 2005; Johnson et al., 2012; Kennedy et al., 1997; Kennedy et al., 2002; McCulloch et al., 2005; Mercier et al., 2012). This approach is largely based on two key assumptions: 1) otoliths are metabolically inert with no evidence that the new material is resorbed or reworked after deposition and 2) otoliths grow continuously throughout the fish lifetime (Campana, 1999).

The main aims of the present study are 1) to describe migration patterns between estuarine and marine habitats of juvenile *Terapon jarbua*, 2) to determine the Planktonic Larval Duration (PLD) and test whether there are differences in PLDs within the studied region, 3) to test whether otolith edge fingerprint signature allow reliable assignments to specific estuarine nurseries and 4) to verify if the population structure observed in *T. jarbua* between estuaries (Chapter 4) could be explained by sub-populations contributing more than other to the recruitment in particular estuaries.

## **Materials and methods**

### ***Terapon jarbua***

*Terapon jarbua* (Forsskål, 1775) (Terapontidae, Perciformes) locally known as “Dirhar” in Yemen mainland and “Habraham” on Socotra Island, inhabits marine and brackish waters of the Indo-West Pacific, from the Red Sea and East coast of Africa to Samoa. Its juveniles have been observed to thrive even in coastal freshwater courses. In their study of the role of South African estuaries in providing nursery habitats for juvenile fish, Wallace and colleagues (1984; 1975)

observed that the reproduction, spawning and early larval life of *T. jarbua* is limited to the marine environment but estuarine recruitment seems to take place at an early stage. Like the majority of tropical and subtropical marine spawners, they have an extended breeding season and are fractional spawners. Although advances have been made in the taxonomy and biology of the Terapontidae (Miu et al., 1990; Vari, 1978; Whitfield and Blaber, 1978), no in-depth studies of the reproductive ecology, life history strategy or population structure of *T. jarbua* have been conducted so far. Yet, its wide distribution beyond the North-Western Indian Ocean and its ability to cope with contrasted environments (salinity: 0-39 ‰, temperatures: up to 36°C) indicate that this species can be considered as an excellent sentinel species (multi-stress: temperature, salinity and pollution) for the estuaries of the region.

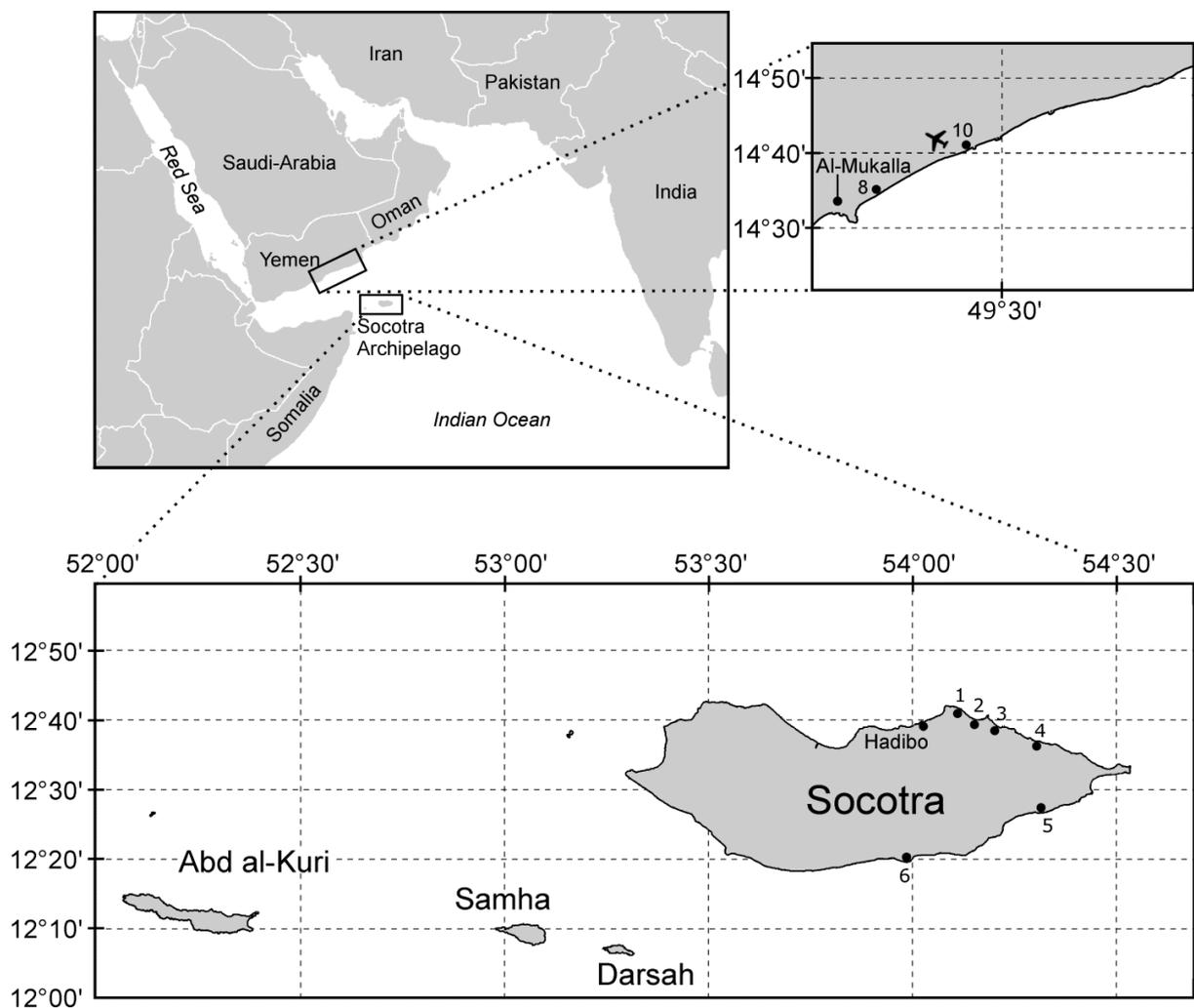
**Table 5.1: Sampling locations**

Locations	Coordinates (Lat., Long.)	
<b>Socotra Island:</b>		
1-Khor Delisha	12°41'11.3''N, 54°07'47.8''E	Shallow khor isolated by a sand berm, with a very low water level during the dry period. Very eutrophicated, many <i>Chara</i> sp. and filamentous algae. A “bridge” should allow water to circulate but disintegrating construction material (rocks) reduces significantly the water flow.
2-Khor Dubena	12°40'16.3''N, 54°09'01.6''E	Shallow khor periodically isolated by a sand berm. Continuous slow flow of very clear fresh to brackish water crossing a date palm plantation.
3-Khor Quariya	12°38'31.8''N, 54°13'29.1''E	Large khor connected to the sea at the time of the survey, only rarely isolated by a sand berm. Stagnant to very slow flowing water from the hinterland.
4-Arhen	12°36'44.0''N, 54°18'16.0''E	Very small freshwater stream running from karst caves in the coastal escarpment.
5-Khor Matief	12°26'48.5''N, 54°18'17.6''E	Large khor isolated by a gravelly berm resting on a sandy bottom, which may imply slight interstitial water exchange when not connected to the sea. Opened during the monsoon storms and associated floodwaters.
6-Khor Bidholeh	12°19'45.8''N, 54°00'29.5''E	Khor opened to the sea with highly limited freshwater input, used by local fishermen as a fish landing site.
<b>Yemen Mainland:</b>		
8-Khor Rukup	14°34'34.5''N, 49°13'43.6''E	Khor periodically isolated by a sand berm. The wadi is crossed up stream by a large road.
10-Khor Sahier	14°39'55.4''N, 49°24'55.6''E	Khor periodically isolated by a sand berm. The wadi is crossed up stream by a large road.

### **Sampling**

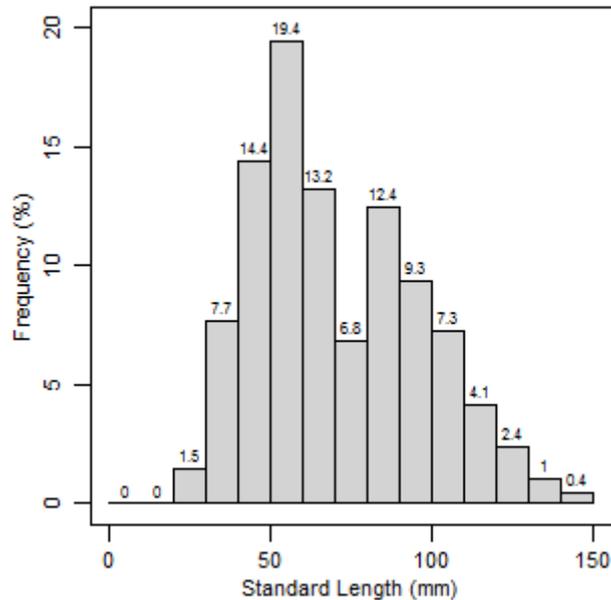
Specimens of *T. jarbua* were collected at eight different locations on Socotra Island and the Hadhramout coast of Yemen (Fig. 5.1, Table 5.1) from 2007 to 2008, during pre- and post-south-west monsoon periods. The two sagittae were removed, washed with milli-Q water and dried in desiccated boxes containing silica gel bags before being stored in properly labeled vials. Otoliths have been removed from the fish within few hours after capture when possible (Panfili

et al., 2002). During all sample preparation, samples were handled in the same way and only came in contact with nonmetallic and acid-washed instruments in order to minimize contamination. A total of 74 left otoliths from individuals caught at three locations (Fig. 5.1) was selected to determine the mean Planktonic Larval Duration (PLD) of *Terapon jarbua*. The right otoliths from 15 individuals per location for eight locations (Fig. 5.1) were reserved for microchemistry analyses. As two cohorts were observed in estuaries, individuals were randomly selected in each location around the mean size of the 0+ age class (50 – 60 mm) in order to avoid any potential temporal bias on otolith elemental chemical analysis (Fig. 5.2).



**Figure 5.1: Map of sampling locations**

1 – Khor Delisha, 2 – Khor Dubena, 3 – Khor Quariya, 4 – Arhen, 5 – Khor Matief, 6 – Khor Bidholeh, 8 – Khor Rukup, 10 – Khor Sahier. This study is part of a larger research project including the faunistic and ecological baseline study of Socotra estuaries and lagoon fishes (Chapter 1) and the analyses of the genetic structure of *T. jarbua* (Chapter 4). As it was desirable to use a consistent location numbering across studies and because not all locations of the project were involved in the present study, some locations are not presented here.

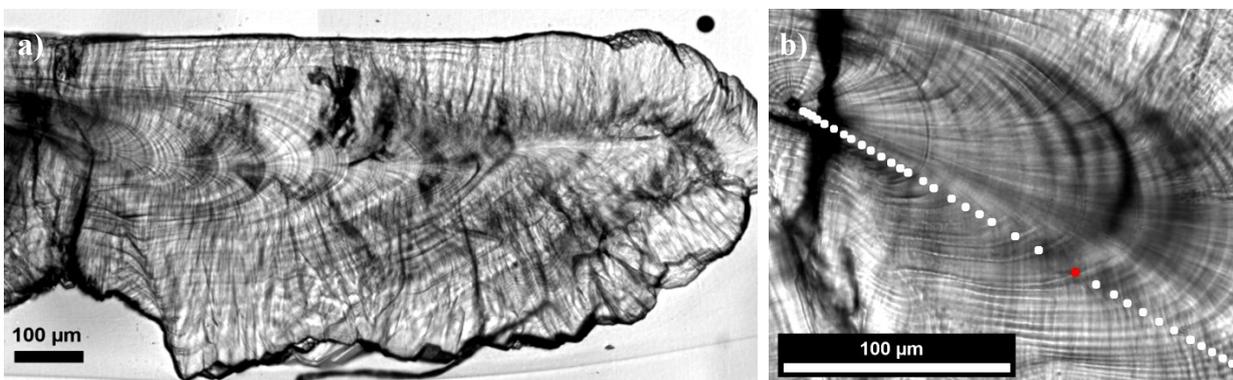


**Figure 5.2: Length frequency distribution of *T. jarbua***  
The frequencies are based on the *T. jarbua* caught in the eight studied estuaries in 2007 and 2008 ( $n = 675$ )

### *Otolith preparation and analysis*

#### *Laval stage duration*

Left otoliths of 74 specimens in Khors Dubena ( $n = 22$ ), Matief ( $n = 27$ ) and Rukup ( $n = 25$ ), were embedded in polyester resin (Sody™ 33) and cut transversally on either side of the nucleus, which had been previously located in the resin block, using a low speed diamond saw to reveal otolith internal structures. The section was then mounted on a microscope slide with thermoplastic glue at 150°C, grounded with wet abrasive disc paper (600 to 2,000 grades) and polished with alumina pastes (3, 1 and  $\frac{1}{4}$   $\mu\text{m}$ ) until the nucleus becomes visible and the surface smooth. The section was then turned over to repeat the previous operation until the core was reached on this face. The section thickness ranges from 60 to 100  $\mu\text{m}$ .



**Figure 5.3: a) Transversal section of a left otolith of *T. jarbua*, b) PLD microincrement counts (white dots) along the otolith growth axis from the core (black spot on the left side) to the settlement-mark (red dot)**

Microincrements were counted under a light microscope (Olympus™ BX41) at 400× and 1000× magnification, along the otolith growth axis from the core to the settlement marks characterized by a rapid decrease in increment width over settlement (Raventos and Macpherson, 2001; Wilson and McCormick, 1997, 1999) (Fig. 5.3). Otolith increments were read without a priori knowledge on the specimens' origin, later a second reading was carried out by the same reader.

Experiments to validate the hypothesis of otolith daily increment for *T. jarbua* in the region were carried out in 2008 in two estuaries on Socotra Island and Yemen mainland using two fish size class (< 50 mm and > 50 mm). Unfortunately, the two tetracycline marking experiments were destroyed due to an unexpectedly strong rainy season and only bigger specimens have been recovered. As growth is lowering when fish are getting older, microincrements could not be read all the way up to the edge of the otolith although the fluorescent marks were clearly visible. Consequently, microincrements were assumed to be deposited daily based on the daily increment validation of several other species (*Sarotherodon melanotheron* Rüppell, 1852 and *Oreochromis niloticus* Linnæus, 1758) from West Africa (Labonne et al., 2009; Panfili and Tomas, 2001).

#### *Otolith elemental analyses*

Right otoliths of 80 specimens caught in Khor Delisha (2007  $n = 10$ ), Khor Dubena (2007  $n = 10$ , 2008  $n = 5$ ), Khor Quariya (2007  $n = 10$ ), Arhen (2007  $n = 10$ ), Khor Matief (2007  $n = 10$ ), Khor Bidholeh (2008  $n = 5$ ), Khor Rukup (2007  $n = 10$ , 2008  $n = 5$ ) and Khor Sahier (2008  $n = 5$ ), were embedded in epoxy resin Araldite® 2020 and mounted on glass slides after sectioning was performed on an Accutom-50 microcutting instrument (Struers™). Otoliths were grounded on several grades of chemically neutral abrasive paper and polished with 3 and 1 µm diamond paste until the surface was smooth and the core was reached (Labonne et al., 2009). Sections were kept thick enough, ranging from 100 to 150 µm, in order not to be transpierced during the laser ablation. The polished sections were then cleaned in an ultrasonic bath, rinsed with Milli-Q water and stocked in a desiccation cabinet (Milton and Chenery, 2005; Panfili et al., 2002). To reduce equilibration and manipulation time associated with changing samples in the LA-ICP-MS sample chamber, ten otoliths were randomly placed on each slide.

Otolith elemental composition was measured using LA-ICP-MS at the European Institute for Marine Studies (IUEM, France). The material used was the Coherent Laser ( $\lambda = 193$  nm, COMPexPro™ 102) mounted on an Element 2 mass spectrometer (Thermo Electron™). The laser was operated with a repetition rate of 5 Hz and a constant fluence on target of 15 J.cm<sup>-2</sup>. The ablated material was transported within a helium gas flow in order to enhance sensitivity and reduce particle condensation on the surface (Eggins et al., 1998). An argon gas flow was then

admixed to resulting aerosol prior the elemental analysis into the ICP-MS. At the beginning of each day of analysis, the argon gas flow and lens voltage was adjusted to optimize sensitivity. The background level was collected during 12 scans, followed by an ablation period of 40 scans. The background level was then subtracted from each measurement in order to use the resulting counts for the calculation of elemental concentrations. Calibration was achieved using the certified reference material NIST 612 (National Institute of Standards and Technology) (Pearce et al., 1997), BIR-1G and BCR-2G (Gao et al., 2002). Otoliths were analyzed for  $^{11}\text{B}$ ,  $^{26}\text{Mg}$ ,  $^{43}\text{Ca}$ ,  $^{55}\text{Mn}$ ,  $^{66}\text{Zn}$ ,  $^{85}\text{Rb}$ ,  $^{88}\text{Sr}$ ,  $^{118}\text{Sn}$ ,  $^{138}\text{Ba}$ ,  $^{208}\text{Pb}$  and  $^{238}\text{U}$ ,  $^{43}\text{Ca}$  was used as an internal standard. Limits of detection (in ppm) at three standard deviations on the blank (i.e.:  $3\sigma$ ) were calculated as:  $^{11}\text{B} = 0.12$ ,  $^{26}\text{Mg} = 25.21$ ,  $^{43}\text{Ca} = 670.59$ ,  $^{55}\text{Mn} = 1.00$ ,  $^{66}\text{Zn} = 0.30$ ,  $^{85}\text{Rb} = 0.05$ ,  $^{88}\text{Sr} = 68.24$ ,  $^{118}\text{Sn} = 0.07$ ,  $^{138}\text{Ba} = 0.23$ ,  $^{208}\text{Pb} = 0.006$  and  $^{238}\text{U} = 0.0004$ . The resin was analyzed as well, and was several orders of magnitude lower in elemental concentrations than the otoliths. The reproducibility of LA-ICP-MS was evaluated from the mean relative standard deviation (RSD, in %) of all certified reference material. The reproducibility for individual elements was  $^{11}\text{B} = 14.8\%$ ,  $^{26}\text{Mg} = 4.1\%$ ,  $^{55}\text{Mn} = 5.1\%$ ,  $^{66}\text{Zn} = 6.8\%$ ,  $^{85}\text{Rb} = 9.9\%$ ,  $^{88}\text{Sr} = 2.6\%$ ,  $^{118}\text{Sn} = 4.7\%$ ,  $^{138}\text{Ba} = 4.1\%$ ,  $^{208}\text{Pb} = 4.6\%$  and  $^{238}\text{U} = 8.6\%$ . The LA-ICP-MS accuracy for some elements determined as mean percentage recovery from USGS (United States Geological Survey) carbonate reference materials MACS-1 (non-certified but chemically closer to an otolith than the NIST 612 reference) was  $^{26}\text{Mg} = 57.5\%$ ,  $^{55}\text{Mn} = 95.6\%$ ,  $^{66}\text{Zn} = 112.6\%$ ,  $^{85}\text{Rb} = 266\%$ ,  $^{88}\text{Sr} = 103.8\%$ ,  $^{118}\text{Sn} = 92.4\%$ ,  $^{138}\text{Ba} = 105.4\%$ ,  $^{208}\text{Pb} = 108.5\%$  and  $^{238}\text{U} = 379.8\%$ .

All assays were based on two measurement procedures: 1) ablations of 60  $\mu\text{m}$  diameter spots along the growth axis from the core to the rim of five selected otoliths per locations were performed. Spots were separated from each other by 30  $\mu\text{m}$  in order to avoid any effect of the previous ablation; 2) ablations of 60  $\mu\text{m}$  diameter spots at the outer edge and the nucleus were performed on five additional otoliths per location when possible.

### **Data analysis**

#### *Planktonic Larval Duration*

A coefficient of variation (*CV*) was calculated in order to determine the level of agreement of the two readings (Campana and Jones, 1992; Campana and Thorrold, 2001; Panfili et al., 2002):

$$CV = 100 \times \frac{\sqrt{\sum_{i=1}^R \frac{(X_{ij} - \bar{X}_j)^2}{R - 1}}}{\bar{X}_j}$$

where  $\bar{X}_j$  is the average of the readings for the  $j^{\text{th}}$  fish,  $X_{ij}$  is the  $i^{\text{th}}$  estimation of the microincrement counts of the  $j^{\text{th}}$  fish and  $R$  is the number of readings. Two otoliths presented a  $CV$  over 10 % and were discarded from the analysis. As normality (Shapiro and Wilk, 1965) and homocedasticity (Bartlett, 1937) hypotheses of the two readings data set were not rejected ( $p > 0.05$ ), the difference between the two readings was tested by a paired two-sample  $t$  test using the *t.test* function from the R package *stats* (Ihaka and Gentleman, 1996). As no difference was found between the two readings ( $p > 0.05$ ) the average between the two readings of each otolith was calculated to estimate the PLD (Campana and Jones, 1992).

Differences in PLD among the three locations (Socotra: Khors Dubena and Matief and Yemen mainland: Khor Rukup) were investigated using ANOVA (Chambers et al., 1992), as hypotheses of normality and homogeneity of the variance at each location were not rejected ( $p > 0.05$ ). Analyses were performed using the *shapiro.test*, *bartlett.test* and *aov* functions of the R package *stats*.

#### *Otolith elemental analyses*

Sr:Ca and Ba:Ca relative concentrations presented an inverse relationship along the otolith growth axis. Indeed, in the marine environment Sr:Ca relative concentration is high and very uniform when adjusted to salinity, while Ba:Ca relative concentration is low and *vice versa* in brackish and freshwater environments (Panfili et al., 2002; McCulloch et al., 2005). Sr:Ba ratio was then used to increase the signal and investigate fish movements between marine and brackish water. Indeed McCulloch et al. (2005) have demonstrated that Sr:Ba ratio is a suitable fingerprint marker for transitional environment such as estuaries. This is particularly true when salinity is higher than 5 ‰ and when strontium isotope ratio  $^{87}\text{Sr}:^{86}\text{Sr}$  cannot be used (Kennedy et al., 1997).

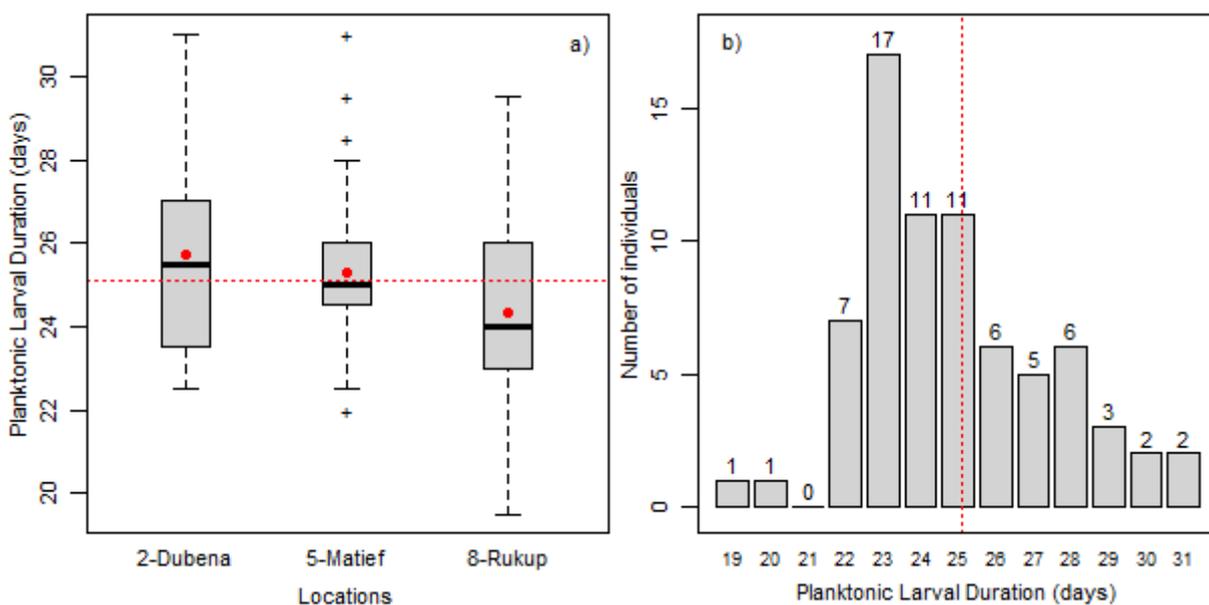
Differences between relative element concentrations of the otolith edge, representing the environmental signature of the location in which individuals have been caught, were tested using Multivariate Analysis of Variance (MANOVA,  $\alpha = 0.05$ ). This allowed determining which elements were most important in segregating each location. Due to the small sample size ( $n = 5$  to 10 per location) we assumed the hypothesis of normality and homogeneity of the variance of the dataset. Unlike principal component analysis (PCA) which maximizes the total variance explained, linear discriminant function analysis (LDFA) maximizes the total variance between groups, thus LDFA was performed on  $\log(x + 1)$  transformed data to diminish the influence of high element relative concentration (i.e.: Sr:Ca) compare to trace elements, in order to test whether otolith edge elemental signature is effective in discriminating estuaries. Analysis was performed using the *lda* function of the R package *mass* (Venables and Ripley, 2002).

The same analyses were performed on elemental composition of otolith nuclei in order to assess whether the juveniles from each estuary originated from the same or different sub-populations. In addition, Ward's hierarchical joining clustering analysis based on previously determined pairwise estimator of genetic differentiation among estuaries ( $F_{ST}$  statistics, considering microsatellite markers: Chapter 4) including all individuals of the present study, was then used to group estuaries according to their genetic similarity representing potential pseudo isolated sub-population. As Ward's method maximizes the differences among clusters and minimizes the differences within clusters (Kindt and Coe, 2005), linear DFA was used to test whether otolith nuclei elemental signature was effective in discriminating potential sub-populations detected by the population genetics approach. Assignment analyses were only performed on data from 2007 to avoid temporal bias.

## Results

### *Planktonic Larval Duration*

All sampled juvenile *T. jarbua* were between 27.4 and 149.1 mm in standard length and represented 0+ and 1+ age class specimens (Fig. 5.2). Respective PLD averages of *T. jarbua* for Khors Dubena, Matief and Rukup were 25.7, 25.3 and 24.3 days and no significant differences were found between the three PLD's ( $F = 3.922$ ,  $p > 0.05$ ) (Fig. 5.4a). The total PLD average was 25.1 days (~150  $\mu\text{m}$ ) ranging from 19.5 to 31 days (Fig. 5.4b).



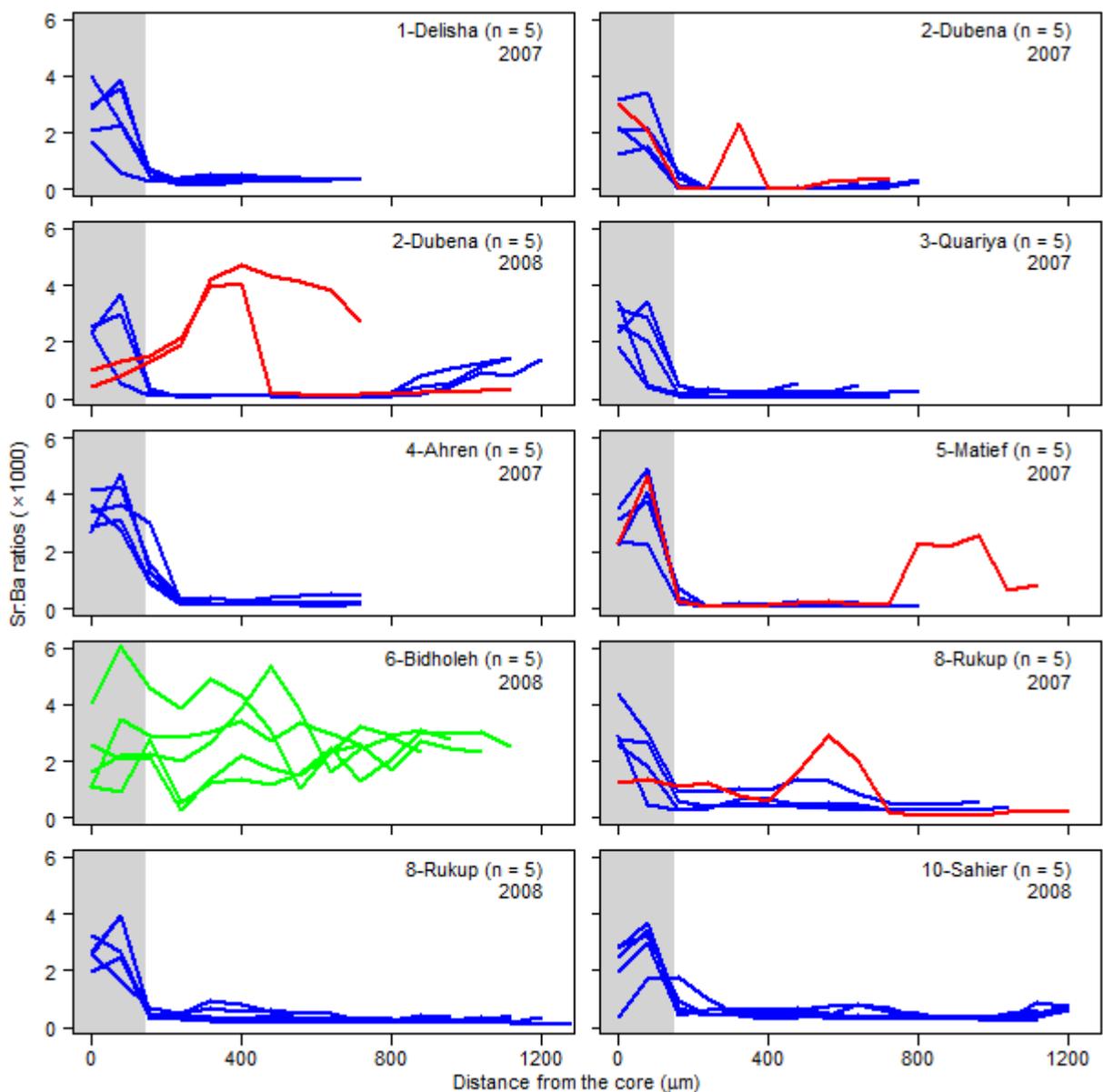
**Figure 5.4: *Terapon jarbua* Planktonic Larval Duration**

a) Boxplot of PLD for Khors Dubena, Matief and Rukup, red dots represent PLD means while the black horizontal bars represent the PLD medians, boxes encompass 50 % of the data, whiskers encompass 95 % and small crosses represent outliers. b) PLD distribution.

The red dotted lines correspond to the overall PLD mean of 25.1 days (~150  $\mu\text{m}$ ).

**Otolith microchemistry***Migratory life history*

The migratory life history of juvenile *T. jarbua* was well resolved by using Sr:Ba ratios. Laser ablation analyses from the otolith core to the edge revealed large variation in Sr:Ba ratios ranging from 19 to 6031 (Fig. 5.5). Three patterns can be drawn from those profiles, the first and most common one (in blue) presents high ratio values at the core and decrease to very low values outside the core (180  $\mu\text{m}$ ), indicating that the species hatch at sea and enter estuaries after a short PLD of 25 days ( $\sim 150 \mu\text{m}$ ). Discrepancy between PLD and the appearance of the estuarine chemical signal in the otolith (180  $\mu\text{m}$ ) might be due to the ablation resolution (60  $\mu\text{m} \text{ } \varnothing$ ) and the latency necessary for the otolith to incorporate environmental signature in their increments.



**Figure 5.5: Profiles of Sr:Ba ratios measured along otolith growth axes of *T. jarbua***

The Sr:Ba ratios show evidence of migration between marine and brackish habitats. Colors were used to differentiate the three migratory patterns. The grey and white backgrounds represent the marine larval stage and the estuarine juvenile phase respectively

The second pattern was found in Khor Bidholeh (in green) where Sr:Ba ratios are highly variable and remains high (>1000), indicating that Khor Bidholeh receiving very limited freshwater inputs is permanently connected to the sea. A third pattern (in red) was observed in few individuals ( $n = 5$ ) at Khors Dubena, Matief and Rukup where profiles start to follow the first pattern, however Sr:Ba ratios increase and then decrease again in the middle or at the end of the profiles (Fig. 5.5). This third pattern suggested that individuals might have experienced early migration outside or close to the opening of the estuaries before returning to more inland habitats. Moreover for three of those individuals, Sr:Ba ratios at the core, although high, were lower than all other individual core ratios, suggesting a more coastal natal origin.

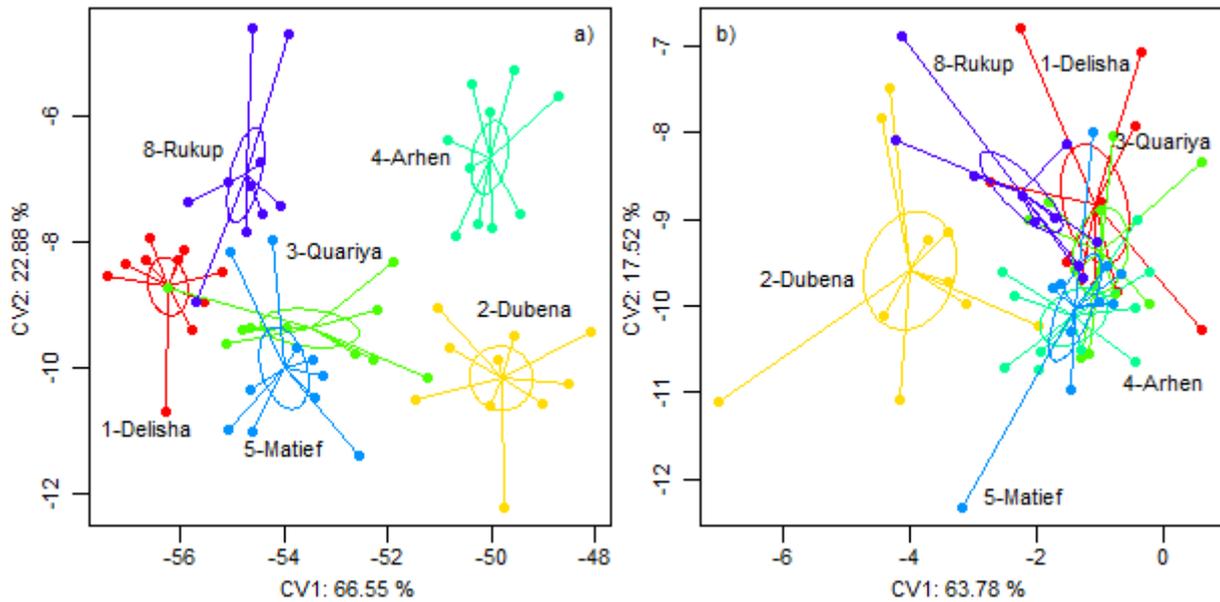
#### *Estuarine and birth place elemental fingerprints*

A MANOVA was used to compare the mean relative concentrations of all ten elements ( $^{11}\text{B}$ ,  $^{26}\text{Mg}$ ,  $^{55}\text{Mn}$ ,  $^{66}\text{Zn}$ ,  $^{85}\text{Rb}$ ,  $^{88}\text{Sr}$ ,  $^{118}\text{Sn}$ ,  $^{138}\text{Ba}$ ,  $^{208}\text{Pb}$  and  $^{238}\text{U}$ ) in the otolith edges between each of the sampled estuaries. The discrimination among locations was significant (MANOVA  $F = 4.665$ ,  $p < 0.001$ ) and five out of the ten analyzed elements presented significant differences among estuaries:  $^{26}\text{Mg}$ ,  $^{55}\text{Mn}$ ,  $^{85}\text{Rb}$ ,  $^{88}\text{Sr}$  and  $^{138}\text{Ba}$  ( $p < 0.001$ ) and an other element tends to show differences although non significant:  $^{208}\text{Pb}$  ( $p = 0.07$ ). LDFA on the elemental signature of otolith edges (Fig. 5.6a) allowed discriminating among locations. Indeed the assignment test to each location was successful with an average cross-validated accuracy of 80 % (Table 5.2) and the first two discriminate functions which jointly accounted for 91.65 % of the variance between locations.

A MANOVA was also used to compare the mean relative concentrations of all ten elements in the otolith nuclei between each of the estuaries. The discrimination among locations was significant (MANOVA  $F = 0.758$ ,  $p < 0.01$ ) and four out of the ten analyzed elements presented significant differences among estuaries:  $^{26}\text{Mg}$ ,  $^{66}\text{Zn}$ ,  $^{138}\text{Ba}$  ( $p < 0.05$ ) and  $^{85}\text{Rb}$  ( $p < 0.01$ ) and an other element tends to show differences although non significant:  $^{118}\text{Sn}$  and  $^{208}\text{Pb}$  ( $p < 0.1$ ). Although non significant, both element were included in the LDFA as it increased the assignment test accuracy. The LDFA on the elemental signature of otolith nuclei (Fig. 5.6b) did not allow a very accurate discrimination among locations or drawing natal origin patterns. Indeed the assignment test to each location was only moderately successful with an average cross-validated accuracy of 40 % (Table 5.2) and the first two discriminant functions which jointly accounted for 81.30 % of the variance between locations.

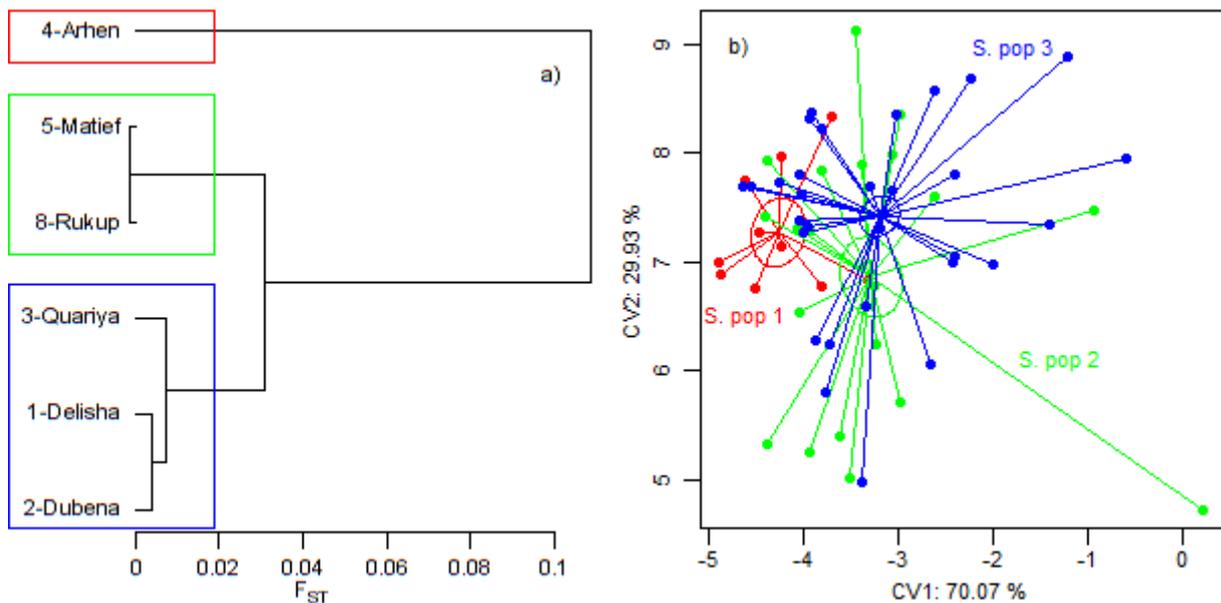
**Table 5.2: Assignment test**

Locations	Accuracy of the prediction (%)	
	Otolith edge	Otolith nucleus
1-Delisha – 2007	100	10
2-Dubena – 2007	70	80
3-Quariya – 2007	60	20
4-Arhen – 2007	100	40
5-Matief – 2007	80	50
8-Rukup – 2007	70	40
<b>Total accuracy</b>	<b>80</b>	<b>40</b>



**Figure 5.6: Linear Discriminant Function Analysis on the elemental composition of a) otolith edges (Accuracy: 80 %) and b) otolith nuclei (Accuracy: 40 %)**

LDFA were performed on  $\log(x + 1)$  transformed data. Colored star like figures represent fingerprint signature of estuaries sampled in 2007. Colored ellipses represent the 95 % confidence error. The meaning of the 95 % confidence error ellipse is that if more points are added to improve the calculation of the circle, there is 95 % probability that the center of the circle will remain within the area specified by the ellipse.



**Figure 5.7: a) Ward hierarchical clustering analysis on  $F_{ST}$ , b) Linear Discriminant Function Analysis on the elemental composition of otolith nuclei (Accuracy: 53.33 %)**

Clustering analyses were performed on pairwise  $F_{ST}$  values (Chapter 4). LDFA was performed on  $\log(x + 1)$  transformed data. Colored rectangles and star like figures represent the three genetically different groups. Colored ellipses represent the 95 % confidence error.

Ward's hierarchical clustering analysis derived from pairwise  $F_{ST}$  produced three groups (potential sub-populations). Group 1 is represented by Ahren, Group 2 includes Khors Matief and Rukup and Group 3 includes Khors Delisha, Dubena and Quariya (Fig. 5.7a). A MANOVA was used to compare the mean relative concentrations of all ten elements in the otolith nuclei between each of the sub-population group. Although the discrimination among groups was not significant (MANOVA  $F = 1.089$ ,  $p > 0.05$ ) one element presented significant differences among groups:  $^{138}\text{Ba}$  ( $p < 0.05$ ). Although non significant, the element  $^{26}\text{Mg}$  and  $^{55}\text{Mn}$  were included in the LDFA as it increased the assignment test accuracy. LDFA on the elemental signature of otolith nuclei (Fig. 5.7b) did not allow a very accurate discrimination among groups. Indeed the assignment test to each groups was only moderately successful with an average cross-validated accuracy of 53.33 % and the first two discriminant functions which jointly accounted for 100 % of the variance between groups.

## Discussion

Although, the dissection process was performed in conditions as clean as possible, contamination was unavoidable. However, otoliths were treated in exactly the same way, thus measurement errors were likely to be the same for all otoliths. Migration profiles showed that *T. jarbua* in the studied region have flexible life histories. The key geochemical markers distinguishing residence salinities and movements was the Sr:Ba ratio (Fig. 5.5) with high ratios indicating a more marine character. Most *T. jarbua* exhibited a natal marine phase, migrating into estuarine systems after a short planktonic larval stage as post larvae or young juveniles in which they remained for at least two years (Fig. 5.2). PLD of *T. jarbua* was relatively short but not uncommon (Raventos and Macpherson, 2001) compare to other tropical species where it can last up to 2 months (Victor, 1986). Indeed estuarine settlement of *T. jarbua* occurred at 25 days old in average and was stable over the studied region. This result and the most commonly observed migration profile (Fig. 5.5) agrees with previous observations of this species by Miu et al. (1990) and Wallace et al. (1984).

Profiles observed in Khor Bidholeh exhibited relatively wide range of Sr:Ba ratios ( $> 1000$ ) throughout their lifespan consistent with marine signature, in addition some specimens presented back and forth profiles between brackish and marine habitats, thus refuting the hypothesis that juveniles *T. jarbua* is an estuarine dependent species which requires freshwater input, but rather an opportunist species that uses estuaries as shelter and source of prey. However, no *T. jarbua* was observed in coastal waters of the three small outer islands of the archipelago where no freshwater input are found, indicating that although lower salinity might not be a physiological requirement, the detection and physiological adaptation of the species to sheltered freshwater and

brackish habitats like estuaries and stream (e.g.: Arhen) procure to *T. jarbua* post larvae a higher chance to survive and to contribute to the adult population.

Statistically significant differences were found in the otolith edge elemental composition ( $^{26}\text{Mg}$ ,  $^{55}\text{Mn}$ ,  $^{85}\text{Rb}$ ,  $^{88}\text{Sr}$  and  $^{138}\text{Ba}$ ) of juvenile *T. jarbua* collected in Socotra and Yemen mainland estuaries in 2007. Assignment test suggested that otolith edge chemical signature was adequate to discriminate nurseries (Fig. 5.6a) even those separated by less than 10 km (e.g.: Khors Delisha and Dubena). Such resolution might be link with the particular geology of Socotra Island (Fleitmann et al., 2004). However inter-annual differences (not shown) in the otolith elemental signatures exceeded intra-annual variation. Such limitation prevents the use of fish otoliths collected in different years in a single data set (Miller and Shanks, 2004). Additional studies on the juvenile otolith signature of marine adult specimens might help resolving spatial issues on connectivity between estuarine and marine habitats of Socotra.

Statistically significant differences between estuaries were also found in the otolith nuclei elemental composition ( $^{26}\text{Mg}$ ,  $^{66}\text{Zn}$ ,  $^{138}\text{Ba}$  and  $^{85}\text{Rb}$ ). However, the discriminatory power of the nucleus signature to characterize larval origin of *T. jarbua* was weak (Fig. 5.6b). Although, the relation between the assay spot size and the temporal scale of movement (i.e.: days, weeks, months) might increase misclassification rate (Bradbury et al., 2008), the spot size of 60  $\mu\text{m}$  diameter used in this study corresponding to 30  $\mu\text{m}$  radius of growth at the nucleus was smaller than the PLD ( $\sim 150$ ), thus being unlikely the reason of misclassification. However, there are several other potential reasons such as otolith elemental composition which does not reflect the composition of the ambient environment, movement of larvae between locations, homogeneity of the environment (Gillanders, 2005; Gillanders and Kingsford, 2003; Thresher, 1999) and large variations within locations that mask differences between locations. The lack of influence of the surrounding environmental composition on otolith signature is unlikely for several elements ( $^{88}\text{Sr}$ ,  $^{138}\text{Ba}$  and  $^{26}\text{Mg}$ ). Indeed relationship between water composition and otolith finger print has been demonstrated by several authors (Bradbury et al., 2011; Campana, 1999; Elsdon et al., 2008; Honda et al., 2012; McCulloch et al., 2005; Milton and Chenery, 2005; Patterson et al., 1999). A suitable reason would be the dynamic marine environment of the region, homogenizing the water chemistry, especially during the period when estuaries are open and allowing *T. jarbua* post larvae from different sub-populations to settle in the same estuary, thus possibly increasing misclassification rate. However a certain differentiation level could be detected suggesting that despite probable mixing events, some subpopulations were restricted to settle in specific estuaries.

This hypothesis was congruent with previous microsatellite genotyping analysis (Chapter 4) which suggested that *T. jarbua* population structure followed probably a metapopulation model

composed of open subpopulations (i.e.: multiple sources producing more or less pronounced mixtures of larvae) and thus leading to significant genetic differentiation between the nurseries (i.e.: the estuaries). Random demographic event linked to TOCE functioning system might be responsible of increasing such genetic differentiation. Finally, this was partially confirmed by nucleus elemental signature assignment test (Accuracy 53.33 %, Fig. 5.7b) to empirical subpopulations determined using Ward's hierarchical clustering analysis on pairwise  $F_{ST}$  previously determined in Chapter 4 (Fig. 5.7a). Indeed, despite the moderate accuracy of the assignment test, the discrepancy between the otolith nucleus fingerprints reflected differences in the chemical composition of their natal environments and therefore suggest that 1) several spawning areas with different water composition might exist and 2) passive mixing of larvae stemming from those areas might take place in the region.

Finally, this study highlighted that elemental fingerprints of the otolith edge have great potential for discriminating nursery areas at both small and large geographical scales and for reconstructing early life migration histories of *T. jarbua*. On the other side, elemental fingerprints of the otolith nuclei have a low potential for discriminating *T. jarbua* marine spawning grounds but point out the existence of several natal areas, thus supporting the metapopulation model hypothesis. In the light of increasing development on Socotra Island, disturbances of connectivity between estuaries and marine habitats and derived consequences to local fishery and ecosystem services (Chapter 1) are very likely. The present study suggests that new tools are available for a possible estimation of the contribution of specific coastal nurseries to adult stocks (Fromentin et al., 2009) and should be used in the future to build pertinent management and conservation programs devoted to the Socotra estuaries.

## **Acknowledgments**

The present study was mainly funded by the Total Foundation, Paris. It was partially conducted at the Socotra Field Research Station of the Biodiversity and Climate Research Centre (BiK-F), Frankfurt a.M., based on financial support of the research-funding programme “LOEWE – Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz” of Hesse's Ministry of Higher Education, Research, and the Arts. Additional mobility funds were provided by scholarships from the GRADE - Goethe Graduate Academy of the Goethe University Frankfurt a.M. and the International Doctoral College of the European University of Brittany (UEB). His Excellency the former Minister of Water and Environment of the Republic of Yemen, Eng. Abdul-Rahman F. Al-Eryani, and His Excellency the Chairman of the Environment Protection Authority, Eng. Mahmoud Shidiwa, are cordially acknowledged for their continued support and for granting research and sample export permits. The Socotra Conservation and Development Program (SCDP-UNDP) is thanked for providing indispensable support during the field work. We would like to thank the People of Socotra and in particular the members of the coastal communities which kindly facilitated field work and provided access to the areas in their care. We wish to express our gratitude to Fouad Naseeb and Motea Sheikh Aideed for their efficient assistance in the field, to Dr. El-Mashjary and Dr. Ali of the Hadhramout University for granting the authors access to the University wet laboratory, to Claire Bassoullet and Jean-Marie Munaron for their help with the ICP-MS and to Edric Dabas and Claire Geffroy for their help with otolith preparation and measurements. We are also grateful to Eric Morize for his scientific support and comments on this work. Friedhelm Krupp is cordially acknowledged for his support to the Ph.D. project of the first author.



# Conclusion





## Conclusion

In this study a multidisciplinary approach was developed to understand the functioning and importance of Socotra estuaries and lagoon for marine fishes. Several tools from different fields of biology and chemistry, i.e.: taxonomy, ecology, phylogenetics, population genetics, otolith microstructure and otolith microchemistry, were used. A funnel approach, from the study of estuarine fish community to the functioning of *T. jarbua* population, was used because little was known about North-Western Indian Ocean estuaries and particularly those of the Socotra Island recognised in July 2008 as a natural world heritage site by UNESCO. Socotra Island has been isolated from massive human development until the late 90's. Recent uncontrolled development raised some environmental issues for Socotra pristine habitats and unique biodiversity and particularly estuaries which providing shelters for juvenile fishes and other groups.

Understanding connectivity between estuarine nurseries and marine habitats is fundamental to studies of fish population dynamics and to the design of effective conservation and fisheries management strategies (Gillanders, 2005). In this general context the aim of this work was to provide the first faunistic and ecological baseline of Socotra estuaries and lagoon fishes for governmental coastal managers and decision makers, with a particular focus on a sentinel species, *Terapon jarbua*, to better understand the connectivity between estuarine and marine habitats, the functioning and the importance of Socotra temporarily open / closed estuarine system. Socotra Island is under strong influence of the alternating monsoon seasons in the Northern Indian Ocean driven by the ITCZ. The combine geographical and climatic characteristics control the volume of freshwater input on the Island, and monsoon seasons are also responsible for estuary opening and closing.

Taking into account the limited knowledge on Socotra Island estuarine fishes (Krupp et al., 2006; Steindachner, 1902, 1903; Taschenberg, 1883) despite numerous faunistic surveys on the island (Kemp, 1998; Zajonz and Khalaf, 2002), the first important step in this work was to provide a faunistic account of estuarine and lagoon fish species of Socotra Island and the Hadhramout mainland coast of Yemen and describe for the first time fish species diversity and assemblage composition at key sites. Then a narrower focus on one particular sentinel species (*T. jarbua*) for the estuaries of the region was carried out in order to better understand phylogenetics, population structure and life history strategy of this species and to explore the complex connectivity between estuarine and marine habitats.

---

**Faunistic account, fish species diversity and assemblage composition: baseline information of paramount importance for the conservation management on Socotra.**

Socotra Island and Yemen mainland estuaries and lagoon are relatively small; however they contain high fish diversity, with a total of 66 species in 31 families among which 23 species represent new records. Including the critically assessed historic records, the total fish diversity might reach 75-80 species. On all estuarine fish species of South Africa recorded by Harrison (2005) 15 were also recorded in this study, 14 in Socotra estuaries and only seven in Yemen mainland. This provides further support to Socotra's function as a biogeographic "stepping stone" for certain species on the one hand, as proposed by De Vantier et al. (2004), Kemp (1998) and Zajonz et al. (2000). On the other hand, this distribution pattern also suggests that for certain species it is not possible to bridge the gap between the African coasts and Socotra and the Eastern Arabian coast. Moreover 33 out of the 66 recorded species were considered relevant species for the local economy (i.e.: 18 highly important and 15 medium important species to the local fishery). This underscores the paramount importance of these coastal water bodies as spawning and nursery sites, and for the sustainability of vital provisioning ecosystem services.

**High Resolution Melting Analysis as a new tool to explore CO1 polymorphism**

The first step in the phylogenetic analysis of *T. jarbua* was to develop a new tool to study the polymorphism of the Cytochrome c Oxydase sub-unit 1 (CO1). Indeed at the beginning of this Ph.D. work, sequencing costs were much higher than nowadays, thus HRMA appeared to be a much cheaper, faster and accurate alternative to mass sequencing (Liew et al., 2004; Wittwer et al., 2003). Although this technique aroused a great interest of the scientific community, especially for medical diagnostics (Do et al., 2008), it has been employed only recently for environmental research and was used in detecting heterozygosity and DNA sequence variations and in identifying organisms (Dalmaso et al., 2007). However, this analysis relies on software usually provided with the thermocycler which was not developed for the number of samples needed for phylogenetics and population studies, thus increasing post-analysis data treatment time. Despite the high reliability of the analysis, errors derived from data treatment are more likely than sequencing errors. Taking into account the actual lower costs of mass sequencing, HRMA should be reserved for studies that do not require sequencing such as heterozygote detection or the polymorphism of candidate genes (Calves et al., in prep).

**The contribution of genetics to better understand *T. jarbua* population dynamics**

The study of *T. jarbua* CO1 sequences, included sequences from other regions highlighted two patterns of genetic structure. A high and significant genetic differentiation was observed at

the scale of the Indo-West Pacific. Three population clusters could be drawn, the North-Western Indian Ocean cluster which includes all haplotypes sequenced in this study and haplotypes from the Arabian (Persian) Gulf, the West Indian Shelf cluster and the Chinese Sea cluster. At the restricted scale of the North-Western Indian Ocean, analysis resolution was higher and a small but significant genetic structure was observed principally between the Khors Delisha and Matief and the other estuaries, indicating that in Socotra Island, Khor Sahier the most Eastern estuary of the mainland also appeared to be differentiated. However, the large number of nucleotide differences (100 out of 619 nucleotides) between the North-Western Indian Ocean and Chinese sequences raised some issues concerning the species identification despite the fact that *T. jarbua* has a characteristic color pattern easily identifiable. Such genetic differences might be explained by the presence of marked biogeographical barriers such as the one between the Arabian Sea and the Indian Ocean (Kemp, 1998), and the Indo-Pacific Barrier (IPB) between the South Chinese Sea and the Indian Ocean (Gaither et al., 2010). The Indo-West Pacific speciation process probably occurred in the Pliocene–Early Pleistocene driven by sea-level changes isolating populations between major oceans (Pillans et al., 1998; Voris, 2000).

Meanwhile microsatellites genotyping for Socotra and Yemen mainland estuaries highlighted a relatively high and significant genetic differentiation between estuaries. The highest differentiation was between the Ahren – Khor Bidholeh group and the other locations, and the relative isolation of the Khors Delisha – Dubena group. Geographical distance did not appear to be a major structuring factor for *T. jarbua* populations in this region, but rather the strict link between juvenile *T. jarbua* and TOCE's and random demographic bottleneck, increasing the local differentiation among estuaries. However, random demographic events could not be the only factor responsible for such atypical genetic differentiation. Although the dynamic environment of the region driven by the monsoon system could reduce genetic differences of *T. jarbua*, the short larval stage duration of 25 days of the species and potential larval retention in particular sectors might reduce homogenization over larger geographical scale.

### **Life history strategy of *Terapon jarbua* in a complex dynamic environment**

The use of otolith microstructures and LA-ICP-MS to understand life history strategy of *T. jarbua* in a complex climatic and biogeographic region appeared to be highly valuable. Although elemental fingerprint assignment tests to natal origin were not satisfactory with high misclassification rate, this analysis allowed pointing out the existence of several marine spawning grounds with a certain level of mixing, thus confirming the population genetics approach suggesting a regional model of a metapopulation composed of open subpopulations (i.e.: multiple sources and more or less pronounced mixtures of larval flows). In addition,

transect analyses along the otolith growth axis showed clear pattern of post larval migrations into estuarine nurseries. Low salinity did not appear to be a requirement but rather a potential signal for the species juveniles to find safe harbors to survive and contribute to the adult population. Finally, elemental fingerprint assignation tests to nurseries were highly accurate and could be used to study at which scales a particular nursery might contribute to the adult population. However a major limitation in the use of this marker is its high temporal variability.

## **Perspectives**

### ***Estuarine fish diversity, conservation management, sustainable resource use and local development: a complex temporal – spatial equation***

Additional work need to be done to finish the identification of the collected specimens and the Steindachner's voucher specimens located at the museum of Vienna should be reexamined according to current literature in order to produce a monograph on estuarine fishes of Socotra.

Basic Length-Weight Relationship and condition factor analyses have demonstrated their utility by showing the strong influence of the monsoon driven climate on estuarine fish fitness. However, Socotra Island remains a remote location where monthly surveys were difficult to implement especially during the monsoon season when transportation with the mainland are restricted or stopped. Fortunately, the new Socotra Field Research Station provides a real opportunity to investigate seasonal and annual variation of species assemblages and recruitment patterns at a higher temporal resolution, in order to better understand the functioning rythme of TOCE's. Moreover the assessment of fish demography and the estimation of biomass productivity of selected (commercial) species is part of a current M.Sc. study of Moteah Sheikh Aideded from the Hadhramout University (Yemen).

This kind of surveys is of prime importance for Socotra conservation and the local fishery management. Indeed contribution of estuarine juvenile fishes to the local fishery resources in terms of fish food or commercially important species is poorly understood yet and requires further studies of the general and functional estuarine ecology and fisheries biology in support of appropriate management.

### ***High resolution phylogenetic analysis of T. jarbua over its distribution range***

*Terapon jarbua* displayed interesting phylogeographical characteristics over large geographical scale. Finer resolution of the phylogeny of the species over its whole geographical distribution range including the specimen from the Mediterranean Sea describe by Golani and Appelbaum-Golani (2011), would lead to very promising answers on 1) the taxonomical status of the species, indeed according to Gill and Kemp (2002), most of the wide Indo-Pacific

distribution shore fishes could in fact belong to more than one taxon and 2) the reconstruction of Red Sea – Indian Ocean colonization history after the Pleistocene glaciations.

**Scale of connectivity, coupling genetic markers with otolith composition analysis.**

Knowledge of scale of connectivity is necessary to protect important habitats such as nurseries contributing more than others to the adult reproductive population. Spatial and temporal geochemical mapping of Socotra estuaries would allow establishing a clear geographical link to distinct nursery habitats, inferred from otolith microchemistry of juveniles and adults *T. jarbua* respectively caught in estuaries and at sea; coupled with microsatellite analysis, this temporal approach might tackle the issue of determining to which extend a particular nursery contribute to the adult reproductive population. Most of the studies including the present one are based on few year classes of a single species (Gillanders et al., 2012), thus increasing the number of studied species over longer timescales would lead to more flexible management practices in phase with variability in connectivity. Future developments of new quantitative approaches on the combine use of both genetic and otolith markers provide encouraging tools to better understand wild fish population (Fromentin et al., 2009).



# References





## References

- Abraham, K.J., Joshi, K.K. and Murty, V.S.R. (2011). Taxonomy of the fishes of the family Leiognathidae (Pisces, Teleostei) from the west coast of India. *Zootaxa*, **2886**:1–18.
- Akazaki, M. (1994). *Comments on the taxonomic status of the sparid fish, Acanthopagrus bifasciatus*. Faculty of Fisheries, Kasetsart University, Bangkok, Thailand.
- Allen, G.R. (1985). *Snappers of the world*. Food and Agriculture Organization of the United Nations, Rome.
- Allen, G.R. (1991). *Field guide to the freshwater fishes of New Guinea*. Christensen Research Institute, Madang, Papua New Guinea.
- Allen, G.R. and Swainston, R. (1988). The marine fishes of North-Western Australia. A field guide for anglers and divers. Western Australian Museum, Perth.
- Allen, G.R. and Adrim, M. (2003). Coral reef fishes of Indonesia. *Zoological Studies*, **42(1)**:1–72.
- Allen, G.R., Swainston, R. and Ruse, J. (1997). *Marine fishes of tropical Australia and South-East Asia*. Western Australian Museum, Perth, W.A.
- Anderson, M.E. and Heemstra, P.C. (2003). Review of the glassfishes (Perciformes Ambassidae) of the Western Indian Ocean. *Cybium*, **27(3)**:199–209.
- Asgharian, H., Sahafi, H.H., Ardalan, A.A., Shekarriz, S. and Elahi, E. (2011). Cytochrome *c* oxidase subunit 1 barcode data of fish of the Nayband National Park in the Persian Gulf and analysis using meta-data flag several cryptic species. *Molecular Ecology Resources*, **11(3)**:461–472. DOI: 10.1111/j.1755-0998.2011.02989.x.
- Avise, J.C. (2004). *Molecular markers, natural history, and evolution*. Sinauer Associates, Sunderland, Mass.
- Avise, J.C. and Saunders, N.C. (1984). Hybridization and introgression among species of sunfish (*lepomis*): analysis by mitochondrial dna and allozyme markers. *Genetics*, **108(1)**:237–255.
- Avise, J.C., Arnold, J., Ball, R.M., Bermingham, E., Lamb, T., Neigel, J.E., Reeb, C.A. and Saunders, N.C. (1987). Intraspecific Phylogeography: The Mitochondrial DNA Bridge Between Population Genetics and Systematics. *Annual Review of Ecology and Systematics*, **18**:489–522.
- Bachtrog, D., Thornton, K., Clark, A. and Andolfatto, P. (2006). Extensive introgression of mitochondrial dna relative to nuclear genes in the *drosophila yakuba* species group. *Evolution*, **60(2)**:292–302. DOI: 10.1111/j.0014-3820.2006.tb01107.x.

- Baker, A.M., Hughes, J.M., Dean, J.C. and Bunn, S.E. (2004). Mitochondrial DNA reveals phylogenetic structuring and cryptic diversity in Australian freshwater macroinvertebrate assemblages. *Marine and Freshwater Research*, **55(6)**:629. DOI: 10.1071/MF04050.
- Balloux, F. and Lugon-Moulin, N. (2002). The estimation of population differentiation with microsatellite markers. *Molecular Ecology*, **11(2)**:155–165.  
DOI: 10.1046/j.0962-1083.2001.01436.x.
- Banfield, L., Van Damme, K. and Miller, A.G. (2011). Evolution and biogeography of the flora of the Socotra Archipelago (Yemen), in: D. Bramwell and J. Caujapé-Castells (eds.). *The biology of island floras*. Cambridge University Press, Cambridge ;, New York.
- Banister, K.E. and Clarke, M.A. (1977). The freshwater fishes of the Arabian peninsula. In: The scientific results of the Oman flora and fauna survey 1975. *Journal Oman Studies (Special Report)* pp111–154.
- Bartlett, M.S. (1937). Properties of sufficiency and statistical tests. *Proceedings of the Royal Society of London Series A - Matematical and Physical Sciences*, **160(A901)**:268–282.
- Bay, L.K., Choat, J.H., van Herwerden, L. and Robertson, D.R. (2004). High genetic diversities and complex genetic structure in an Indo-Pacific tropical reef fish (*Chlorurus sordidus*): evidence of an unstable evolutionary past? *Marine Biology*, **144(4)**:757–767.  
DOI: 10.1007/s00227-003-1224-3.
- Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B.S., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F. and Weinstein, M.P. (2001). The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates. *BioScience*, **51(8)**:633.  
DOI: 10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2.
- Beck, M.W., Heck Jr., K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B.S., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F. and Weinstein, M.P. (2003). The Role of Nearshore Ecosystems as Fish and Shellfish Nurseries. *Issues in Ecology*, **11**:1–12.
- Belkhir, K., Borsa, P., Chikhi, L., Raufaste, N. and Bonhomme, F. (2004). *GENETIX* v.4.05. Logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5171, Université de Montpellier II, Montpellier (France).
- Ben Souissi, J., Mejri, H., Zaouali, J. and Capapé, C. (2006). Occurrence of an exotic silverside most closely related to *Atherinomorus lacunosus* (Atherinidae) in southern Tunisia (central Mediterranean) . *Cybium*, **30(4)**:379–381.

- Ben-Tuvia, A. (1973). Man-made changes in the eastern Mediterranean Sea and their effect on the fishery resources. *Marine Biology*, **19**:197–203. DOI: 10.1007/BF02097138.
- Bennett, B.A. (1989). A comparison of the fish communities in nearby permanently open, seasonally open and normally closed estuaries in the South-Western Cape, South Africa. *South African Journal of Marine Science*, **8**(1):43–55. DOI: 10.2989/02577618909504550.
- Bennett, J.W. (1830). *A selection from the most remarkable and interesting fishes found on the coast of Ceylon.*, London.
- Bilecenoglu, M., Taskavak, E., Mater, S. and Kaya, M. (2002). Checklist of the marine fishes of Turkey. *Zootaxa*, **113**:1–194.
- Bleeker, P. (1854). Spécies piscium bataviensium novae vel minus cognitae. *Natuurkundig Tijdschrift voor Nederlandsch Indië*, **6**:191–202.
- Bleeker, P. (1863). Onzième notice sur la faune ichthyologique de l'île de Ternate. *Nederlandsch Tijdschrift voor de Dierkunde*, **1**:228–238.
- Bloch, M.E. (1795). *Naturgeschichte der ausländischen Fische.*, Berlin.
- Bloch, M.E. and Schneider, J.G., editors (1801). *Systema Ichthyologiae.*
- Bonfil, R. and Abdallah, M. (2004). *Field identification guide to the sharks and rays of the Red Sea and Gulf of Aden.* Food and Agriculture Organization of the United Nations, Rome.
- Borkenhagen, K., Esmaeili, H.R., Mohsenzadeh, S., Shahryari, F. and Gholamifard, A. (2011). The molecular systematics of the *Carasobarbus* species from Iran and adjacent areas, with comments on *Carasobarbus albus* (Heckel, 1843). *Environmental Biology of Fishes*, **91**(3):327–335. DOI: 10.1007/s10641-011-9787-1.
- Bowen, B.W., Muss, A., Rocha, L.A. and Grant, W.S. (2006). Shallow mtDNA Coalescence in Atlantic Pygmy Angelfishes (Genus *Centropyge*) Indicates a Recent Invasion from the Indian Ocean. *Journal of Heredity*, **97**(1):1–12. DOI: 10.1093/jhered/esj006.
- Bradbury, I.R., Campana, S.E. and Bentzen, P. (2008). Estimating contemporary early life-history dispersal in an estuarine fish: integrating molecular and otolith elemental approaches. *Molecular Ecology*, **17**(6):1438–1450. DOI: 10.1111/j.1365-294X.2008.03694.x.
- Bradbury, I.R., Laurel, B., Snelgrove, P.V., Bentzen, P. and Campana, S.E. (2008). Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. *Proceedings of the Royal Society B: Biological Sciences*, **275**(1644):1803–1809. DOI: 10.1098/rspb.2008.0216.
- Bradbury, I.R., DiBacco, C., Thorrold, S.R., Snelgrove, P.V. and Campana, S.E. (2011). Resolving natal tags using otolith geochemistry in an estuarine fish. *Marine Ecology Progress Series*, **433**:195–204. DOI: 10.3354/meps09178.

- Brookfield, J.F.Y. (1996). A simple new method for estimating null allele frequency from heterozygote deficiency. *Molecular Ecology*, **5(3)**:453–455.  
DOI: 10.1046/j.1365-294X.1996.00098.x.
- Bucciarelli, G., Golani, D. and Bernardi, G. (2002). Genetic cryptic species as biological invaders: the case of a Lessepsian fish migrant, the hardyhead silverside *Atherinomorus lacunosus*. *Journal of Experimental Marine Biology and Ecology*, **273(2)**:143–149.  
DOI: 10.1016/S0022-0981(02)00138-7.
- Buratti, C. and Santos, B. (2010). Otolith microstructure and pelagic larval duration in two stocks of the Argentine hake, *Merluccius hubbsi*. *Fisheries Research*, **106(1)**:2–7.  
DOI: 10.1016/j.fishres.2010.05.007.
- Calves, I., Claireaux, G., Amérand, A., Théron, M., Loizeau, V., Labonne, M., Sanchez, W., Cabral, H., Vasconcelos, R.P., França, S., Pedron, N., Quiniou, L. and Laroche, J. (in prep). Phenotypic variation of the European flounder (*Platichthys flesus*) under field conditions, considering the possible effects of climate change, hypoxia and chemical stress.
- Campana, S.E. (1992). Measurement and Interpretation of the Microstructure of Fish Otoliths. Pages 59–71, in: D.K. Stevenson and S.E. Campana (eds.). *Otolith microstructure examination and analysis*. Department of Fisheries and Oceans, Ottawa.
- Campana, S.E. (1999). Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Marine Ecology Progress Series*, **188**:263–297. DOI: 10.3354/meps188263.
- Campana, S.E. and Jones, C.M. (1992). Analysis of Otolith Microstructure Data. Pages 73–100, in: D.K. Stevenson and S.E. Campana (eds.). *Otolith microstructure examination and analysis*. Department of Fisheries and Oceans, Ottawa.
- Campana, S.E. and Thorrold, S.R. (2001). Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? *Canadian Journal of Fisheries and Aquatic Sciences*, **58(1)**:30–38. DOI: 10.1139/cjfas-58-1-30.
- Carpenter, K.E. and Allen, G.R. (1989). *Emperor fishes and large-eye breams of the world (family Lethrinidae)*. Food and Agriculture Organization of the United Nations, Rome.
- Carpenter, K.E. and Niem, V.H. (1999). *Species identification guide for fishery purposes*. Food and Agriculture Organization of the United Nations, Rome.
- Carpenter, K.E., Krupp, F., Jones, D.A. and Zajonz, U. (1997). *Living marine resources of Kuwait, eastern Saudi Arabia, Bahrain, Qatar, and the United Arab Emirates*. Food and Agriculture Organization of the United Nations, Rome.
- Cavalli-Sforza, L.L. and Edwards, A.W. (1967). Phylogenetic analysis. Models and estimation procedures. *American journal of human genetics*, **19(3 Pt 1)**:233–257.

- Cerny, V., Pereira, L., Kujanová, M., Vašíková, A., Hájek, M., Morris, M. and Mulligan, C.J. (2009). Out of Arabia-The settlement of Island Soqatra as revealed by mitochondrial and Y chromosome genetic diversity. *American Journal of Physical Anthropology*, **138(4)**:439–447. DOI: 10.1002/ajpa.20960.
- Chakrabarty, P., Amarasinghe, T. and Sparks, J.S. (2009). Redescription of Ponyfishes (Teleostei: Leiognathidae) of Sri Lanka and the Status of *Aurigequula* Fowler 1918. *Ceylon Journal of Science (Biological Sciences)*, **37(2)**:143-161. DOI: 10.4038/cjsbs.v37i2.502.
- Chakrabarty, P., Sparks, J.S. and Ho, H.-C. (2010). Taxonomic review of the ponyfishes (Perciformes: Leiognathidae) of Taiwan. *Marine Biodiversity*, **40(2)**:107–121. DOI: 10.1007/s12526-010-0037-0.
- Chambers, J.M., Freeny, A.E. and Heiberger, R.M. (1992). Analysis of Variance; Designed Experiments, in: J.M. Chambers and T. Hastie (eds.). *Statistical models in S*. Wadsworth & Brooks, Pacific Grove, California.
- Chang, E.H., Menezes, M., Meyer, N.C., Cucci, R.A., Vervoort, V.S., Schwartz, C.E. and Smith, R.J. (2004). Branchio-oto-renal syndrome: The mutation spectrum in EYA1 and its phenotypic consequences. *Human Mutation*, **23(6)**:582–589. DOI: 10.1002/humu.20048.
- Chapuis, M.-P. and Estoup, A. (2006). Microsatellite Null Alleles and Estimation of Population Differentiation. *Molecular Biology and Evolution*, **24(3)**:621–631. DOI: 10.1093/molbev/msl191.
- Charrier, G., Chenel, T., Durand, J., Girard, M., Quiniou, L. and Laroche, J. (2006). Discrepancies in phylogeographical patterns of two European anglerfishes (*Lophius budegassa* and *Lophius piscatorius*). *Molecular Phylogenetics and Evolution*, **38(3)**:742–754. DOI: 10.1016/j.ympev.2005.08.002.
- Chien, L.-T., Hwang, D.-F. and Jeng, S.-S. (1999). Thermal Stress on Dietary Requirement of Vitamin C in Thronfish *Terapon jarbua*. *Fisheries Science*, **65(5)**:731–735.
- Clark, F.N. (1928). The weight–length relationship of the California sardine (*Sardina caerulea*) at San Pedro. *Division of Fish and Game, Fish Bull*, **12**:59.
- Clarke, K.R. and Green, R.H. (1988). Statistical design and analysis for a 'biological effects' study. *Marine Ecology Progress Series*, **46**:213–226. DOI: 10.3354/meps046213.
- Clement, M., Posada, D. and Crandall, K.A. (2000). TCS v.1.21. a computer program to estimate gene genealogies. *Molecular Ecology* **9(10)**: 1657-1660.
- Coad, B.W. (1991). Fishes of the Tigris-Euphrates Basin: a critical checklist. *Sylogus*, **68**:1–49.
- Coad, B.W. (1996). Freshwater fishes of Iranian and Pakistani Baluchistan. *Biologia*, **42**:1–18.
- Collette, B.B. (2004). Family Hemiramphidae Gill, 1859 - halfbeaks. *California Academy of Sciences Annotated Checklists of Fishes*, **22**:1–35.

- Collie, J.S., Wood, A.D. and Jeffries, H.P. (2008). Long-term shifts in the species composition of a coastal fish community. *Canadian Journal of Fisheries and Aquatic Sciences*, **65(7)**:1352–1365. DOI: 10.1139/F08-048.
- Corlett, R.T. (2010). Invasive aliens on tropical East Asian islands. *Biodiversity and Conservation*, **19(2)**:411–423. DOI: 10.1007/s10531-009-9624-4.
- Cowley, P.D. and Whitfield, A.K. (2001). Ichthyofaunal characteristics of a typical temporarily open/closed estuary on the south east coast of South Africa. *Ichthyological Bulletin*, **71**:1–17.
- Craig, M.T., Eble, J.A., Bowen, B.W. and Robertson, D.R. (2007). High genetic connectivity across the Indian and Pacific Oceans in the reef fish *Myripristis berndti* (Holocentridae). *Marine Ecology Progress Series*, **334**:245–254. DOI: 10.3354/meps334245.
- Crandall, K.A. and Templeton, A.R.S.C.F. (1994). Intraspecific phylogenetics: problems and solutions. Pages 273–297, in: R.W. Scotland, D.J. Siebert and D.M. Williams (eds.). *Models in phylogeny reconstruction*. Published for the Systematics Association by Clarendon Press; Oxford University Press, Oxford, New York.
- Currie, R.J., Fisher, A.E. and Hargreaves, P.M. (1973). Arabian Sea Upwelling. Pages 37–52, in: B. Zeitzschel and S.A. Gerlach (eds.). *The biology of the Indian Ocean*.
- Cuvier, G. (1816). *Le Règne Animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*.
- Cuvier, G. (1829). *Le Règne Animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*.
- Cuvier, G. and Valenciennes, A. (1828). *Histoire naturelle des poissons - Tome 2*.
- Cuvier, G. and Valenciennes, A. (1829). *Histoire naturelle des poissons - Tome 3*.
- Cuvier, G. and Valenciennes, A. (1830). *Histoire naturelle des poissons - Tome 4*.
- Dalmaso, A., Fontanella, E., Piatti, P., Civera, T., Secchi, C. and Bottero, M. (2007). Identification of Four Tuna Species by Means of Real-Time PCR and Melting Curve Analysis. *Veterinary Research Communications*, **31(S1)**:355–357. DOI: 10.1007/s11259-007-0036-1.
- De Vantier, L., De'ath, G., Klaus, R., Al-Moghrabi, S., Abdulaziz, M., Reinicke, G.N. and Cheung, C. Reef-building corals and coral communities of the Socotra Archipelago, a zoogeographic “crossroads” in the Arabian Sea. *Fauna of Arabia*, **20**:117–168.
- Dempster, A.P., Laird, N.M. and Rubin, D.B. (1977). Maximum Likelihood from Incomplete Data via the EM Algorithm. *Journal of the Royal Statistical Society. Series B (Methodological)*, **39(1)**:1–38.

- Di Franco, A., Gillanders, B.M., Benedetto, G. de, Pennetta, A., Leo, G.A. de, Guidetti, P. and Unsworth, R.K.F. (2012). Dispersal Patterns of Coastal Fish: Implications for Designing Networks of Marine Protected Areas. *PLoS ONE*, **7(2)**:e31681.  
DOI: 10.1371/journal.pone.0031681.
- Dixey, F.A., Burr, M. and Pickard-Cambridge, O. (1898). On a Collection of Insects and Arachnids made by Mr. E. N. Bennett in Socotra, with Descriptions of new Species. *Proceedings of the Zoological Society of London*, **66(3)**:372–383.  
DOI: 10.1111/j.1096-3642.1898.tb03156.x.
- Do, H., Krypuy, M., Mitchell, P.L., Fox, S.B. and Dobrovic, A. (2008). High resolution melting analysis for rapid and sensitive EGFR and KRAS mutation detection in formalin fixed paraffin embedded biopsies. *BMC Cancer*, **8(1)**:142.  
DOI: 10.1186/1471-2407-8-142.
- Dor, M. (1984). Checklist of the fishes of the Red Sea. *CLOFRES*.
- Dorenbosch, M., Pollux, B.J.A., Pustjens, A.Z., Rajagopal, S., Nagelkerken, I., Velde, G. and Staay, S.Y.M. (2006). Population structure of the Dory snapper, *Lutjanus fulvivflamma*, in the western Indian Ocean revealed by means of AFLP fingerprinting. *Hydrobiologia*, **568(1)**:43–53. DOI: 10.1007/s10750-006-0020-8.
- Drummond, A.J. and Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, **7(1)**:214. DOI: 10.1186/1471-2148-7-214.
- Drummond, A.J., Ashton, B., Buxton, S., Cheung, M., Cooper, A., Duran, C., Field, M., Heled, J., Kearse, M., Markowitz, S., Moir, R., Stones-Havas, S., Sturrock, S., Thierer, T. and Wilson, A. (2011). *Geneious* v.5.4. Available from: <http://www.geneious.com>.
- Drummond, A.J., Suchard, M.A., Xie, D. and Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*.  
DOI: 10.1093/molbev/mss075.
- Duran, S., Palacin, C., Becerro, M.A., Turon, X. and Giribet, G. (2004). Genetic diversity and population structure of the commercially harvested sea urchin *Paracentrotus lividus* (Echinodermata, Echinoidea). *Molecular Ecology*, **13(11)**:3317–3328.  
DOI: 10.1111/j.1365-294X.2004.02338.x.
- Eggins, S., Kinsley, L. and Shelley, J. (1998). Deposition and element fractionation processes during atmospheric pressure laser sampling for analysis by ICP-MS. *Applied Surface Science*, **127-129**:278–286. DOI: 10.1016/S0169-4332(97)00643-0.
- Elsdon, T.S., Wells, B.K., Campana, S.E., Gillander, B.M., Jones, C.M., Limburg, K.E., Secor, D.H., Thorrold, S.R. and Walther, B.D. (2008). Otolith chemistry to describe movements and life -history parameters of fishes: hypotheses, assumptions, limitations and inferences. Pages

- 297–330, in: R.N. Gibson, R.J.A. Atkinson and J.D.M. Gordon (eds.). *Oceanography and Marine Biology. An Annual Review*. C.R.C. Press LLC Taylor & Francis, Boca Raton, Florence.
- Eschmeyer, W.N. (2011). *Catalog of Fishes*. Available from: <http://research.calacademy.org>
- Excoffier, L. and Lischer, H.E.L. (2010). Arlequin suite v.3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, **10(3)**:564–567. DOI: 10.1111/j.1755-0998.2010.02847.x.
- Excoffier, L., Smouse, P.E. and Quattro, J.M. (1992). Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics*, **131(2)**:479–491.
- Fauvelot, C., Bernardi, G. and Planes, S. (2003). Reductions in the mitochondrial dna diversity of coral reef fish provide evidence of population bottlenecks resulting from Holocene sea-level change. *Evolution*, **57(7)**:1571–1583. DOI: 10.1111/j.0014-3820.2003.tb00365.x.
- Fischer, J.G. (1885). II. Üeber einige afrikanische Fische des Naturhistorischen Museums in Hamburg. Pages 66-77, in: *Ichthyologische und herpetologische Bemerkungen. Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten v.2: 49-121, Pls. 1-4*.
- Fischer, W. and Bianchi, G., editors (1984). *FAO Species identification sheets for fishery purposes. Western Indian Ocean (Fishing Area 51). Prepared and printed with the support of the Danish International Development Agency (DANIDA). Rome, Food and Agricultural Organization of the United Nations*.
- Fleitmann, D., Matter, A., Burns, S.J., Al-Subbary, A. and Al-Aowah, M.A. (2004). Geology and Quaternary climate history of Socotra. *Fauna of Arabia*, **20**:27–43.
- Forsskål, P. (1775). *Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit*. Copenhagen, Mölleri.
- Forster (1801), in: M.E. Bloch and J.G. Schneider (eds.). *Systema Ichthyologiae*.
- Fratantoni, D.M., Bower, A.S., Johns, W.E. and Peters, H. (2006). Somali Current rings in the eastern Gulf of Aden. *Journal of Geophysical Research*, **111(9)**:1-19.  
DOI: 10.1029/2005JC003338.
- Fratini, S. and Vannini, M. (2002). Genetic differentiation in the mud crab *Scylla serrata* (Decapoda: Portunidae) within the Indian Ocean. *Journal of Experimental Marine Biology and Ecology*, **272(1)**:103–116. DOI: 10.1016/S0022-0981(02)00052-7.
- Fricke, R., Mulochau, T., Durville, P., Chabanet, P., Tessier, E. and Letourneur, Y. (2009). Annotated checklist of the fish species (Pisces) of La Réunion, including a Red List of threatened and declining species. *Stuttgarter Beiträge zur Naturkunde A, Neue Serie*, **2**:1-168.

- Froese, R. (2006). Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology*, **22(4)**:241–253.  
DOI: 10.1111/j.1439-0426.2006.00805.x.
- Froese, R., Pauly, D. (2011). *FishBase. World Wide Web electronic publication version (12/2011)*. Available from: [www.fishbase.org](http://www.fishbase.org).
- Fromentin, J.-M., Ernande, B., Fablet, R. and Pontual, H. de (2009). Importance and future of individual markers for the ecosystem approach to fisheries. *Aquatic Living Resources*, **22(4)**:395–408. DOI: 10.1051/alr/2009035.
- Fu, Y.X. (1997). Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics*, **147(2)**:915–925.
- Gaither, M.R., Toonen, R.J., Robertson, D.R., Planes, S. and Bowen, B.W. (2010). Genetic evaluation of marine biogeographical barriers: perspectives from two widespread Indo-Pacific snappers (*Lutjanus kasmira* and *Lutjanus fulvus*). *Journal of Biogeography*, **37(1)**:133–147.  
DOI: 10.1111/j.1365-2699.2009.02188.x.
- Gao, S., Liu, X., Yuan, H., Hattendorf, B., Günther, D., Chen, L. and Hu, S. (2002). Determination of Forty Two Major and Trace Elements in USGS and NIST SRM Glasses by Laser Ablation – Inductively Coupled Plasma – Mass Spectrometry. *Geostandards and Geoanalytical Research*, **26(2)**:181–196. DOI: 10.1111/j.1751-908X.2002.tb00886.x.
- Gauthier, O., Sarrazin, J. and Desbruyères, D. (2010). Measure and mis-measure of species diversity in deep-sea chemosynthetic communities. *Marine Ecology Progress Series*, **402**:285–302. DOI: 10.3354/meps08395.
- Giacalone, V.M., D’Anna, G., Badalamenti, F. and Pipitone, C. (2010). Weight-length relationships and condition factor trends for thirty-eight fish species in trawled and untrawled areas off the coast of northern Sicily (central Mediterranean Sea). *Journal of Applied Ichthyology*, **26(6)**:954–957. DOI: 10.1111/j.1439-0426.2010.01491.x.
- Gill, A.C. (2004). *Revision of the Indo-Pacific dottyback fish subfamily Pseudochrominae (Perciformes:Pseudochromidae)*. South African Institute for Aquatic Biodiversity, Grahamstown, South Africa.
- Gill, A.C. and Kemp, J.M. (2002). Widespread Indo-Pacific Shore-fish Species: A Challenge for Taxonomists, Biogeographers, Ecologists, and Fishery and Conservation Managers. *Environmental Biology of Fishes*, **65(2)**:165–174. DOI: 10.1023/A:1020044616889.
- Gill, A.C. and Zajonz, U. (2011). Pseudochromine and pseudoplesiopine dottyback fishes from the Socotra Archipelago, Indian Ocean, with descriptions of two new species of *Pseudochromis* Rüppell (Perciformes: Pseudochromidae). *Zootaxa*, **3106**:1–23.

- Gillanders, B. (2005). Using elemental chemistry of fish otoliths to determine connectivity between estuarine and coastal habitats. *Estuarine, Coastal and Shelf Science*, **64**(1):47–57. DOI: 10.1016/j.ecss.2005.02.005.
- Gillanders, B. and Kingsford, M. (2003). Spatial variation in elemental composition of otoliths of three species of fish (family Sparidae). *Estuarine, Coastal and Shelf Science*, **57**(5-6):1049–1064. DOI: 10.1016/S0272-7714(03)00009-X.
- Gillanders, B.M., Elsdon, T.S. and Roughan, M. (2012). Connectivity of Estuaries, in: D. McLusky and E. Wolanski (eds.). *Treatise on Estuarine and Coastal Science*. Elsevier Science Technology.
- Glynn, P.W. (1993). Monsoonal upwelling and episodic *Acanthaster* predation as probable controls of coral reef distribution and community structure in Oman, Indian Ocean. *Atoll Research Bulletin*, **379**:1–66.
- Golani, D. (1998). Distribution of Lessepsian migrant fish in the Mediterranean. *Italian Journal of Zoology*, **65**(S1):95-99.
- Golani, D. (2002). The Indo-Pacific striped eel catfish, *Plotosus lineatus* (Thunberg, 1787), (Osteichthyes: Siluriformes), a new record from the Mediterranean. *Scientia Marina*, **66**(3):321-323. DOI: 10.3989/scimar.2002.66n3321.
- Golani, D. and Appelbaum-Golani, B. (2010). First record of the Indo-Pacific fish the Jarbua terapon (*Terapon jarbua*) (Osteichthyes: Terapontidae) in the Mediterranean with remarks on the wide geographical distribution of this species. *Scientia Marina*, **74**(4):717–720. DOI: 10.3989/scimar.2010.74n4717.
- Golani, D., Fricke, R. and Tikochinski, Y. (2011). Rehabilitation of *Sillago erythraea* Cuvier, and redescription of *Sillago sihama* (Forsskål) (Teleostei: Sillaginidae) from the Red Sea. *Stuttgarter Beiträge zur Naturkunde A, Neue Serie*, **4**:465–171.
- Gotelli, N.J. and Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**(4):379–391. DOI: 10.1046/j.1461-0248.2001.00230.x.
- Gopurenko, D., Hughes, J.M. and Keenan, C.P. (1999). Mitochondrial DNA evidence for rapid colonisation of the Indo-West Pacific by the mudcrab *Scylla serrata*. *Marine Biology*, **134**(2):227–233. DOI: 10.1007/s002270050541.
- Goren, M. and Dor, M. (1994). *An updated checklist of the fishes of the Red Sea. CLOFRES II*.
- Goren, M. and Galil, B.S. (1998). First record of the Indo-Pacific, coral reef fish *Abudefduf vaigiensis* (Quoy & Gaimard, 1825) in the Levant. *Israel Journal of Zoology*, **44**:57–59.
- Gower, J.C. (1966). Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika*, **53**(3-4):325–338. DOI: 10.1093/biomet/53.3-4.325.

- Grant, W.S. and Waples, R.S. (2000). Spatial and temporal scales of genetic variability in marine and anadromous species. Implications for fisheries oceanography. Pages 61–93, in: P.J. Harrison and T.R. Parsons (eds.). *Fisheries oceanography. An integrative approach to fisheries ecology and management*. Blackwell Science, Oxford.
- Gray, J.E. (1851). List of the specimens of fish in the collection of the British Museum. Part I - Chondropterygii. London. 1–160.
- Guindon, S. and Gascuel, O. (2003). A Simple, Fast, and Accurate Algorithm to Estimate Large Phylogenies by Maximum Likelihood. *Systematic Biology*, **52(5)**:696–704.  
DOI: 10.1080/10635150390235520.
- Guo, S.W. and Thompson, E.A. (1992). Performing the exact test of Hardy-Weinberg proportion for multiple alleles. *Biometrics*, **48(2)**:361–372.
- Günter, G. (1945). *Studies of Marine Fishes of Texas*. Publications of the Institute of Marine Science, University of Texas.
- Günter, G. (1967). Some relationships of estuaries to the fisheries of the Gulf of Mexico. – *American Association for the Advancement of Science Publications*, **83**:621–638.
- Harold, A.S., Winterbottom, R., Munday, P.L. and Chapman, R.W. (2008). Phylogenetic relationships of Indo-Pacific coral gobies of the genus *Gobiodon* (Teleostei Gobiidae), based on morphological and molecular data. *Bulletin of Marine Science*, **82(1)**:119–136.
- Harpending, H.C. (1994). Signature of ancient population growth in a low-resolution mitochondrial DNA mismatch distribution. *Human biology*, **66(4)**:591–600.
- Harrison, T.D. (2001). Length–weight relationships of fishes from South African estuaries. *Journal of Applied Ichthyology*, **17(1)**:46–48.
- Harrison, T.D. (2005). Ichthyofauna of South African estuaries in relation to the zoogeography of the region. *Smithiana*, **6**:1–27.
- Harrison, T.D. and Whitfield, A.K. (1995). Fish community structure in three temporarily open/closed estuaries on the Natal coast. *Ichthyological Bulletin Smithsonian Institute of Ichthyology*, **64**:1–80.
- Hartl, D.L. and Borot, N. (1994). *Génétique des populations*. Flammarion Médecine-Sciences, Paris.
- Hastings, A. and Botsford, L.W. (2006). Persistence of spatial populations depends on returning home. *Proceedings of the National Academy of Sciences*, **103(15)**:6067–6072.  
DOI: 10.1073/pnas.0506651103.
- He, L., Zhang, A., Zhu, C., Weese, D. and Qiao, Z. (2011). Phylogeography of the mud crab (*Scylla serrata*) in the Indo-West Pacific reappraised from mitochondrial molecular and

- oceanographic clues: transoceanic dispersal and coastal sequential colonization. *Marine Ecology*, **32(1)**:52–64. DOI: 10.1111/j.1439-0485.2010.00406.x.
- Heemstra, P.C. and Heemstra, E. (2004). *Coastal fishes of Southern Africa*. NISC, Grahamstown.
- Ho, H.-C. and Shao, G. (2011). Annotated checklist and type catalog of fish genera and species described from Taiwan. *Zootaxa*, **2957**:1–74.
- Ho, S.Y.W. (2005). Time Dependency of Molecular Rate Estimates and Systematic Overestimation of Recent Divergence Times. *Molecular Biology and Evolution*, **22(7)**:1561–1568. DOI: 10.1093/molbev/msi145.
- Hoarau, G., Rijnsdorp, a.D., van der Veer, H.W., Stam, W.T. and Olsen, J.L. (2002). Population structure of plaice (*Pleuronectes platessa* L.) in northern Europe: microsatellites revealed large-scale spatial and temporal homogeneity. *Molecular Ecology*, **11(7)**:1165–1176. DOI: 10.1046/j.1365-294X.2002.01515.x.
- Hoareau, T.B., Bosc, P., Valade, P. and Berrebi, P. (2007). Gene flow and genetic structure of *Sicyopterus lagocephalus* in the South-western Indian Ocean, assessed by intron-length polymorphism. *Journal of Experimental Marine Biology and Ecology*, **349(2)**:223–234. DOI: 10.1016/j.jembe.2007.05.015.
- Hollander, M. and Wolfe, D.A. (1999). *Nonparametric statistical methods*. John Wiley & Sons, New York ; Chichester.
- Honda, K., Arai, T., Kobayashi, S., Tsuda, Y. and Miyashita, K. (2012). Migratory patterns of exotic brown trout *Salmo trutta* in south-western Hokkaido, Japan, on the basis of otolith Sr:Ca ratios and acoustic telemetry. *Journal of Fish Biology*, **80(2)**:408–426. DOI: 10.1111/j.1095-8649.2011.03183.x.
- Hureau, J.-C. and Monod, T. (1973). *Check-list of the fishes of the north-eastern Atlantic and of the Mediterranean*. Unesco, Paris.
- Ihaka, R. and Gentleman, R. (1996). R: A Language for Data Analysis and Graphics. *Journal of Computational and Graphical Statistics*, **5(3)**:299-314.
- Ivanova, N.V., Dewaard, J.R. and Hebert, P.D.N. (2006). An inexpensive, automation-friendly protocol for recovering high-quality DNA. *Molecular Ecology Notes*, **6(4)**:998–1002. DOI: 10.1111/j.1471-8286.2006.01428.x.
- Iwatsuki, Y. and Kimura, S. (1998). A new species, *gerres infasciatus*, from the gulf of thailand (perciformes: Gerreidae). *Ichthyological Research*, **45**:79–84. DOI: 10.1007/BF02678577.
- Iwatsuki, Y. and Heemstra, P.C. (2001). *Gerres phaiya*: A new species of gerreid fish (Teleostei Perciformes: Gerreidae) from India, with comments on *Gerres poieti* and the *Gerres erythrourus* complex. *Copeia*, **2001(4)**:1043–1049.

- Iwatsuki, Y. and Heemstra, P.C. (2007). A new Gerreid fish species and redescription of *Gerres maldivensis* Regan, 1902 from the Indian Ocean (Perciformes: Perciformes: Gerreidae). *Copeia*, **2007(1)**:85-92.
- Iwatsuki, Y. and Carpenter, K.E. (2009). *Acanthopagrus randalli* (Perciformes: Sparidae), a new black seabream from the Persian Gulf. *Zootaxa*, **2267**:43–54.
- Iwatsuki, Y. and Heemstra, P.C. (2010). Taxonomic Review of the Western Indian Ocean Species of the Genus *Acanthopagrus* Peters, 1855 (Perciformes: Sparidae), with Description of a New Species from Oman. *Copeia*, **2010(1)**:123–136.
- Iwatsuki, Y., Kimura, S., Kishimoto, H. and Yoshino, T. (1996). Validity of the gerreid fish, *Gerres macracanthus* Bleeker, 1854, with designation of a lectotype, and designation of a neotype for *G. filamentosus* Cuvier, 1829. *Ichthyological Research*, **43(4)**:417-429.
- Iwatsuki, Y., Kimura, S. and Yoshino, T. (1998). Redescription of *Gerres erythrourus* (Bloch, 1791), a senior synonym of *G. abbreviatus* Bleeker, 1850 (Teleostei Perciformes: Gerreidae). *Copeia*, **1998(1)**:165–172.
- Iwatsuki, Y., Kimura, S. and Yoshino, T. (1999a). Redescriptions of *Gerres baconensis* (Evermann & Seale, 1907), *G. equulus* Temminck & Schlegel, 1844 and *G. oyena* (Forsskal, 1775), included in the "*G. oyena* complex", with notes on other related species (Perciformes: Gerreidae). *Ichthyological Research*, **46(4)**:377–395.
- Iwatsuki, Y., Satapoomin, U. and Matsuura, K. (1999b). The Rare Haemulid Fish, *Pomadasys andamanensis* McKay & Satapoomin, 1994, and comparisons with Other Striped Species of *Pomadasys* (Teleostei, Perciformes). *Bulletin of the National Science Museum. Series A, Zoology*, **25(1)**:79–86.
- Iwatsuki, Y., Djawad, M.I., Burhanuddin, A.I., Motomura, H. and Hidaka, K. (2000). A preliminary list of the epipelagic and inshore fishes of Makassar (= Ujung Panang), South Sulawesi, Indonesia, collected mainly from fish markets between 23-27 January 2000, with notes on fishery catch statistics. *Bulletin of the Faculty of Agriculture of Miyazaki University*, **47(1-2)**:95–114.
- Iwatsuki, Y., Kimura, S. and Yoshino, T. (2001a). *Gerres limbatus* Cuvier and *G. lucidus* Cuvier from the Indo-Malay Archipelagos, the latter corresponding to young of the former (Perciformes: Gerreidae). *Ichthyological Research*, **48(3)**:307–314.  
DOI: 10.1007/s10228-001-8151-4.
- Iwatsuki, Y., Kimura, S. and Yoshino, T. (2001b). New species of *Gerres* from the southern Malay Peninsula, belonging to the *Gerres setifer* complex (Perciformes: Gerreidae). *Copeia*, **2001(1)**:164–168.

- Iwatsuki, Y., Kimura, S. and Yoshino, T. (2001c). Redescription of *Gerres longirostris* (Lacepede, 1801) and *Gerres oblongus* Cuvier in Cuvier and Valenciennes, 1830, included in the *Gerres longirostris* complex (Perciformes: Gerreidae). *Copeia*, **2001(4)**:954–965.
- Iwatsuki, Y., Kimura, S. and Yoshino, T. (2002). A new species: *Gerres microphthalmus* (Perciformes: Gerreidae) from Japan with notes on limited distribution, included in the "*G. filamentosus* complex". *Ichthyological Research*, **49(2)**:133–139.  
DOI: 10.1007/s102280200017.
- Iwatsuki, Y., Kume, M. and Yoshino, T. (2010). A new species, *Acanthopagrus pacificus* from the Western Pacific (Pisces, Sparidae). v. 36 (no. 4):. *Bulletin of the National Science Museum. Series A, Zoology*, **36(4)**:115–130.
- James, N.C., Cowley, P.D., Whitfield, A.K. and Lamberth, S.J. (2007). Fish communities in temporarily open/closed estuaries from the warm- and cool-temperate regions of South Africa: A review. *Reviews in Fish Biology and Fisheries*, **17(4)**:565–580.  
DOI: 10.1007/s11160-007-9057-7.
- Johnson, M.S. and Black, R. (2006). Islands increase genetic subdivision and disrupt patterns of connectivity of intertidal snails in a complex archipelago. *Evolution*, **60(12)**:2498.  
DOI: 10.1554/06-211.1.
- Johnson, R.C., Weber, P.K., Wikert, J.D., Workman, M.L., MacFarlane, R.B., Grove, M.J., Schmitt, A.K. and Krkosek, M. (2012). Managed Metapopulations: Do Salmon Hatchery ‘Sources’ Lead to In-River ‘Sinks’ in Conservation? *PLoS ONE*, **7(2)**:e28880.  
DOI: 10.1371/journal.pone.0028880.
- Jones, K.C., Levine, K.F. and Banks, J.D. (2002). Characterization of 11 polymorphic tetranucleotide microsatellites for forensic applications in California elk (*Cervus elaphus canadensis*). *Molecular Ecology Notes*, **2(4)**:425–427.  
DOI: 10.1046/j.1471-8286.2002.00264.x.
- Jordan, D.S. and Evermann, B.W. (1993). Descriptions of new genera and species of fishes from the Hawaiian Islands. *Bulletin of the U. S. Fish Commission*, **22**:161–208.
- Jost, L. (2006). Entropy and diversity. *Oikos*, **113(2)**:363–375.  
DOI: 10.1111/j.2006.0030-1299.14714.x.
- Jurasinski, G. and Koch, M. (2011). Commentary: do we have a consistent terminology for species diversity? We are on the way. *Oecologia*, **167(4)**:893–902.  
DOI: 10.1007/s00442-011-2126-6.
- Karlsson, S. and Mork, J. (2005). Deviation from Hardy–Weinberg equilibrium, and temporal instability in allele frequencies at microsatellite loci in a local population of Atlantic cod. *ICES Journal of Marine Science*, **62(8)**:1588–1596. DOI: 10.1016/j.icesjms.2005.05.009.

- Kennedy, B.P., Folt, C.L., Blum, J.D. and Chamberlain, C.P. (1997). Natural isotope markers in salmon. *Nature*, **387(6635)**:766–767. DOI: 10.1038/42835.
- Kennedy, B.P., Klaue, A., Blum, J.D., Folt, C.L. and Nislow, K.H. (2002). Reconstructing the lives of fish using Sr isotopes in otoliths. *Canadian Journal of Fisheries and Aquatic Sciences*, **59(6)**:925–929. DOI: 10.1139/f02-070.
- Kemp, J.M. (1998). Zoogeography of the coral reef fishes of the Socotra Archipelago. *Journal of Biogeography*, **25(5)**:919–933. DOI: 10.1046/j.1365-2699.1998.00249.x.
- Kemp, J.M. (2000). Zoogeography of the coral reef fishes of the North-Eastern Gulf of Aden, with eight new records of coral reef fishes from Arabia. *Fauna of Arabia*, **18**:293–321.
- Keys, A.B. (1928). The Weight-Length Relation in Fishes. *Proceedings of the National Academy of Sciences*, **14(12)**:922-925.
- Khalaf, M.A. and Disi, A. (1997). *Fishes of the Gulf of Aqaba*. Marine Science Station, Aqaba, Jordan.
- Khalaf, M.A. and Krupp, F. (2003). Two new records of fishes from the Red Sea. *Zoology in the Middle East*, **30**:55–59.
- Khalaf, M. and Zajonz, U. (2007). Fourteen additional fish species recorded from below 150 m depth in the Gulf of Aqaba, including *Liopropoma lunulatum* (Pisces: Serranidae), new record for the Red Sea. *Fauna of Arabia*, **23**:421–433.
- Kimura, S., Satapoomin, U. and Matsuura, K. (2009). *Fishes of Andaman Sea*. National Museum of Nature and Science, Tokyo.
- Kindt, R. and Coe, R. (2005). *Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies*. World Agroforestry Centre (ICRAF), Nairobi, 196 pp.
- Klaus, R. and Turner, J.R. (2004). The marine biotopes of the Socotra Island Group. *Fauna of Arabia*, **20**:45–115.
- Klaus, R., West, F. and Turner, J.R. (2002). The marine biotopes of the Socotra Island Group, in: M. Apel, F. Krupp and K.I. Hariri (eds.). *Conservation and Sustainable Use of Biodiversity of Socotra Archipelago. Marine Habitat, Biodiversity and Fisheries Surveys and Management. Final Report of Phase III (UNOPS YEM/96/G32, C-972248)*. Senckenberg Research Institute, Frankfurt a.M., Germany.
- Klaus, R., Jones, D., Turner, J., Simões, N. and Vousden, D. (2003). Integrated Marine and coastal management: a strategy for the conservation and sustainable use of marine biological resources in the Socotra Archipelago, Yemen. *Journal of Arid Environments*, **54(1)**:71–80. DOI: 10.1006/jare.2001.0889.

- Klausewitz, W. and Nielsen, J.G. (1965). On Forsskål's collection in the Zoological Museum of Copenhagen. *Spolia zoological museum Hauniensis, Copenhagen*, 1-29.
- Kornfield, I.L. and Nevo, E. (1976). Likely pre-Suez occurrence of a Red Sea fish *Aphanius dispar* in the Mediterranean. *Nature*, **264**:289–291. DOI: 10.1038/264289a0.
- Krupp, F. (1983). Fishes of Saudi Arabia. Freshwater fishes of Saudi Arabia and adjacent regions of the Arabian Peninsula. *Fauna of Saudia Arabia*, **5**:568–636.
- Krupp, F. (1988). Freshwater fishes of the Wadi Batha drainage. *Journal of Oman Studies Special Report*, **3**:401–404.
- Krupp, F. and Schneider, W. (1989). The fishes of the Jordan River drainage basin and Azraq Oasis. *Fauna of Saudia Arabia*, **10**:347–416.
- Krupp, F., Almarri, M., Zajonz, U., Carpenter, K., Almatar, S. and Zetzsche, H. (2000). Twelve new records of fishes from the Gulf. *Fauna of Arabia*, **18**:323–335.
- Krupp, F., Zajonz, U. and Naseeb, F. (2006). Box 4.8: Socotra's Freshwater and Estuarine Fishes, in: C. Cheung, K. Van Damme and L. DeVantier (eds.). *Socotra. A natural history of the islands and their people*. Odyssey, Hong Kong.
- Krupp, F., Khalaf, M., Malek, M., Streit, B. and Al-Jumaily, M. (2009). The Middle Eastern Biodiversity Network: Generating and sharing knowledge for ecosystem management and conservation. *ZooKeys*, **31**:3–15. DOI: 10.3897/zookeys.31.371.
- Kruskal, W.H. and Wallis, W.A. (1952). Use of ranks in one-criterion variance analysis. *Journal of the American Statistical Association*, **47(260)**:583–621.
- Kuang, Y.D., editor (1986). *The freshwater and estuarine fishes of Hainan Island*.
- Kulbiki, M., Guillemot, N. and Amand, M. (2005). A general approach to length-weight relationships for New Caledonian lagoon fishes. *Cybium*, **29(3)**:235-252.
- Kyushin, K., Amaoka, K. and Nakaya, K. (1977). *Fishes of Indian Ocean*. Japan Marine Fishery Resource Center, Tokyo.
- Kyushin, K., Amaoka, K., Nakaya, K., Ida, H., Tanino, Y. and Senta, T. (1982). *Fishes of the south China Sea*, Tokyo.
- Labonne, M., Morize, E., Scolan, P., Lae, R., Dabas, E. and Bohn, M. (2009). Impact of salinity on early life history traits of three estuarine fish species in Senegal. *Estuarine, Coastal and Shelf Science*, **82(4)**:673–681. DOI: 10.1016/j.ecss.2009.03.005.
- Lacépède, B.G.E. (1800). *Histoire naturelle des poissons*.
- Lacépède, B.G.E. (1801). *Histoire naturelle des poissons*.
- Lacépède, B.G.E. (1802). *Histoire naturelle des poissons*.
- Lacépède, B.G.E. (1803). *Histoire naturelle des poissons*.

- Lakra, W.S., Verma, M.S., Goswami, M., Lal, K.K., Mohindra, V., Punia, P., Gopalakrishnan, A., Singh, K.V., Ward, R.D. and Hebert, P.D.N. (2011). DNA barcoding Indian marine fishes. *Molecular Ecology Resources*, **11(1)**:60–71. DOI: 10.1111/j.1755-0998.2010.02894.x.
- Lamarck, J.B. and Monet, P.A. de (1822). *Histoire naturelle des animaux sans vertèbres*. Verdière, Paris.
- Laroche, J., Baran, E. and Rasoanandrasana, N.B. (1997). Temporal patterns in a fish assemblage of a semiarid mangrove zone in Madagascar. *Journal of Fish Biology*, **51(1)**:3-20. DOI: 10.1111/j.1095-8649.1997.tb02509.x.
- Larsen, L.A., Jespersgaard, C. and Andersen, P.S. (2007). Single-strand conformation polymorphism analysis using capillary array electrophoresis for large-scale mutation detection. *Nature Protocols*, **2(6)**:1458–1466. DOI: 10.1038/nprot.2007.200.
- Larson, R.J. and Julian, R.M. (1999). Spatial and temporal genetic patchiness in marine populations and their implications for fisheries management. *CalCOFI Rep*, **40**:94–99.
- Laurel, B.J. and Bradbury, I.R. (2006). “Big” concerns with high latitude marine protected areas (MPAs): trends in connectivity and MPA size. *Canadian Journal of Fisheries and Aquatic Sciences*, **63(12)**:2603–2607. DOI: 10.1139/f06-151.
- Lavergne, E., Calves, I., Zajonz, U. and Laroche, J. (2011). Isolation and characterization of nine microsatellite loci of *Terapon jarbua* (Forsskål, 1775) from Socotra Island (Gulf of Aden) using multiplex PCR. Electronic supplement to Agostini et al. Permanent Genetic Resources added to Molecular Ecology Resources Database 1 October 2010-30 November 2010. *Molecular Ecology Resources*, **11(2)**:418–421. DOI: 10.1111/j.1755-0998.2010.02970.x.
- Lavergne, E., Krupp, F., Saeed, F.N., Pulch, H., Ziegler, M., Klaus, R., Alpermann, T. and Zajonz, U. (2011). BiK-F Field Research Station Socotra. *Tayf - The Socotra newsletter, Issued by Friends of Soqotra and Socotra Conservation Fund*, **8**:17.
- Legendre, P. (2005). Species associations: the Kendall coefficient of concordance revisited. *Journal of Agricultural, Biological, and Environmental Statistics*, **10(2)**:226–245. DOI: 10.1198/108571105X46642.
- Legendre, P. and Legendre, L. (1998). *Numerical ecology*. Elsevier, Amsterdam, New York.
- Legendre, P. and Gallagher, E. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129(2)**:271–280. DOI: 10.1007/s004420100716.
- Leroy, S., Gente, P., Fournier, M., d'Acremont, E., Patriat, P., Beslier, M.-O., Bellahsen, N., Maia, M., Blais, A., Perrot, J., Al-Kathiri, A., Merkouriev, S., Fleury, J.-M., Ruellan, P.-Y., Lepvrier, C. and Huchon, P. (2004). From rifting to spreading in the eastern Gulf of Aden: a geophysical survey of a young oceanic basin from margin to margin. *Terra Nova*, **16(4)**:185–192. DOI: 10.1111/j.1365-3121.2004.00550.x.

- Letourneur, Y., Kulbiki, M. and Labrosse, P. (1998). Length-weight relationships of fish from coral reefs and lagoons of New Caledonia, southwestern Pacific Ocean: an update. *Naga ICLARM Q*, **21(4)**:39-46.
- Librado, P. and Rozas, J. (2009). DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, **25(11)**:1451–1452.  
DOI: 10.1093/bioinformatics/btp187.
- Liew, M., Pryor, R., Palais, R., Meadows, C., Erali, M., Lyon, E. and Wittwer, C. (2004). Genotyping of Single-Nucleotide Polymorphisms by High-Resolution Melting of Small Amplicons. *Clinical Chemistry*, **50(7)**:1156–1164. DOI: 10.1373/clinchem.2004.032136.
- Linnæus, C. (1758). *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata, 824 pp. Holmiæ. (Salvius).*
- Liu, C., Whittaker, R.J., Ma, K. and Malcolm, J.R. (2007). Unifying and distinguishing diversity ordering methods for comparing communities. *Population Ecology*, **49(2)**:89–100.  
DOI: 10.1007/s10144-006-0026-0.
- Liu, J.-X., Tataronkov, A., Beacham, T.D., Gorbachev, V., Wildes, S. and Avise, J.C. (2011). Effects of Pleistocene climatic fluctuations on the phylogeographic and demographic histories of Pacific herring (*Clupea pallasii*). *Molecular Ecology*, **20(18)**:3879–3893.  
DOI: 10.1111/j.1365-294X.2011.05213.x.
- Ludwig, J.A. and Reynolds, J.F. (1988). *Statistical ecology*. Wiley, New York.
- Malewski, T., Draber-Mońko, A., Pomorski, J., Łoś, M. and Bogdanowicz, W. (2010). Identification of forensically important blowfly species (Diptera: Calliphoridae) by high-resolution melting PCR analysis. *International Journal of Legal Medicine*, **124(4)**:277–285.  
DOI: 10.1007/s00414-009-0396-x.
- Manilo, L.G. and Bogorodsky, S.V. (2003). Taxonomic composition, diversity and distribution of coastal fishes of the Arabian Sea. *Journal of Ichthyology*, **43**:75–149.
- Mantel, N. (1967). The Detection of Disease Clustering and a Generalized Regression Approach. *Cancer Research*, **27(2 Part 1)**:209–220.
- Marshall, D.C., Hill, K.B.R., Cooley, J.R. and Simon, C. (2011). Hybridization, Mitochondrial DNA Phylogeography, and Prediction of the Early Stages of Reproductive Isolation: Lessons from New Zealand Cicadas (Genus *Kikihia*). *Systematic Biology*, **60(4)**:482–502.  
DOI: 10.1093/sysbio/syr017.
- Masuda, H., Amaoka, K., Araga, C., Uyeno, T. and Yoshino, T. (1984). *The Fishes of the Japanese Archipelago*. Tokai Daigaku Shuppankai, Tokyo.

- McClelland, J. (1844). Apodal fishes of Bengal. *Calcutta Journal of Natural History*, **5(18)**:151–226.
- McCulloch, M., Cappo, M., Aumend, J. and Müller, W. (2005). Tracing the life history of individual barramundi using laser ablation MC-ICP-MS Sr-isotopic and Sr/Ba ratios in otoliths. *Marine and Freshwater Research*, **56(5)**:637. DOI: 10.1071/MF04184.
- McKay, R.J. and McCarthy, L.J. (1989). A revision of the sillaginid fishes of the Arabian Gulf with a description of *Sillago arabica* new species. *Memoirs of the Queensland Museum*, **27(2)**:551–553.
- Meistertzheim, A.L., Calves, I., Artigaud, S., Friedman, C.S., Paillard, C., Laroche, J. and Ferec, C. (2012) High Resolution Melting Analysis for fast and cheap polymorphism screening of marine populations. *Nature Reviews Genetics*, DOI:10.1038/protex.2012.015.
- Mercier, L., Mouillot, D., Bruguier, O., Vigliola, L. and Darnaude, A.M. (2012). Multi-element otolith fingerprints unravel sea–lagoon lifetime migrations of gilthead sea bream *Sparus aurata*. *Marine Ecology Progress Series*, **444**:175–194. DOI: 10.3354/meps09444.
- Metzker, M.L. (2009). Sequencing technologies – the next generation. *Nature Reviews Genetics*, **11(1)**:31–46. DOI: 10.1038/nrg2626.
- Miller, A.G. and Morris, M. (2004). *Ethnoflora of the Soqatra Archipelago*. Royal Botanic Garden Edinburgh, Edinburgh.
- Miller, J.A. and Shanks, A.L. (2004). Evidence for limited larval dispersal in black rockfish (*Sebastes melanops*): implications for population structure and marine-reserve design. *Canadian Journal of Fisheries and Aquatic Sciences*, **61(9)**:1723–1735. DOI: 10.1139/F04-111.
- Milton, D.A. and Chenery, S.R. (2005). Movement patterns of barramundi *Lates calcarifer*, inferred from  $^{87}\text{Sr}/^{86}\text{Sr}$  and Sr/Ca ratios in otoliths, indicate non-participation in spawning. *Marine Ecology Progress Series*, **301**:279-291.
- Miu, T.-C., Lee, S.-C. and Tzeng, W.-N. (1990). Reproductive biology of *Terapon jarbua* from the estuary of Tamshui River. *Journal of the Fisheries Society of Taiwan*, **17(1)**:9–20.
- Mora, C. and Sale, P.F. (2002). Are populations of coral reef fish open or closed? *Trends in Ecology & Evolution*, **17(9)**:422–428. DOI: 10.1016/S0169-5347(02)02584-3.
- Moran, M. (2003). Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos*, **100(2)**:403-405. DOI: 10.1034/j.1600-0706.2003.12010.x.
- Moreno, C.E. and Rodríguez, P. (2011). Commentary: Do we have a consistent terminology for species diversity? Back to basics and toward a unifying framework. *Oecologia*, **167(4)**:889–892. DOI: 10.1007/s00442-011-2125-7.

- Morgan, D.L., Allen, G.R., Pusey, B.J. and Burrows, D.W. (2011). A review of the freshwater fishes of the Kimberley region of Western Australia. *Zootaxa*, **2816**:1–64.
- Motomura, H., Kimura, S. and Haraguchi, Y. (2007). Two Carangid Fishes (Actinopterygii: Perciformes), *Caranx heberi* and *Ulua mentalis*, from Kagoshima: the First Records from Japan and Northernmost Records for the Species. *Species Diversity*, **12**:223–235.
- Muchlisin, Z.A., Musman, M. and Siti Azizah, M.N. (2010). Length-weight relationships and condition factors of two threatened fishes, *Rasbora tawarensis* and *Poropuntius tawarensis*, endemic to Lake Laut Tawar, Aceh Province, Indonesia. *Journal of Applied Ichthyology*, **26(6)**:949–953. DOI: 10.1111/j.1439-0426.2010.01524.x.
- Nelson, G. and Rothman, M.N. (1973). The species of gizzard shads (Dorosomatinae) with particular reference to the Indo-Pacific Region. *Bulletin of the American Museum of Natural History*, **150**:131–206.
- Nelson, G. and McCarthy, L. (1995). Two new species of gizzard shads of the genus *Nematalosa* (Teleostei, Clupeidae, Dorosomatinae) from the Persian/Arabian Gulf. *Japanese Journal of Ichthyology*, **41(4)**:379–383.
- Neubert, E. (2005). The continental malacofauna of Arabia and adjacent areas, IV. Revision of the family Cerastidae in the Soqotran Archipelago, I: The genus *Passamaella* L. Pfeiffer 1877, with description of a new genus and species (Gastropoda: Pulmonata: Cerastidae). *Archiv für Molluskenkunde: International Journal of Malacology*, **134(1)**:1–21.  
DOI: 10.1127/arch.moll/0003-9284/134/001-021.
- Neubert, E. (2006). Land snails of the Socotra Archipelago. Pages 125–127, in: C. Cheung, K. Van Damme and L. DeVantier (eds.). *Socotra. A natural history of the islands and their people*. Odyssey, Hong Kong.
- Neubert, E. (2009). The continental malacofauna of Arabia and adjacent areas: VI. Pomatiidae of Arabia, Socotra and Northeast Africa, with descriptions of new genera and species (Gastropoda: Caenogastropoda: Littorinoidea). *Fauna of Arabia*, **24**:47–127.
- Nicolas, D., Lobry, J., Lepage, M., Sautour, B., Le Pape, O., Cabral, H., Uriarte, A. and Boët, P. (2010). Fish under influence: A macroecological analysis of relations between fish species richness and environmental gradients among European tidal estuaries. *Estuarine, Coastal and Shelf Science*, **86(1)**:137–147. DOI: 10.1016/j.ecss.2009.11.006.
- Nielsen, J.G. (1974). Fish types in the Zoological Museum of Copenhagen. *Zoological Museum, University of Copenhagen, Denmark*, 115.
- Nielsen, E.E., Nielsen, P.H., Meldrup, D. and Hansen, M.M. (2004). Genetic population structure of turbot (*Scophthalmus maximus* L.) supports the presence of multiple hybrid zones

- for marine fishes in the transition zone between the Baltic Sea and the North Sea. *Molecular Ecology*, **13(3)**:585–595. DOI: 10.1046/j.1365-294X.2004.02097.x.
- O'Connell, M. and Wright, J.M. (1997). Microsatellite DNA in fishes. *Reviews in Fish Biology and Fisheries*, **7(3)**:331–363. DOI: 10.1023/A:1018443912945.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L. and Stevens, M.H.H. (2008). *vegan: community ecology package* v.1.11-0. R package. Available from: <http://cran.r-project.org/package=vegan>.
- Olsen, E.M., Knutsen, H., Gjøsæter, J., Jorde, P.E., Knutsen, J.A. and Stenseth, N.C. (2008). Small-scale biocomplexity in coastal Atlantic cod supporting a Darwinian perspective on fisheries management. *Evolutionary Applications*, **1(3)**:524–533. DOI: 10.1111/j.1752-4571.2008.00024.x.
- Pan, J.H., Zhong, L., Zheng, C.Y., Wu, H.L. and Liu, J.H., editors (1991). *The freshwater fishes of Guangdong Province*. Guangdong Science and Technology Press, Guangzhou.
- Panfili, J. and Tomas, J. (2001). Validation of age estimation and back-calculation of fish length based on otolith microstructures in tilapias (Pisces, Cichlidae). *Fishery Bulletin*, **99(1)**:139–150.
- Panfili, J., Pontual, H. de, Troadec, H. and Wright, P.J., editors (2002). *Manual of fish sclerochronology*. IFREMER, Plouzané, France.
- Parin, N.V., Collette, B.B. and Shcherbachev, Y.N. (1980). Preliminary review of the marine halfbeaks (Hemiramphidae, Beloniformes) of the tropical Indo-West-Pacific. *Transactions of the P. P. Shirshov Institute of Oceanology*, **97**:7–173.
- Pastore, M.A. (2009). *Sphyraena intermedia* sp. nov. (Pisces: Sphyraenidae): a potential new species of barracuda identified from the central Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, **89(6)**:1299-1303. DOI: 10.1017/S0025315409000575.
- Patterson, H.M., Thorrold, S.R. and Shenker, J.M. (1999). Analysis of otolith chemistry in Nassau grouper (*Epinephelus striatus*) from the Bahamas and Belize using solution-based ICP-MS. *Coral Reefs*, **18(2)**:171–178. DOI: 10.1007/s003380050176.
- Pauly, D. (1984). *Fish population dynamics in tropical waters*. International Center for Living Aquatic Resources Management, Manila, Philippines.
- Pauly, D., Cabanban, A. and Torres, F.S.B., JR (1996). Fishery biology of 40 trawl-caught teleosts of western Indonesia. Pages 135-216, in: D. Pauly and P. Martosubroto (eds.). *Baseline studies of biodiversity: the fish resource of western Indonesia*. ICLARM.

- Paxton, J.R., Hoese, D.F., Allen, G.R. and Hanley, J.E. (1989). Zoological Catalogue of Australia. Volume 7. Pisces. Petromyzontidae to Carangidae. Australian Government Publishing Service, Canberra. 1-665.
- Pearce, N.J., Perkins, W.T., Westgate, J.A., Gorton, M.P., Jackson, S.E., Neal, C.R. and Chenery, S.P. (1997). A Compilation of New and Published Major and Trace Element Data for NIST SRM 610 and NIST SRM 612 Glass Reference Materials. *Geostandards and Geoanalytical Research*, **21(1)**:115–144. DOI: 10.1111/j.1751-908X.1997.tb00538.x.
- Pearse, A.S. and Günter, G. (1957). Salinity. Pages 129–157, in: J.W. Hedgpeth (ed.). *Ecology – Treatise on marine ecology and paleoecology, Vol. 1*. Geological Society of America, New York.
- Peters, W.C.H. (1869). Über neue oder weniger bekannte Fische des Berliner Zoologischen Museums. *Monatsberichte der Akademie der Wissenschaft zu Berlin*, pp703-711.
- Pielou, E. (1966). The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology*, **13**:131–144. DOI: 10.1016/0022-5193(66)90013-0.
- Pillans, B., Chappell, J. and Naish, T.R. (1998). A review of the Milankovitch climatic beat: template for Plio–Pleistocene sea-level changes and sequence stratigraphy. *Sedimentary Geology*, **122(1-4)**:5–21. DOI: 10.1016/S0037-0738(98)00095-5.
- Planes, S. and Lenfant, P. (2002). Temporal change in the genetic structure between and within cohorts of a marine fish, *Diplodus sargus*, induced by a large variance in individual reproductive success. *Molecular Ecology*, **11(8)**:1515–1524. DOI: 10.1046/j.1365-294X.2002.01521.x.
- Platnick, N.I. (2011). *The World Spider Catalog* v.12.0. American Museum of Natural History. Available from: <http://research.amnh.org/iz/spiders/catalog>.
- Posada, D. (2008). jModelTest: Phylogenetic Model Averaging. *Molecular Biology and Evolution*, **25(7)**:1253–1256. DOI: 10.1093/molbev/msn083.
- Pulch, H.W., Zajonz, U, Pfenninger, M. (*in prep.*). Population structure, past demography and intrageneric relationships of the endemic dottyback fish *Pseudochromis socotraensis* (Perciformes: Pseudochromidae) from Socotra Archipelago, inferred from cytochrome *c* oxidase subunit I sequences.
- Qing-chao, C., editor (1997). *Fishes from Nansha Islands to South China coastal waters*. Science Press, Beijing, China.
- Quoy, J.R.C. and Gaimard, J.P. (1825). *Description des Poissons. Chapter IX. In: de Freycinet, L. - Voyage autour du Monde...Paris*.
- Rafinesque, C.S. (1810). *Caratteri di alcuni nuovi generi e nuove specie di animali e piante della Sicilia, con varie osservazioni sopra i medisimi*.

- Rambaut, A. (2009). *FigTree* v.1.3.1. Available from: <http://beast.bio.ed.ac.uk/FigTree>.
- Rambaut, A. and Drummond, A.J. (2007). *Tracer* v.1.4. Available from: <http://beast.bio.ed.ac.uk/Tracer>.
- Randall, J.E. (2005). *Reef and shore fishes of the South Pacific*. University of Hawai'i Press, Honolulu.
- Randall, J.E. (2007). *Reef and shore fishes of the Hawaiian Islands*. Sea Grant College Program, University of Hawai'i, Honolulu.
- Randall, J.E. and Hoover, J.P. (1995). *Coastal fishes of Oman*. University of Hawai'i Press, Honolulu.
- Randall, J.E. and Lim, K.K. (2000). A checklist of the fishes of the South China Sea. *Raffles Bulletin of Zoology*, **Supp. 8**:569–667.
- Randall, J.E., Allen, G.R. and Steene, R.C. (1997). *Fishes of the Great Barrier Reef and Coral Sea*. University of Hawaii Press, Honolulu.
- Randall, J.E., Williams, J.T., Smith, D.G., Kulbicki, M., Mou Tham, G., Labrosse, P., Kronen, M., Clua, E. and Mann, B.S. (2003). Checklist of the shore and epipelagic fisheries of Tonga. *Atoll Research Bulletin*, **502**:1–35.
- Raventos, N. and Macpherson, E. (2001). Planktonic larval duration and settlement marks on the otoliths of Mediterranean littoral fishes. *Marine Biology*, **138(6)**:1115–1120.  
DOI: 10.1007/s002270000535.
- Raymond, M. and Rousset, F. (1995). Genepop v.1.2 - Population Genetics Software for Exact Tests and Ecumenicism. *Journal of Heredity*, **86(3)**:248–249.
- Regan, C.T. (1905). On fishes from the Persian Gulf, the Sea of Oman, and Karachi, collected by Mr. F. W. Townsend. *Journal of the Bombay Natural History Society*, **16**:318–333.
- Regan, C.T. (1917). A revision of the clupeoid fishes of the genera *Pomolobus*, *Brevoortia* and *Dorosoma* and their allies. *Annals and Magazine of Natural History (Series 8)*, **19(112)**:297–316.
- Rice, W.R. (1989). Analyzing Tables of Statistical Tests. *Evolution*, **43(1)**:223–225.
- Richardson, J. (1845). Ichthyology - Part 2., in: Hinds R. B. (ed.). *The zoology of the voyage of H. M. S. Sulphur, under the command of Captain Sir Edward Belcher during the years 1836-42, No. 9. London: Smith, Elder & Co.*
- Riede, K. (2004). *Global Register of Migratory Species – from Global to Regional Scales. Final Report of the R&D Project 808-05-081*. Federal Agency for Nature Conservation, Bonn, Germany.
- Roberts, T.R. (1978). An ichthyological survey of the Fly River in Papua New Guinea with descriptions of new species. *Smithsonian Contributions to Zoology*, **281**:1–72.

- Robinet, T., Réveillac, E., Kuroki, M., Aoyama, J., Tsukamoto, K., Rabenevanana, M.W., Valade, P., Gagnaire, P.-A., Berrebi, P. and Feunteun, E. (2008). New clues for freshwater eels (*Anguilla* spp.) migration routes to eastern Madagascar and surrounding islands. *Marine Biology*, **154**(3):453–463. DOI: 10.1007/s00227-008-0938-7.
- Rogers, A.R. and Harpending, H. (1992). Population growth makes waves in the distribution of pairwise genetic differences. *Molecular biology and evolution*, **9**(3):552–569.
- Roman, J. and Palumbi, S.R. (2004). A global invader at home: population structure of the green crab, *Carcinus maenas*, in Europe. *Molecular ecology*, **13**(10):2891–2898. DOI: 10.1111/j.1365-294X.2004.02255.x.
- Rousset, F. (2008). genepop'007: a complete re-implementation of the genepop software for Windows and Linux. *Molecular Ecology Resources*, **8**(1):103–106. DOI: 10.1111/j.1471-8286.2007.01931.x.
- Rüppell, W.P.E.S. (1829). *Atlas zu der Reise im nördlichen Afrika. Fische des Rothen Meers. Frankfurt am Main (Heinrich Ludwig Brönnner)*, 141 pp.
- Rüppell, W.P.E.S. (1838). *Neue Wirbelthiere zu der Fauna von Abyssinien gehörig. Fische des Rothen Meeres. Frankfurt-am-Main.*
- Rüppell, W.P.E.S. (1852). *Verzeichniss der in dem Museum der Senckenbergischen naturforschenden Gesellschaft aufgestellten Sammlungen. Vierte Abtheilung. Fische und deren Skelette. pp 1-40, Frankfurt a.M., Germany.*
- Sale, P.F. (2004). Connectivity, Recruitment Variation, and the Structure of Reef Fish Communities. *Integrative and Comparative Biology*, **44**(5):390–399. DOI: 10.1093/icb/44.5.390.
- Sato, T. (1978). A synopsis of the sparoid fish genus *Lethrinus*, with the description of a new species. *Bulletin of the University Museum*, **15**:1–70.
- Schmitt, T. and Hewitt, G.M. (2004). The genetic pattern of population threat and loss: a case study of butterflies. *Molecular Ecology*, **13**(1):21–31. DOI: 10.1046/j.1365-294X.2004.02020.x.
- Scholte, P. and De Geest, P. (2010). The climate of Socotra Island (Yemen): A first-time assessment of the timing of the monsoon wind reversal and its influence on precipitation and vegetation patterns. *Journal of Arid Environments*, **74**(11):1507–1515. DOI: 10.1016/j.jaridenv.2010.05.017.
- Scholte, P., Al-Okaishi, A. and Suleyman, A.S. (2011). When conservation precedes development: a case study of the opening up of the Socotra archipelago, Yemen. *Oryx*, **45**(03):401–410. DOI: 10.1017/S0030605310001535.

- Scribner, K.T., Page, K.S. and Bartron, M.L. (2000). Hybridization in freshwater fishes: a review of case studies and cytonuclear methods of biological inference. *Reviews in Fish Biology and Fisheries*, **10(3)**:293–323. DOI: 10.1023/A:1016642723238.
- Secor, H. and Rooker, J.R. (2005). Connectivity in the life histories of fishes that use estuaries. *Estuarine, Coastal and Shelf Science*, **64(1)**:1–3. DOI: 10.1016/j.ecss.2005.02.001.
- Sedov, A.V., Naumkin, V.V., Vinogradov, Y.A., Zhukov, V.A., Vinogradova, E.M., Kurkina, E.A. and Sarabjev, A.V. (2009). Preliminary report of the Russian Interdisciplinary Mission to the Republic of Yemen submitted to the general organization of antiquities and museums (G.O.A.M.). – Moscow, 19 pp.
- Seegers, L., Vos, L. de and Okeyo, D.O. (2003). Annotated Checklist of the Freshwater Fishes of Kenya (excluding the lacustrine haplochromines from Lake Victoria). *Journal of East African Natural History*, **92(1)**:11–47. DOI: 10.2982/0012-8317(2003)92[11:ACOTFF]2.0.CO;2.
- Shadbolt, A.B. and Ragai, R. (2010). Effects of habitat fragmentation on the movement patterns and dispersal ability of the brown spiny rat (*Maxomys rajah*) in the Planted Forest Zone of Sarawak, Eastern Malaysia. *Biodiversity and Conservation*, **19(2)**:531–541. DOI: 10.1007/s10531-009-9729-9.
- Shannon, C.E. and Weaver, W. (1949). *The mathematical theory of communication*. University of Illinois Press, Urbana.
- Shapiro, S.S. and Wilk, M.B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, **52**:591.
- Simões, N. and Jones, D. (2000). Intertidal and coastal lagoons ecology survey. Socotra Report of Phase II.
- Simões, N., Apel, M. and Jones, D.A. (2001). Intertidal habitats and decapod faunal assemblages (Crustacea: Decapoda) of Socotra Island, Republic of Yemen. *Hydrobiologia*, **449(1)**:81–97. DOI: 10.1023/A:1017541019388.
- Sinclair, M. (1988). *Marine populations*. Washington Sea Grant Program, Seattle Wash.
- Slatkin, M. (1995). A measure of population subdivision based on microsatellite allele frequencies. *Genetics*, **139(1)**:457–462.
- Smith, M.M. and Heemstra, P.C. (1986). *Smiths' sea fishes*. Springer-Verlag, Berlin, New York.
- Smith, J.L.B., Smith, M.M. and Heemstra, P.C. (2003). *Smiths' Sea fishes*. Struik, Cape Town.
- Smith-Vaniz, W.F. and Staiger, J.C. (1973). *Comparative revision of Scomberoides, Oligoplites, Parona and Hypacanthus*, San Francisco.
- Sponaugle, S. (2010). Otolith microstructure reveals ecological and oceanographic processes important to ecosystem-based management. *Environmental Biology of Fishes*, **89(3-4)**:221–238. DOI: 10.1007/s10641-010-9676-z.

- Steindachner, F. (1902). Wissenschaftliche Ergebnisse der südarabischen Expedition in den Jahren 1898 bis 1899. Fische von Südarabien und Socotra. [Species date to this abstract, main work published in 1903]. *Anzeiger der Akademie der Wissenschaften Wien*, **39(24)**:316–318.
- Steindachner, F. (1903). Fische aus Südarabien und Sokotra. [Dated as Nov. 1902, published in 1903. Species date to abstract. Separate pages 1-46.]. *Denkschriften der Akademie der Wissenschaften Wien*, **71**:123–168.
- Storey, J.D. (2002). A direct approach to false discovery rates. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, **64(3)**:479–498.  
DOI: 10.1111/1467-9868.00346.
- Storey, J.D. (2003). The positive false discovery rate: a Bayesian interpretation and the q -value. *The Annals of Statistics*, **31(6)**:2013–2035. DOI: 10.1214/aos/1074290335.
- Storey, J.D. and Tibshirani, R. (2003). Statistical significance for genomewide studies. *Proceedings of the National Academy of Sciences*, **100(16)**:9440–9445.  
DOI: 10.1073/pnas.1530509100.
- Storey, J.D., Taylor, J.E. and Siegmund, D. (2004). Strong control, conservative point estimation and simultaneous conservative consistency of false discovery rates: a unified approach. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, **66(1)**:187–205.  
DOI: 10.1111/j.1467-9868.2004.00439.x.
- Sylva, D.P. de (1975). Barracudas (Pisces: Sphyraenidae) of the Indian Ocean and adjacent seas. a preliminary review of their systematics and ecology. *Journal of the Marine Biological Association of India*, **15(1)**:74–94.
- Taiti, S. and Checcucci, I. (2009). New species and records of terrestrial Isopoda (Crustacea, Oniscidea) from Socotra Island, Yemen. *ZooKeys*, **31(0)**. DOI: 10.3897/zookeys.31.140.
- Tajima, F. (1989). Statistical Method for Testing the Neutral Mutation Hypothesis by DNA Polymorphism. *Genetics*, **123(3)**:585–595.
- Tamura, K. and Nei, M. (1993). Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution*, **10(3)**:512–526.
- Taschenberg, O. (1883). Beiträge zur Fauna der Insel Sokotra, vorzüglich nach dem von Herrn Dr. Emil Riebeck aus Halle a.S. gesammelten Materiale zusammengestellt. *Zeitschrift für Naturwissenschaften*, **56**:157–185.
- Templeton, A.R., Crandall, K.A. and Sing, C.F. (1992). A Cladistic Analysis of Phenotypic Associations With Haplotypes Inferred From Restriction Endonuclease Mapping and DNA Sequence Data. III. Cladogram Estimation. *Genetics*, **132(2)**:619–633.

- Teng, H.-Y., Lin, Y.-S. and Tzeng, C.-S. (2009). A New *Anguilla* Species and a Reanalysis of the Phylogeny of Freshwater Eels. *Zoological Studies*, **48(6)**:808–822.
- Thieme, M.L. (2005). *Freshwater ecoregions of Africa and Madagascar*. Island Press, Washington.
- Thresher, R. (1999). Elemental composition of otoliths as a stock delineator in fishes. *Fisheries Research*, **43(1-3)**:165–204. DOI: 10.1016/S0165-7836(99)00072-7.
- Thunberg, C.P. (1787). *Museum naturalium Academiae Upsaliensis*.
- Turner, J.R., Klaus, R., Simões, N. and Jones, D. (1999). Littoral and sublittoral ground-truthing survey of the Socotra Archipelago. Socotra Report of phase I.
- UNEP/WCMC (2008). Socotra Archipelago, Yemen. UNESCO Fact Sheet. World Heritage Sites – Protected Areas and World Heritage. United Nations Environment Programme & World Conservation Monitoring Centre. Available from: [www.unep-wcmc.org/medialibrary/2011/06/29/f525b1b2/Socotra%20Archipelago.pdf](http://www.unep-wcmc.org/medialibrary/2011/06/29/f525b1b2/Socotra%20Archipelago.pdf).
- Van Damme, K. (2009). Socotra Archipelago. Pages 846–851, in: R.G. Gillespie and D.A. Clague (eds.). *Encyclopedia of islands*. University of California Press, Berkeley.
- Van Damme, K. and Banfield, L. (2011). Past and present human impacts on the biodiversity of Socotra Island (Yemen): implications for future conservation. *Zoology in the Middle East, Supplementum 3*:31–88.
- Van der Elst, R. (1993). *A guide to the common sea fishes of Southern Africa*. Struik Publishers, Cape Town.
- Van Oosterhout, C., Hutchinson, W.F., Wills, D.P.M. and Shipley, P. (2004). Micro-Checker: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, **4(3)**:535–538. DOI: 10.1111/j.1471-8286.2004.00684.x.
- Vari, R.P. (1978). The terapon perches (Percoidei, Teraponidae): a cladistic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History*, **159(5)**:175–340.
- Venables, W.N. and Ripley, B.D. (2002). *Modern applied statistics with S*. Springer, New York.
- Victor, B.C. (1986). Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). *Marine Biology*, **90(3)**:317–326.  
DOI: 10.1007/BF00428555.
- Visram, S., Yang, M.-C., Pillay, R.M., Said, S., Henriksson, O., Grahn, M. and Chen, C.A. (2010). Genetic connectivity and historical demography of the blue barred parrotfish (*Scarus ghobban*) in the western Indian Ocean. *Marine Biology*, **157(7)**:1475–1487.  
DOI: 10.1007/s00227-010-1422-8.

- Vogler, C., Benzie, J., Lessios, H., Barber, P.A. and Worheide, G. (2008). A threat to coral reefs multiplied? Four species of crown-of-thorns starfish. *Biology Letters*, **4(6)**:696–699.  
DOI: 10.1098/rsbl.2008.0454.
- Voris, H.K. (2000). Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography*, **27(5)**:1153–1167.  
DOI: 10.1046/j.1365-2699.2000.00489.x.
- Waldman, B. and McKinnon, J.S. (1993). Inbreeding and outbreeding in fishes, amphibians and reptiles. Pages 250–282, in: N.W. Thornhill (ed.). *The Natural history of inbreeding and outbreeding. Theoretical and empirical perspectives*. University of Chicago Press, Chicago.
- Wallace, J.H. and Van der Elst, R. (1975). The estuarine fishes of the East Coast of South Africa. IV. Occurrence of Juveniles in Estuaries. V. Ecology, Estuarine Dependence and Status. *Investigational Report of the Oceanographic Research Institute*, **42**:1–63.
- Wallace, J.H., Koh, H.M., Beckley, L.E., Bennett, B., Blaber, S.J.M. and Whitfield, A.K. (1984). South African estuaries and their importance to fishes. *South African Journal of Science*, **80**:203–207.
- Ward, R.D., Ward, R.D., Zemplak, T.S., Innes, B.H., Last, P.R. and Hebert, P.D.N. (2005). DNA barcoding Australia's fish species. *Philosophical transactions*, **360(1462)**:1847–1857.  
DOI: 10.1098/rstb.2005.1716.
- Weatherley, A.H. and Gill, H.S. (1987). *The biology of fish growth*. Acad. Pr., London [u.a.].
- Weir, B.S. and Cockerham, C.C. (1984). Estimating F-Statistics for the Analysis of Population Structure. *Evolution*, **38(6)**:1358. DOI: 10.2307/2408641.
- Whitfield, A.K. (2010). A century of fish research in South African estuaries. *African Journal of Aquatic Science*, **35(3)**:211–225. DOI: 10.2989/16085914.2010.538510.
- Whitfield, A.K. and Blaber, S.J.M. (1978). Scale-eating habits of the marine teleost *Terapon jarbua* (Forsskål, 1775). *Journal of Fish Biology*, **12(1)**:61–70.  
DOI: 10.1111/j.1095-8649.1978.tb04151.x.
- Whitfield, A.K. and Cowley, P.D. (2010). The status of fish conservation in South African estuaries. *Journal of Fish Biology*, **76(9)**:2067–2089.  
DOI: 10.1111/j.1095-8649.2010.02641.x.
- Whitehead, P.J., Nelson, G.J. and Thosaporn Wongratana (1985). *Clupeoid fishes of the world (suborder Clupeoidei)*. Part 1. Chirocentridae, Clupeidae and Pristigasteridae. Food and Agriculture Organization of the United Nations, Rome.
- Whitehead, P.J., Nelson, G.J. and Wongratana, T. (1988). *Clupeoid fishes of the world (suborder Clupeoidei)*. Part 2: Engraulididae. Food and Agriculture Organization of the United Nations, Rome.

- Whitley, G.P. (1943). Ichthyological notes and illustrations (Part 2). *Australian Zoologist*, **10**:167–187.
- Wilson, D.T. and McCormick, M.I. (1997). Spatial and temporal validation of settlement-marks in the otoliths of tropical reef fishes. *Marine Ecology Progress Series*, **153**:259–271.  
DOI: 10.3354/meps153259.
- Wilson, D.T. and McCormick, M.I. (1999). Microstructure of settlement-marks in the otoliths of tropical reef fishes. *Marine Biology*, **134**(1):29–41. DOI: 10.1007/s002270050522.
- Winters, K.L., Herwerden, L., Choat, J.H. and Robertson, D.R. (2010). Phylogeography of the Indo-Pacific parrotfish *Scarus psittacus*: isolation generates distinctive peripheral populations in two oceans. *Marine Biology*, **157**(8):1679–1691.  
DOI: 10.1007/s00227-010-1442-4.
- Wittwer, C.T., Reed, G.H., Gundry, C.N., Vandersteen, J.G. and Pryor, R.J. (2003). High-Resolution Genotyping by Amplicon Melting Analysis Using LCGreen. *Clinical Chemistry*, **49**(6):853–860. DOI: 10.1373/49.6.853.
- Wongratana, T. (1983). Diagnoses of 24 new species and proposal of a new name for a species of Indo-Pacific clupeoid fishes. *Japanese Journal of Ichthyology*, **29**(4):385–407.
- Yanagawa, H. (1994). Length-weight relationship of Gulf of Thailand fishes. *Naga ICLARM Q*, **17**(4):48–52.
- Zajonz, U. (2006). *Plectranthias klausewitzii* n. spec. (Teleostei, Perciformes, Serranidae), a new anthiine fish from the deep waters of the southern Red Sea. *Aqua – International Journal of Ichthyology*, **12**(1):119–126.
- Zajonz, U. and Khalaf, M.A. (2002). Inshore fishes of the Socotra Archipelago: diversity and community structure. Pages 237–296, in: M. Apel, F. Krupp and K.I. Hariri (eds.). *Conservation and Sustainable Use of Biodiversity of Socotra Archipelago. Marine Habitat, Biodiversity and Fisheries Surveys and Management. Final Report of Phase III (UNOPS YEM/96/G32, C-972248)*. Senckenberg Research Institute, Frankfurt a.M., Germany.
- Zajonz, U. and Saeed, F.N. (2002). Inshore fish monitoring programme for the Socotra Archipelago. Pages 297–337, in: M. Apel, F. Krupp and K.I. Hariri (eds.). *Conservation and Sustainable Use of Biodiversity of Socotra Archipelago. Marine Habitat, Biodiversity and Fisheries Surveys and Management. Final Report of Phase III (UNOPS YEM/96/G32, C-972248)*. Senckenberg Research Institute, Frankfurt a.M., Germany.
- Zajonz, U. and Klaus, R. (2005). [up dated in 2007] *The Pilot CZM Areas of Bir Ali - Burum and Sharma - Jethmun. Coastal Zone Management Plan for Bir Ali-Burum and Sharma-Jethmun (Deliveries B03+B04)*. 257 pp. + XVIII Appendices (2 Vols.). Report to the

- Environment Protection Authority, Yemen and the World Bank-GEF. MacAlister Elliott & Partners Ltd, U.K.; Scientific Council for Systems and Applied Science, Sana'a.
- Zajonz, U. and Krupp, F. (2006). Fish biogeography of Socotra, in: C. Cheung, K. Van Damme and L. DeVantier (eds.). *Socotra. A natural history of the islands and their people*. Odyssey, Hong Kong.
- Zajonz, U., Khalaf, M.A. and Krupp, F. (2000). Coastal fish assemblages of the Socotra Archipelago. Pages 127–170, in: M. Apel, F. Krupp and K.I. Hariri (eds.). *Conservation and Sustainable Use of Biodiversity of Socotra Archipelago. Marine Habitat, Biodiversity and Fisheries Surveys and Management. Progress Report of Phase III (UNOPS YEM/96/G32, C-972248)*. Senckenberg Research Institute, Frankfurt a.M., Germany.
- Zajonz, U., Klaus, R., Pulch, H., Lavergne, E., Naseeb, F., Ziegler, M., Alpermann, T., Goerres, M. and Krupp, F. (2011, unpubl. report). Socotra Research Projects. Summary Progress Report 2009- 2010 to the Environment Protection Authority and the Ministry of Water and Environment of the Republic of Yemen. Tropical Marine Ecosystems Group. 40 pp. + 1 Annex. Biodiversity and Climate Research Centre and Senckenberg Research Institute, Frankfurt am Main, Germany.
- Zemlak, T.S., Ward, R.D., Connell, A.D., Holmes, B.H. and Hebert, P.D.N. (2009). DNA barcoding reveals overlooked marine fishes. *Molecular Ecology Resources*, **9**:237–242. DOI: 10.1111/j.1755-0998.2009.02649.x.
- Zhang, J. (2011). Species Identification of Marine Fishes in China with DNA Barcoding. *Evidence-Based Complementary and Alternative Medicine*, **2011**:1–10. DOI: 10.1155/2011/978253
- Zhang, J., Song, B. and Chen, G. (2002). Study on the age and growth of Therapon jarbua. *Marine Science*, **26**(7):66-70.
- Zhang, J., Hanner, R. and Sarkar, I.N. (2012). Molecular Approach to the Identification of Fish in the South China Sea. *PLoS ONE*, **7**(2):e30621. DOI: 10.1371/journal.pone.0030621.

# ***Curriculum Vitae***





## EDOUARD LAVERGNE, *Biologist*



### CONTACT

Senckenberg Research Institute and Nature History Museum  
\*Marine Zoology / Ichthyology\*  
LOEWE - Biodiversity and Climate Research Centre (BiK-F)  
\*Tropical Marine Ecosystems Group\*

Senckenberganlage 25, 60325 Frankfurt am Main, Germany  
Phone: +49 69 75 42 15 83 - Fax: +49 69 75 42 12 53  
E-mail: [elavergne@senckenberg.de](mailto:elavergne@senckenberg.de)  
[www.bik-f.de](http://www.bik-f.de)

Institut Universitaire Européen de la Mer (IUEM)  
Laboratoire des Sciences de l'Environnement Marin  
LEMAR - UMR 6539 CNRS/IRD/UBO

Rue Dumont d'Urville, 29280 Plouzané, France  
Phone: +33 2 98 49 86 27 - Fax: +33 2 98 22 46 53  
E-mail: [edouard.lavergne@univ-brest.fr](mailto:edouard.lavergne@univ-brest.fr)  
[www-iuem.univ-brest.fr](http://www-iuem.univ-brest.fr)

### PERSONAL INFORMATION

<i>Date of birth</i>	<i>Nationality</i>	<i>Place of birth</i>	<i>Marital status</i>
6/11/1980	French	Pessac, France	Married

#### *Licenses*

Driving license (1999) , Diving license CMAS\* (2000), Boat license (2010)

### RESEARCH INTERESTS & EXPERTISE

#### *Basic research*

Community ecology of tropical marine ecosystems with a focus on fish population connectivity between freshwater, brackish and seawater habitats. Ecology and population genetics of estuarine and coastal fishes. Age, growth & life history of fishes using otolith micro -structures and -chemistry. Local adaptation to multi-stress using transcriptomic.

#### *Transfer and applied research*

Environmental research and consulting at the technical level for institutional and private organizations and stakeholders (expertise, communication and education).

### EDUCATION

- Since 2008**     **Ph.D. in Natural Sciences:** “Estuarine fish biodiversity of Socotra Island (NW Indian Ocean): from the fish community to the functioning of *Terapon jarbua* populations”. University of Western Brittany (UBO, France).  
**Co-Supervisors:** Prof. Jean Laroche  
**Scientific advisors:** Prof. Jean Laroche, Dr. Friedhelm Krupp and Dr. Eric Morize
- 2004**     **M.Res. in Natural Sciences, Distinction (70%),** Bordeaux 1 University and the Oceanological Observatory of Villefranche sur Mer (France).
- 2002 – 2003**     **M.Sc. in Environmental Biology,** Swansea University (Wales).
- 1998 – 2002**     **DEUG SVT, Licence BO, Maîtrise BPE,** Bordeaux 1 University.

### WORK EXPERIENCE

- 2008 – 2010**     **Co-founder of the BiK-F Socotra Field Research Station.**
- 2009** <sup>1 month</sup>     **Scientific consultant** on Socotra for a German TV production company.
- 2005 – 2006**     **Environmental consultant** for MacAlister Eliote and Partner Ltd, Yemen. Evaluate the effect of YLNG and TOTAL Companies on the fishery and advised YLNG on a package of measures to compensate fishermen and their communities. Main task: study of fish reproduction.
- 2005 – 2008**     **Research assistant and technical coordinator** of the zoological survey of Arabia including Socotra coastal and estuarine biodiversity, Senckenberg Research Institute.
- 2005** <sup>2 months</sup>     **Scientific consultant:** CZM Pilot Project in the Yemen Gulf of Aden (World Bank-GEF).
- 2004** <sup>3 months</sup>     **Engineer assistant at the security and environment** department of Thales Avionics: Maintain the ISO 14001 standards on C.M.R. chemicals.

**SUPERVISION & TEACHING EXPERIENCE**

<b>2012</b> <sup>6 months</sup>	Co-supervision of Nicolas Pedron (Graduate student at UBO): « Transcriptomic study of <i>Platichthys flesus</i> local adaptation to multi-stress. »
<b>2012</b> <sup>2 mois</sup>	Co-supervision of Carine Le Goff (Graduate student at the UBO) : « Etude de la réponse du flet européen <i>Platichthys flesus</i> à une contamination expérimentale aux PCBs. »
<b>2012</b> <sup>1 semaine</sup>	Supervision de Cyndie Hervé (IBEP) : « Méthodes et Pratiques en Biologie Moléculaire. »
<b>2011 – 2012</b>	Co-supervision of Motea Sheikh Aideed (Graduate student at the Hadramout University, Yemen): « Spatial and temporal dynamics of fish biomass productivity on Socotra, and the impact of the small-scale fisheries on the fish community structure. »
<b>2010</b> <sup>2 months</sup>	Supervision of Lucie Sellin (Graduate student at the UBO): « Larval stage duration of <i>Terapon jarbua</i> using otolith microstructures. »
<b>2010</b> <sup>1 week</sup>	Supervision of Clémentine Le Jouan (Undergraduate student at the UBO): « DNA extraction, PCR and gel electrophoresis initiation on <i>Terapon jarbua</i> microsatellite loci. »
<b>2010</b> <sup>2 months</sup>	Co-supervision of Romain Morvezen and Nicolas Pedron (Undergraduate students at the UBO): « Methods and Practices in Molecular Biology. »
<b>2005 – 2010</b>	Co-supervision of Yemenite counterpart trainig: Sampling methods; Specimen preservation; coastal, estuarine and freshwater fish identification; Initiation to biological conservation.
<b>2003</b> <sup>1 week</sup>	Organization of practical work on pigments, O <sub>2</sub> and nutrients concentration measurements for undergraduate foreign students visiting the Oceanological Observatory of Villefranche sur Mer.
<b>1998 – 2001</b>	Private tuitions from Junior High level to French Baccalaureate level. Subjects: Mathematics, Biology, Physics and Chemistry.

**SKILLS**

***Trainings, scientific and technical skills***

*Conservation*: Environmental Impact Assessment (EIA), Integrated Coastal Zone Management (ICZM).

*Ecological Niche Modeling* (certificate of the BiK-F).

*Laser Ablation Inductively Coupled Plasma Mass Spectrometry* (certificate of the Goethe-University Frankfurt).

*Molecular Biology*: DNA Extraction, PCR, sequencing, genotyping and transcriptomic (qPCR).

*Otoliths*: Extraction, preparation, age determination and growth estimation of fishes using otoliths.

*Sampling and transects*: Niskin bottles, CTD, fishing and underwater monitoring of benthic and fish communities.

*Statistics with R* (certificate of the Goethe-University Frankfurt)

*Scientific writing*: structure and quality (certificate of the Goethe-University Frankfurt)

*Taxonomy*: Taxonomic determination of marine fishes of the Western Indian Ocean.

*Team management* (University of Western Brittany)

*Water Chemistry*: Pigments, dissolved oxygen and nutrients concentration measurements (fluorescence...).

***Language skills***

French: ■■■■■■■■■■ (Native)

English: ■■■■■■■■■□ (Fluent)

German: ■■■■■□□□□ (A2)

Spanish: ■■■■■□□□□□ (Fair)

Japanese: ■□□□□□□□ (Basic)

Arabic: ■□□□□□□□ (Notion)

***Computer skills***

Office, Image: ■■■■■■■■■□ (Word, Excel, Powerpoint, Access, Gimp)

References: ■■■■■■■■■□ (Citavi, End Note, Zotero)

Genetics: ■■■■■■■■■□ (Geneious, Arlequin, GeneMapper)

Statistics: ■■■■■■■■■□ (R, Matlab, Statistica, SPSS)

GIS: ■■■■■□□□□ (ArcGIS)

Web: ■■■■■□□□□ (Adobe Flash & Dreamweaver)

## FUNDING & SCHOLARSHIPS

---

- 2008 – 2011** TOTAL Foundation – Ph.D. research funding: **160 000 €**.
- 2009 – 2010** GRADE (Goethe Graduate Academy, Frankfurt) – Mobility scholarship: **2 500 €**.
- 2009** UEB (European University of Brittany) & CDI (International Doctoral College) – Mobility scholarship: **4 500 €**.
- 2006 – 2007** DAAD (German Academic Exchange Service) – Research & Mobility scholarship in the framework of the project « Establishment of a Middle Eastern Biodiversity Research, Training & Conservation Network »: **8 000 €**.
- 2001 – 2002** Erasmus and the General Council of la Gironde, France – Mobility scholarship: **1 000 €**.

## PUBLICATIONS, REPORTS & CONFERENCES

---

### *Publications*

- Lavergne, E.**, Zajonz, U. and Sellin, L. (2012) Length-weight relationships of *Terapon jarbua* (Forsskål, 1775) from the North-Western Indian Ocean including Socotra Island. *Journal of Applied Ichthyology (Accepted)*.  
DOI: 10.1111/j.1439-0426.2012.02018.x
- Lavergne, E.**, Calves, I., Zajonz, U. and Laroche, J. (2011). Isolation and characterization of nine microsatellite loci of *Terapon jarbua* (Forsskål, 1775) from Socotra Island (Gulf of Aden) using multiplex PCR. Electronic supplement to Agostini et al. Permanent Genetic Resources added to Molecular Ecology Resources Database 1 October 2010-30 November 2010. *Molecular Ecology Resources*, 11:418–421.  
DOI: 10.1111/j.1755-0998.2010.02970.x
- Calves, I., **Lavergne, E.**, Meistertzheim, A.L., Charrier, G., Cabral, H., Guinand, B., Quiniou, L. and Laroche, J. (2012) Genetic structure of the European flounder (*Platichthys flesus*) considering the Southern limit of the species' range and the potential impact of chemical stress. *Marine Ecology progress Series (Submitted)*.

### *Publications in preparation*

- Lavergne, E.**, Calves, I., Meistertzheim, A.L., Charrier, G., Zajonz, U. and Laroche, J. Complex genetic structure of *Terapon jarbua* (Forsskål, 1775) nurseries in temporarily open closed estuaries from the wider Gulf of Aden (*in prep*).
- Lavergne, E.**, Sellin, L., Labonne, M. and Laroche, J. Early life history of *Terapon jarbua* (Forsskål, 1775) using microstructures and Laser Ablation ICP-MS elemental composition of otoliths. (*in prep*).
- Lavergne, E.**, Zajonz, U., Krupp, F., Naseeb, F. and Aideed, M. S. Diversity and composition of estuarine and lagoon fish assemblages of Socotra Island, including comparative sites over the mainland coast of Yemen (*in prep*).

### *Scientific reports*

- Zajonz, U., Klaus, R., Pulch, H., **Lavergne, E.**, Naseeb, F., Ziegler, M., Alpermann, T., Goerres, M. and Krupp, F. (2011, unpubl. report). Socotra Research Projects. Summary Progress Report 2009- 2010 to the Environment Protection Authority and the Ministry of Water and Environment of the Republic of Yemen. *Tropical Marine Ecosystems Group. 40 pp. + 1 Annex. Biodiversity and Climate Research Centre and Senckenberg Research Institute, Frankfurt am Main, Germany*.
- Lavergne, E.** (2006) Determination of reproductive state of target species – In: Zajonz, U., & Willstedt, R. E. (Eds.): Yemen LNG, Fish Nursery Study Balhaf, Yemen. *Part I/Phase 1 Field Report. MacAlister Elliott & Partners Ltd, U.K.*
- Krupp, F., Apel, M., Schneider, M., **Lavergne, E.**, Amui, A. M. & Janssen, R. (2005) Faunistic Survey of the key taxa: Field Report of the Adjunct Research Team (FIS, HLMW). The Pilot CZM Areas of Bir Ali - Burum and

Sharma – Jethmun Marine and Coastal Habitat and Biodiversity Surveys II: 8-19 pp. – In: Zajonz, U., & Willstedt, R. E. (Eds.): Marine and Coastal Biodiversity Report 2 (Delivery A20c). Report to the Environment Protection Authority, Yemen and the World Bank-GEF. 88 pp. *MacAlister Elliott & Partners Ltd, U.K.; Scientific Council for Systems and Applied Science, Sana'a, Yemen.*

**Lavergne, E.** (2004) Meteorological superposed epoch analysis based on chlorophyll fluorescence key events in Villefranche Bay – In the framework of the PNEC & SOMLIT national projects – M.Res. Thesis 35pp; Villefranche sur Mer, France.

**Lavergne, E.** (2003) Villefranche Bay Monitoring System: Data validation and time series analysis, Chlorophyll a and nutrient concentration anomalies – In the framework of the PNEC & SOMLIT national projects – M.Sc. Thesis 94 pp; Swansea, Wales.

**Lavergne, E.** (2002) The infestation of oyster shells by the borrowing sponge *Clonia celata* – Maîtrise B.P.E. Thesis 25pp; Swansea, Wales; Bordeaux, France.

### **International Scientific Conferences and meetings**

Zajonz, U., Aided, M. D., Saeed, F. N., **Lavergne, E.**, Klaus R., Krupp, F. (2012) Socotra Archipelago: unique fish diversity meets exceptional productivity. 12th International Coral Reef Symposium, Cairns, Queensland, Australia, 9-13 July 2012.

Calves, I., **Lavergne, E.**, Meistertzheim, A.L., Charrier, G., Cabral, H., Guinand, B., Quiniou, L. and Laroche, J. (2011). Genetic structure of the European flounder (*Platichthys flesus*) considering the southern limit of the species' range and the potential impact of chemical stress: *8th International Flatfish Symposium, IJmuiden, Hollande, 9 novembre 2011.*

Zajonz, U., **Lavergne, E.**, Al-Harrani, G and Nishimura, B. (2011) Coastal Zones of Yemen - limited management meets Climate Change. Institution-centered Strategic Environmental Assessment of CZM in Yemen: *International symposium on the vulnerability of coastal ecosystems to global change and extreme events – At the crossroads of knowledge to the benefit of coastal and marine ecosystem services. IFREMER, Centre de la mer, Biarritz, France, 18-21 October 2011.*

Zajonz, U., Aided, M. S., Saeed, F. N., **Lavergne, E.**, Klaus, R. and Krupp, F. (2011) Sustainable traditional fisheries management on Socotra: A tale of wishful thinking?: *Annual General Meeting Friends of Soqotra, Naturhistorisches Museum der Burgergemeinde Bern, Switzerland, 23-25 September 2011.*

Calves, I., Dupuy, C., **Lavergne, E.**, Galland, C., Capitaine, C., Pédrón, N., Charrier, G., Guinand, B., Quiniou, L., and Laroche, J. (2011). Structure génétique et réponses aux multi-stress de populations de flet (*Platichthys flesus*) sur un cline latitudinal (Poster). *ECOBIM 2011: Atelier international sur l'évaluation du stress environnemental (Effets biologiques des contaminants chimiques chez les bivalves et les poissons). Institut Maurice-Lamontagne, Mont-Joli, Québec, 6-9 juin 2011.*

**Lavergne, E.** (2010) Life history strategy of *Terapon jarbua*: Population connectivity in an island environment, inferred from otolith microchemistry and microsatellite DNA. *Poster and oral presentation in: ClimECO<sub>2</sub>, Oceans, Marine Ecosystems, and Society facing Climate Change – A multidisciplinary approach, 23-27 Août 2010 IUEM (Eds.): page 117.*

**Lavergne, E.** (2008) First stab at describing the population structure of *Terapon jarbua* from estuarine habitats of Socotra island and the Yemen mainland, and the composition of the associated fish communities: *The First International Congress «Documenting, Analysing and Managing Biodiversity in the Middle East», 20-23 October 2008. In: Neubert, E., Manasfi, N., Weidig, I., Krupp, F. and M. Schneider (Eds.): page 186.*

**Lavergne, E.** (2007) Life history strategy of *Terapon jarbua*: Population connectivity and comparative advantages in an island environment, inferred from reproductive ecology, otolith microchemistry and microsatellite DNA: *XII European Congress of Ichthyology, 9-13 Sept. 2007. In: Buj I., Zanella L. & Mrakovic M. (Eds.): page 126.*

### **National Scientific Conferences and forums**

- Lavergne, E.** (2010) Approche exploratrice des Khors de Socotra, du peuplement à la structure et connectivité populationnelle - Etude de cas de *Terapon jarbua*: *Les Journées des Doctorants du LEMAR, 28-29 Janvier 2010*.
- Lavergne, E.** (2010) La Biodiversité de Socotra, Galápagos de l'Océan Indien. *Forum des Doctorants (publique de lycéens), 07-08 Avril 2010 Association MerSciDoc / EDSM (Eds.) page 24*.

### **PUBLIC RELATIONS**

---

- Lavergne, E., Dupuy, C., Galland, C., Sardenne, F., Dabas, E., Quiniou, L., Laroche, J.** (2012). Effets du réchauffement climatique sur un poisson de l'Atlantique Nord-Est (Projet ANR EVOLFISH): posters, aquarium, otolithes. *Village des Sciences et Technologies de la Mer à Brest 2012, Port de Brest, 13-14 juillet 2012*.
- Lavergne, E., Krupp, F., Saeed, F. N., Pulch, H., Ziegler, M., Klaus, R., Alpermann, T. and Zajonz, U.** (2011) BiK-F Field Research Station Socotra. *Tayf - The Socotra newsletter, Issued by Friends of Soqotra and Socotra Conservation Fund*, 8:17.
- Stent K. (2010) [Ph.D. Student Interviews](#) for the UEB European University of Brittany Website.
- Walter I., Sick E., Mai P., Schiebener W. & Abraham A. (7/06/2009) [ARD W wie Wissen – Sokotra: Ein neues Galapagos](#) (6:30 min).
- Walter I., Sick E., Mai P., Schiebener W. & Abraham A. (15/11/2009) [WDR Planet Schule – Sokotra: Auf den Spuren der Evolution](#) (15 min).

### **ACTIVITIES**

---

#### **Associations**

- 2011 – 2012** Active member of [Gambalo-Japan](#), an association supporting small Japanese villages dependent on marine resources and impacted by the tsunami in 2011
- 2009 – 2012** Active member of [MerSciDoc](#), the young researcher association of the IUEM.
- Deputy secretary (2011)
  - Co-organization of the yearly Doctoral Forum
  - Communication manager
  - Organization of boat driving license training session

#### **Sport**

- 2007 – 2011** Karate (Brown belt) – Kenshinkai Dojo, Frankfurt, Germany
- 2010 – 2011** Judo (Orange belt) – Shudokan Dojo, Brest, France
- 1990 – 2007** Water-polo – 4 years in the French, Wesch and German second league championship.  
Associate trainer for Saint Médard en Jalles junior team.

### **REFERENCES**

---

- Prof. Jean Laroche:**  
[jean.laroche@univ-brest.fr](mailto:jean.laroche@univ-brest.fr) Team Leader at the LEMAR, IUEM, CNRS/IRD/UBO UMR 6539  
Technopôle Brest Iroise, Rue Dumont d'Urville, 29280 Plouzané, France
- Dr. Friedhelm Krupp:**  
[fkrupp@qma.org.qa](mailto:fkrupp@qma.org.qa) Director of the Qatar Natural History Museum, Qatar Museum Authority  
P.O. Box: 2777, Doha - Qatar  
Formerly Head of the Fish Section at the Senckenberg Research Institute
- Dr. Eric Morize:**  
[eric.morize@ird.fr](mailto:eric.morize@ird.fr) Retired Deputy Director of the LEMAR, IUEM, CNRS/IRD/UBO UMR 6539  
IRD Pointe du Diable, Technopôle Brest Iroise, 29280 Plouzané, France
- Dr. Louis Quiniou**  
[louis.quiniou@univ-brest.fr](mailto:louis.quiniou@univ-brest.fr) Research Engineer at the LEMAR, IUEM, CNRS/IRD/UBO UMR 6539  
Rue Dumont d'Urville, Technopôle Brest Iroise, 29280 Plouzané, France
- Mr. Uwe Zajonz:**  
[u.zajonz@senckenberg.de](mailto:u.zajonz@senckenberg.de) PI in the Tropical Marine Ecosystems Group  
Biodiversity and Climate Research Centre (BiK-F)  
Senckenberganlage 25, 60325 Frankfurt am Main, Germany