

AMERICAN UNIVERSITY OF BEIRUT

ATTRIBUTES OF RED SEA FISH SPECIES THAT ARE
ASSOCIATED WITH THE OVERALL RATE AND
TEMPORAL CHANGE IN LESSEPSIAN MIGRATION

by
Carol Nabil Samaha

A thesis
submitted in partial fulfillment of the requirements
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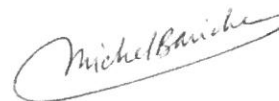
Approved by:

Dr. Heinrich zu Dohna, Assistant Professor
Biology department



Advisor

Dr. Michel J. Bariche, Associate Professor
Biology Department



Committee Member

Dr. Zakaria S. Kambris, Assistant Professor
Biology department



Committee Member

Date of thesis/dissertation defense: [September 15, 2015]

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AN ABSTRACT OF THE THESIS OF

Carol Nabil Samaha for Master of Science
Major: Biology

Title: Attributes of Red Sea fish species that are associated with the overall rate and temporal change in Lessepsian migration

Detecting trends in the introduction rates of invasive species and identifying traits associated with a species' introduction probability are two important approaches in invasion biology research. Our study applied the two approaches to analyze introductions of Red Sea fish species into the Mediterranean Sea. We used Cox regressions to analyze first records in the Mediterranean and demonstrated that many species, with historically low introduction probability, experienced a recent increase in introduction rate. This pattern occurred among demersal fishes and was most pronounced for solitary species living mainly over hard bottoms. The increase in introduction rates for these species cannot be explained by increased detection rates and has important implications for the assessment of future risks posed by species invading the Mediterranean.

CONTENTS

	Page
ACKNOWLEDGEMENTS	VII
ABSTRACT	VII
LIST OF ILLUSTRATIONS	VII
LIST OF TABLES	VII
Chapter	
I. INTRODUCTION	1
II. METHODS	4
A. Species Included in the Analysis	4
B. Predictor Variables Included in the Analysis	5
C. Cox Regression	7
D. Temporal Change of Introduction Rate	8
III. RESULTS	11
A. Variable Screening	11
B. Selection of the Best Model	12
C. Change in Introduction Rate	15
IV. DISCUSSION	16
Appendix	
I. APPENDIX TABLES	25
II. WORK FLOW	57
A. Work Flow Diagram	57
B. Files Used in the Analysis	57

III. R SCRIPTS CODE	59
A. Analyze Fishbase Point Locations script	59
B. Variable Filtering and Analysis HD Survival script	63
C. Penalized Ridge Regression script	99
D. ML_SolowCostello	102
E. Functions	126
1. BestModel_AllCombos_Survival function	126
2. CreateIndicatorVars function	129
3. Plotpath_modified_no_colors function	130
4. QuantileGroups function	133
5. ReplaceNAByGroupMean function	134
 BIBLIOGRAPHY	 136

ILLUSTRATIONS

Figure		Page
1	Flow chart for data pre-processing	5
2	Quantile plot of ranked P -values. Filled circles indicate P -values that passed the screening. Fitted line indicates relationship between rank and value among P -values that do not deviate from the null hypothesis	12
3	Proportion of source pool species with no record from the Mediterranean Sea since the opening of the Suez Canal	14
4	Solution path for the coefficients of predictor variables associated with introduction with respect to variation of λ_2	15
5	SST_{max} values [$^{\circ}C$] in the Indo-Pacific and eastern Mediterranean.....	20
6	Observed and fitted cumulative number of detected introduced species for the three groups that have a different baseline hazard rate according to the proportionality test.....	21
7	Work flow diagram	57

TABLES

Table		Page
1	Estimated coefficients and P-values of predictor variables that are part of the best model	13
2	Correlation estimates among the six traits associated with introductions (predictor variables)	13
3	Results of the five best models fitted to detection times	16
4	List of bony fishes from the Red Sea.....	25
5	List of introduced bony fishes in the Mediterranean Sea from the Indo-Pacific area	48
6	Traits of Red Sea fish species that were analyzed.....	52
7	Files used in the analysis	57

CHAPTER I

INTRODUCTION

The Mediterranean Sea is considered a marine biodiversity hotspot and one of the most invaded marine regions in the world (Coll et al., 2010; Edelist, Rilov, Golani, Carlton, & Spanier, 2013). Due to its enclosed geography and long history of human settlement on its shores, the Mediterranean Sea is exposed to various anthropogenic threats. One such threat is the introduction of alien species from the Red Sea through the Suez Canal, a phenomenon that is referred to as ‘Lessepsian migration’. So far, 90 exotic fish species of Indo-pacific origin have been recorded in the Mediterranean since the construction of the Suez Canal (Golani *et al.*, 2013). There is evidence that some Lessepsian fishes have displaced native Mediterranean species (e.g. Bariche, Letourneur, & Harmelin-vivien, 2004; Edelist et al., 2013; Galil et al., 2014) and have fundamentally altered ecosystems in the Mediterranean (Sala, Kizilkaya, Yildirim, & Ballesteros, 2011; Vergés et al., 2014). In light of the current and potential future impact of Lessepsian migrants, an accurate assessment of the risks posed by the Suez Canal is a pressing task for marine ecologists.

One approach for assessing the risk posed by alien species is to predict which species are likely to pass from the Red Sea into the Mediterranean. Belmaker et al. (2013) worked on such a predictive framework, by analyzing which traits among reef-associated fishes from the Indo-Pacific are significant predictors for the probability of introduction into the Mediterranean. Their analysis confirmed previous observations (e.g. that species forming large schooling groups have higher introduction probabilities)

and produced new results (e.g. that species occurring at higher maximum temperatures have higher introduction probabilities). Based on the latter result, the authors concluded that high sea surface temperature in the Mediterranean constitutes a barrier for introduction of species occurring at lower temperatures in the Indo-Pacific and global warming would therefore be unlikely to accelerate species' introductions from the Red Sea into the Mediterranean.

The detection of traits associated with introduction probabilities provides important information about ecological mechanisms and future risks of such introductions. However, there are several challenges for the detection of these traits. One challenge is that there are numerous correlated traits that can be associated with introduction risk and any particular one could be a strong or poor predictor of introduction risk, depending on other traits included in the analysis. Another challenge is the ecological and geographical definition of the source pool, i.e. the set of species that could potentially become introduced. For example, if the geographic delineation of the source pool is too wide, statistically significant predictors of introduction could simply indicate traits associated with an occurrence close to the Suez Canal, rather than traits associated with the introduction itself. A third challenge is that the introduction risk could change differently over time for different species. In that case a simple introduction probability, as used in earlier studies, does not adequately represent future introduction risk.

The Suez Canal has been widened and deepened multiple times since its initial construction (Rilov & Galil, 2009; Galil et al., 2014). It has been expanded further in 2015 by the digging of a new 35 km long shipping lane and further expansion of another large section is underway. To assess the risk posed by this expansion, it is important to

know whether previous expansions led to an increase in the invasion rate. A key component in answering this question is to determine whether there is evidence that the invasion rate increased over time in the past. Several authors have noted an increase of the rate at which species from the Indo-Pacific are recorded in the Mediterranean (Galil, 2008b; Golani, 2010; Raitos *et al.*, 2010; Edelist *et al.*, 2013). However, an increase in the rate at which alien species are recorded does not necessarily indicate an increase in the introduction rate. Such an increase could occur if detection of alien species improves over time due to increased surveillance. Furthermore, even if the introduction rate and the per-species detection probability stay constant, the rate at which new alien species are recorded can increase over time. This is because alien species are usually not detected immediately upon introduction and unrecorded species can accumulate and contribute to a rise in the detection rate (Costello & Solow, 2003; Solow & Costello, 2004). In fact, a latent-variable model that included undetected introductions, produced no evidence for an increase of the rate at which Indo-Pacific species are introduced into the Mediterranean Sea (Belmaker, Brokovich, China, Golani, & Kiflawi, 2009).

The purpose of the present study is to combine the analysis of temporal trends in introduction risk with the analysis of species traits associated with introduction, while addressing some of the challenges of detecting those traits. Based on careful a priori considerations, we delineated a source pool that differed from source pool definitions of a previous study (Belmaker *et al.*, 2013) and compiled a large set of predictor variables for the source pool species. We employed a Cox-proportional hazard model to identify predictors of introduction risk. We tested the proportionality assumption to reveal whether there are groups of species with different temporal trends in introduction risk.

We fitted latent-variable models to determine whether trends in introduction rates were due to changing introduction or detection rates.

CHAPTER II

METHODS

A. Species included in the analysis

Our analysis considered all bony fish species that were reported from the Red Sea by Golani and Bogorodsky (2010). We excluded species that are native to the Mediterranean Sea, occur in deep water (>100 m upper range depth), or are globally distributed (Table 4, Figure 1A). The resulting list contained a total of 960 fish species. Synonyms were updated according to Froese & Pauly (2015). Since any of these species could theoretically move to the Mediterranean via the Suez Canal, they will be referred to as the “source pool” (Table 4). We used the online CIESM Atlas of Exotic Species in the Mediterranean (Golani *et al.*, 2013) to determine which source pool species have at least one record in the Mediterranean. We did not consider records of *Acanthopagrus bifasciatus*, *Terapon theraps* and the first record of *Pomadasys stridens* as the location of these records in the Mediterranean did suggest a presence not related to a passage through the Suez Canal (Ben Souissi *et al.*, 2014; Golani *et al.*, 2013; Lipej, Mavrič, Žiža, & Dulčić, 2008). Fishes that were recorded in the CIESM’s list (Golani *et al.*, 2013) but were absent from the source pool (Golani & Bogorodsky, 2010) were not included in the analysis to ensure that the definition of the source pool (species that could pass through the Suez Canal) was independent of the measured outcome

(occurrence in the Mediterranean). We identified 78 species from the source pool that have records in the Mediterranean (Golani *et al.*, 2013). They will be referred to as “introduced species” (Table 5).

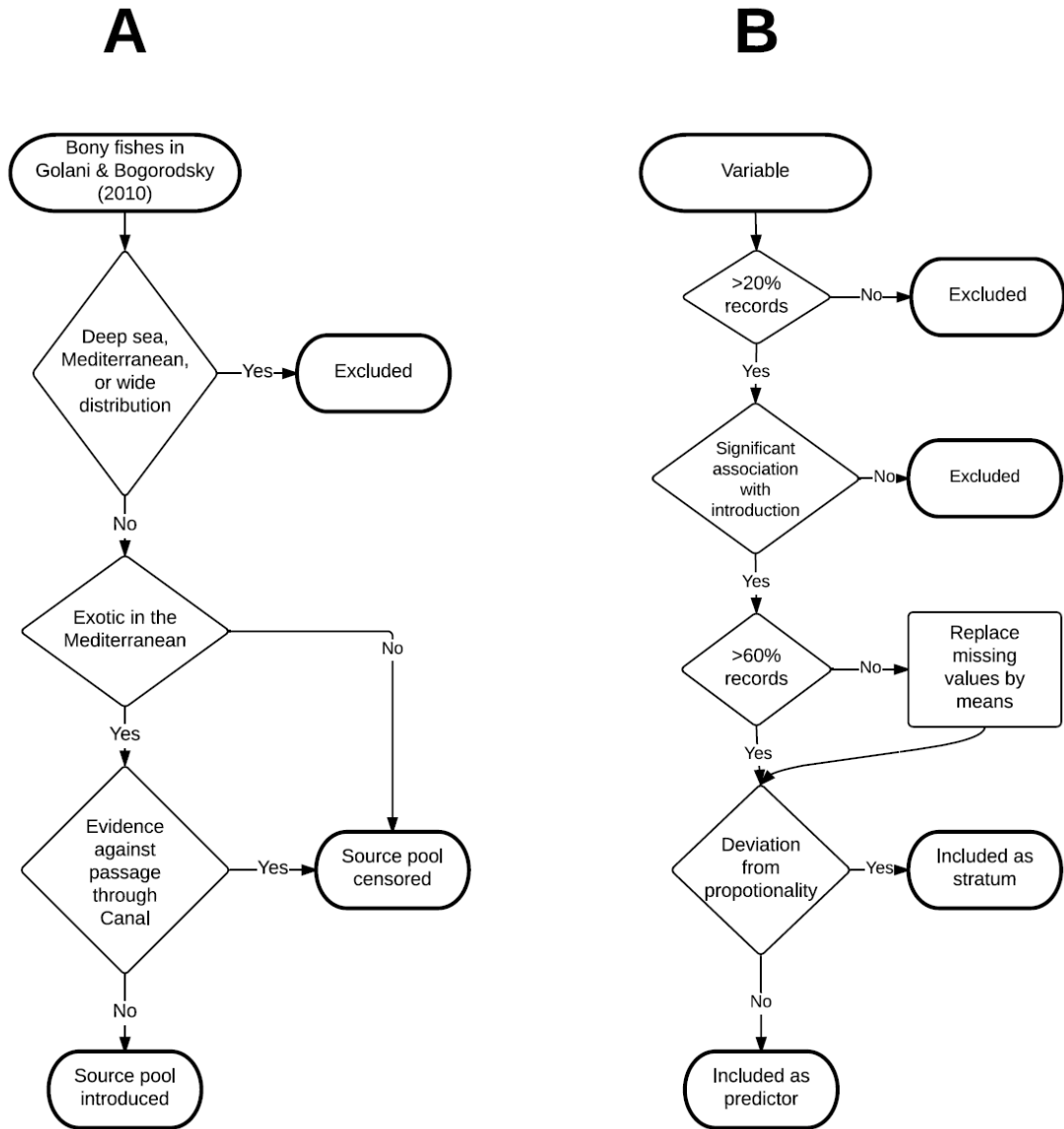


Figure 1: Flow chart for data pre-processing: (A) procedure to select species for inclusion in the source pool and (B) procedure to screen variables for inclusion as predictor or stratifying variable in model selection procedure.

B. Predictor variables included in the dataset

Biological information for all species within the source pool was compiled from a dataset extracted from www.fishbase.org (Froese & Pauly, 2015). For each species, the dataset contained fields with information on taxonomy, ecology, behavior, life history, morphology and an additional field with comments. We extracted from these comments further information and incorporated it manually into the main fields. The number of species present in the Red Sea within each family was included as a separate field. Additional information was obtained from the literature for six variables with missing records. They included information on distribution, longevity, length, activity, type of bottom and food items. We retained for the study only fields with records available for at least 20% of the species in the source pool (Figure 1B).

In addition, we downloaded from www.fishbase.org (Froese & Pauly, 2015) all available sampling location data in the Red Sea and Indian Ocean. This data contained the latitude, longitude and fish species observed per location. These sampling data were not exhaustive, i.e. some source pool species were not recorded in any sampling locations from the Red Sea and some species were not recorded in any sampling locations from the entire Indo-Pacific. We obtained for each of these sampling locations the yearly range and monthly maximum sea surface temperature (*SSTrange* and *SSTmax*, respectively) from the Bio-ORACLE database (Tyberghein *et al.*, 2012). We calculated for each species from the source pool, with at least one record in the location data, the mean *SSTrange* and maximum *SSTmax* among all its sampling locations and included the mean *SSTrange* and maximum *SSTmax* as predictor variables. Furthermore, we determined for each species the sampling location that is closest to the Suez Canal and included the straight line distance from the closest location to the canal

as predictor variable (variable “minimum distance to canal”). The resulting dataset had a total of 33 predictor variables (Table 6).

C. Cox regressions

A Cox proportional hazard model (Cox, 1972) was used to estimate effects of predictor variables on the rate at which new introduced species are recorded in the Mediterranean Sea. Following standard survival analysis terminology, we will refer to this rate as the “hazard rate”. It is important to note that this hazard rate is not the same as the introduction rate, since it is influenced by the rate at which species are introduced and the rate at which introduced species are detected. We will use the term “true introduction rate” when we refer to the rate at which species are introduced. Our analysis considered the year of first record in the Mediterranean as an event time (with the exception of *Pomadasys stridens*, as explained above). All source pool species with no record of introduction were treated as right-censored observations with the year 2013 as censoring time (Figure 1A). The year 2013 was chosen since it coincided with the last update of the CIESM online database at the time of our analysis (Golani *et al.*, 2013). The number of years was counted since the opening of the Suez Canal in 1869 (i.e. year 2013 was treated as year 144). We clustered species by family in each Cox regression to account for phylogenetic non-independence of different fish species.

The analysis contained three parts, the screening of potential predictor variables, the selection of the best combination of predictor variables that passed the screening and an analysis of the temporal change in the hazard rate and true introduction rate. The screening itself was carried out in several steps (Figure 1B). We tested each of the 33 variables individually for an association with the hazard rate using a Cox

regression model and a likelihood ratio test for significant model fit. We adjusted the *P*-values according to the adaptive Benjamini-Hochberg correction (Benjamini & Hochberg, 2000) to keep the false discovery rate among the screened variables below 5%. We tested all variables that passed the screening for a violation of the proportionality assumption. Screened variables entered the model selection procedure as stratifying variables if they violated the proportionality assumption and as predictor variables otherwise. When a screened predictor variable contained missing values for more than 40% of the source pool species, the missing values for this variable were replaced by its mean value among all species that contained a record for this variable. We performed a Cox regression for all possible combinations of screened predictor variables and selected the combination with the lowest Akaike's Information Criterion (AIC) value as the best model (Burnham & Anderson, 2002). We tested the goodness of fit of the best model following the method by Parzen & Lipsitz (1999) using eight rate classes. We calculated the correlations between all variables that passed the screening but did not test whether correlations differed significantly from zero since different species could not be considered independent observations. In addition to the standard Cox regression, we fitted a Cox regression with a ridge penalty (R package penalized) using all predictor variables of the best model to analyze the robustness of the regression coefficients.

D. Temporal change of the introduction rate

To analyze the temporal change in the hazard rate, we assigned species to groups with similar baseline hazard rates. First we tested all variables that passed the screening for a deviation from the proportionality assumption on a global level

(Grambsch & Therneau, 1994). Then we applied the following grouping procedure to each variable that showed a significant deviation: We tested for the deviation from proportionality among all pairs of factor levels within a variable (Grambsch & Therneau, 1994) and pooled pairs of factor levels whose baseline hazard rate did not deviate significantly from proportionality, starting with the pair whose comparison produced the largest P -value. After each pooling, we re-calculated the P -values for the comparisons of the new groups. The procedure stopped once there was a significant deviation from proportionality between all pairs of groups. After we applied this procedure to all predictor variables that showed a deviation from proportionality, we combined the newly created groups from different variables and created a single new variable with a factor level for each group combination. We repeated the grouping procedure for this newly created variable and thereby obtained a single grouping variable that defined groups with different baseline hazard rates.

We fitted different versions of the model by Solow and Costello (2004) to determine the most likely reason for different baseline hazard rates. Different species could have different baseline hazard rates because they experienced a different change in their true introduction rate, a different change in their detection rate or a different change in both. According to the model by Solow and Costello (2004), the true introduction rate μ_t changes with time t according to

$$\mu_t = e^{\beta_0 + \beta_1 t}$$

The introductions described by this rate are not observed directly. The probability of a species becoming detected in year t given that it was introduced in year s is given by

$$\pi_{st} = \frac{\exp(\gamma_0 + \gamma_1 t + \gamma_2 e^{t-s})}{1 + \exp(\gamma_0 + \gamma_1 t + \gamma_2 e^{t-s})}$$

The parameter β_1 estimates how the true introduction rate changed with time, the parameter γ_1 estimates how the detection probability changed with time and the parameter γ_2 estimates how the detection probability changed with time since introduction.

We fitted 16 models of different complexity and used the AIC value to rank them. The trend parameters for introduction (β_1) or detection (γ_1 and γ_2) were either constrained to zero or unconstrained, leading to four possible combinations of trend parameter constraints. Similarly, the parameters of detection and introduction could either be the same for all groups with different baseline hazard rates or be different for each group, leading to four possible combinations of how parameters differed between groups. Combining these two sets of four combinations led to a total of 16 different models.

We estimated the maximum likelihood values for parameters for all 16 models through numerical optimization procedures. We used zero as starting values for the parameters β_1 , γ_0 , γ_1 , and γ_2 and $\log(N/T)$ for β_0 , where N denotes the total number of observed introduced species and T the total number of years. The starting value for β_0 was chosen so that $\exp(\beta_0) = N/T$, i.e. according to the starting values there is no temporal trend in introduction and the yearly introduction rate equals the total number of introduced species divided by the length of the observation period. The observation period started with the first Mediterranean record in 1902 and ended in 2013, the last year CIESM was updated at the time of our analysis. We calculated the AIC values for all models to rank them. In addition, we performed likelihood ratio tests to determine whether individual trend parameters of the highest ranked model differed from zero. All

calculations were performed using the statistical programming language R 3.2.1 (R Core Team, 2013).

CHAPTER III RESULTS

A. Variable screening

Six out of 33 screened traits of fishes living in the Red Sea were significantly associated with introductions, when controlling for a false discovery rate of 5% (Figure 2). These were: schooling, demersal-pelagic distinction, type of bottom, number of species per family, minimum distance to canal, and *SSTmax* (Table 6). The baseline hazard rates of species associated with different categories of the variables “schooling” and “type of bottom” deviated significantly from the proportionality assumption. Our grouping procedure separated species into three groups with distinct baseline hazard rates: group I included all species that had the type of bottom category “none” and any schooling level (i.e. all pelagic species); group II included all species with the type of bottom category “hard” and schooling level 1 (i.e. solitary or species living in pairs on or close to hard bottoms); and group III included all remaining species (i.e. all species living on or close to soft bottoms or alternatively on both types of bottoms and non-solitary species living on or close to hard bottoms). In the subsequent analyses, the Cox proportional hazard model was therefore stratified according to these three groups for which separate baseline introduction rates were estimated. The variables “schooling”, *SSTmax* and “minimum distance to canal” contained each missing records for more than 40% of the species. To include these variables in the model selection procedure, we replaced missing values by means. For all species whose schooling value was missing

but available for at least one member of the same family, we replaced the missing value by the mean schooling value of all species of the same families. For all other species we replaced the missing “schooling” values by the overall mean. We replaced the missing values for *SSTmax* and “minimum distance to canal” by their overall means among all other species.

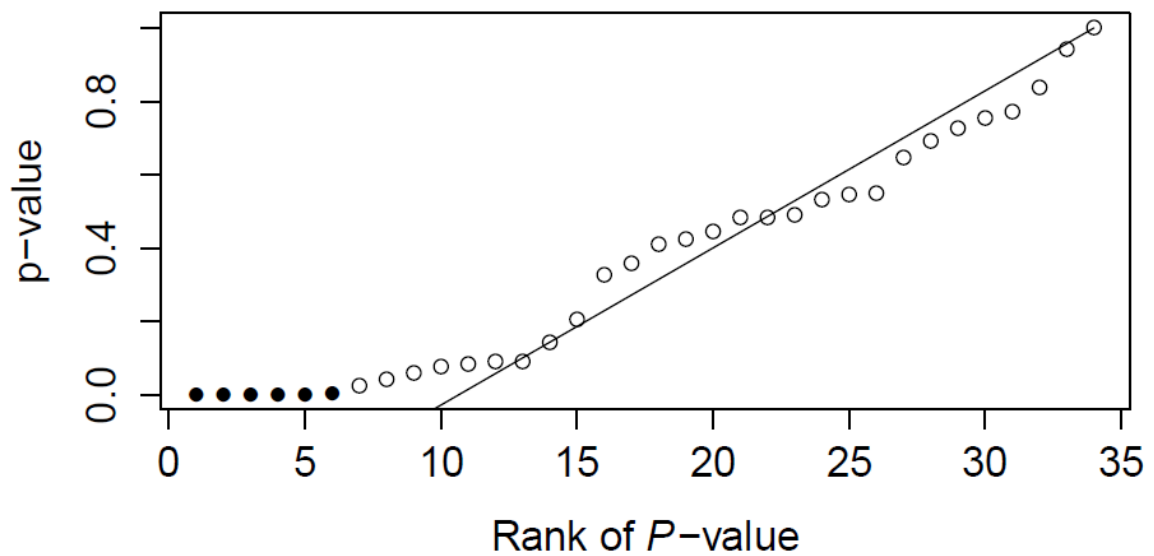


Figure 2: Quantile plot of ranked P -values. Filled circles indicate P -values that passed the screening. Fitted line indicates relationship between rank and value among P -values that do not deviate from the null hypothesis.

B. Selection of the best model

The best combination of predictor variables according to the AIC excluded *SSTmax* and schooling and contained thus four out of the six traits that were associated with introductions (Table 1). According to the best model, the hazard rate was higher among species living close to the surface, among species living over soft bottoms, among species found within species poor families and among species with a low minimum distance to the canal (Table1, Figure 3). The goodness of fit test showed no

significant deviation between the predicted and observed hazard rates. There were moderate correlations among the predictor variables (Table 2). However, a penalized ridge regression analysis showed that, despite these correlations, the sign and magnitude of estimated coefficients were robust (Figure 4).

Table 1: Estimated coefficients and *P*-values of predictor variables that are part of the best model

Variable	Encoding	Estimated coefficient	<i>P</i>
Number of species per family	Integer	-0.01	0.039
Demersal – pelagic	1 = surface 2 = midwater 3 = close to bottom 4 = on the bottom	-0.98	0.0003
Type of bottom	Hard both soft none (pelagic)	-1.1 - 0.46 -	0.001 - 0.17 -
Minimum distance to the canal	real number	-0.0002	0.0007

*Species belonging to multiple categories received the mean value of these categories.

Table 2: Correlation estimates among the six traits associated with introductions (predictor variables).

	Minimum distance to canal	Number of species per family	Demersal – pelagic	Schooling	Type of bottom	<i>SSTmax</i>
Minimum distance to Canal	-	0.02	0.07	-0.11	0	-0.19
Number of species per family	-	-	0.17	-0.31	0.27	-0.06
Demersal – pelagic	-	-	-	-0.57	-0.24	-0.11

Schooling	-	-	-	-	0	0.11
Type of bottom	-	-	-	-	-	-0.06
<i>SSTmax</i>	-	-	-	-	-	-

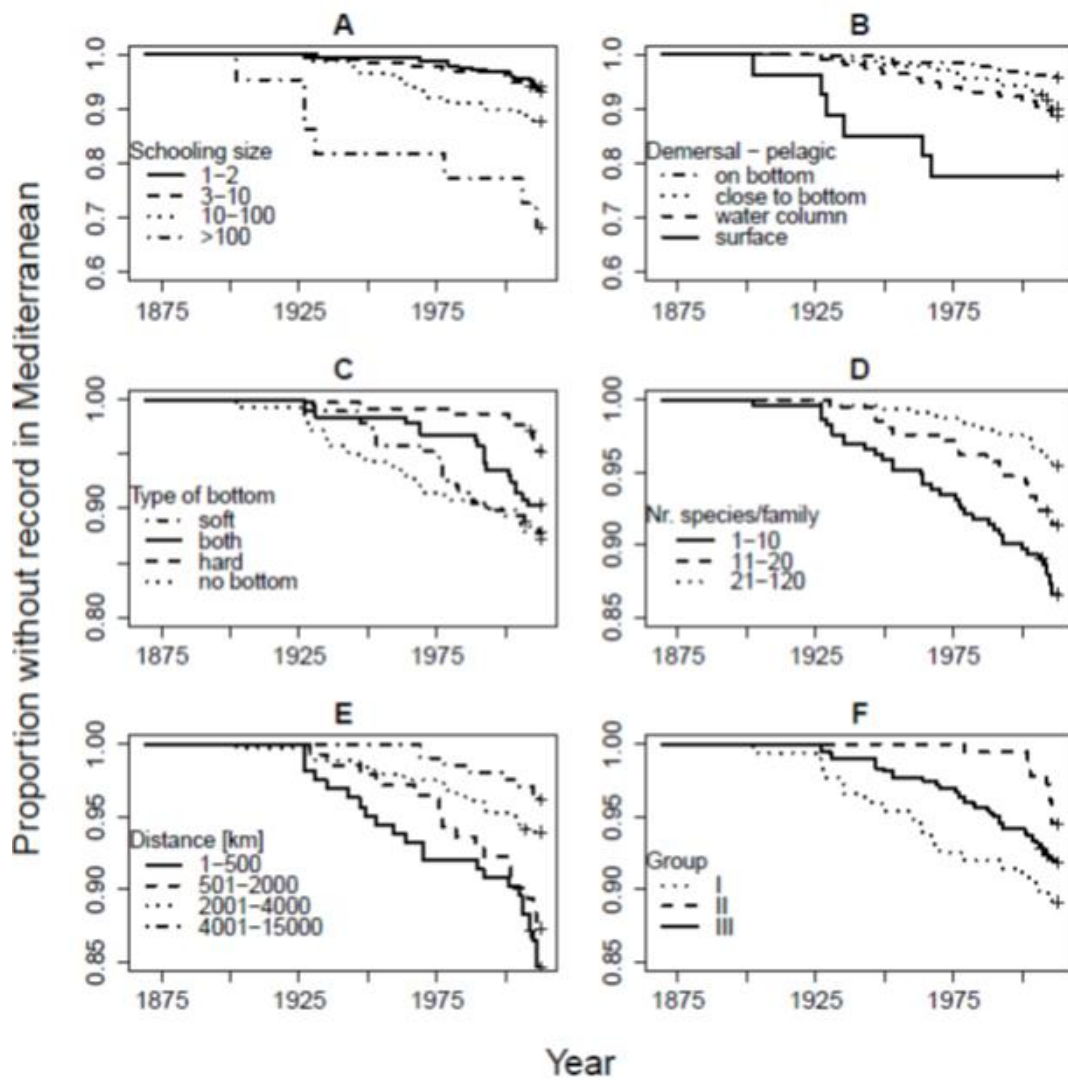


Figure 3: Proportion of source pool species with no record from the Mediterranean Sea since the opening of the Suez Canal. Species were grouped by: (A) Schooling size, (B) their habitat in relation to the bottom; (C) type of bottom; (D) number of species within each family; (E) closest distance to Suez Canal among records from Indo-Pacific sampling locations and (F) groups with different baseline hazard rate.

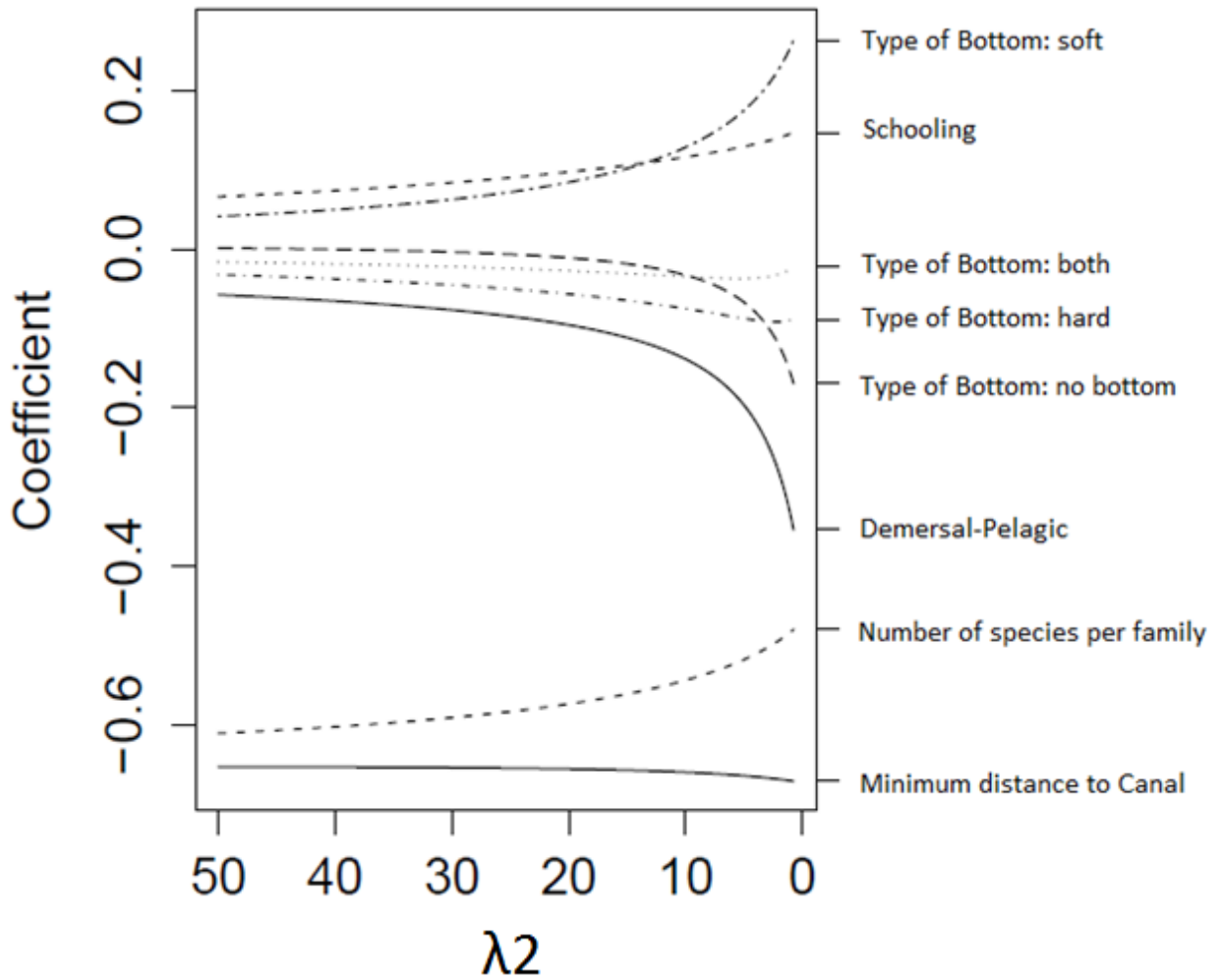


Figure 4: Solution path for the coefficients of predictor variables associated with introduction with respect to variation of λ_2 (tuning parameter of ridge regression).

C. Change in introduction rate

The best fitting model for the change in introduction rate contained a constant detection probability ($\gamma_1 = \gamma_2 = 0$) that was the same for each group and a true introduction rate that changed differently over time for each group (Table 3). The maximum likelihood parameter estimates for this model were $\gamma_0 = 15.8$ for all groups, $\beta_0 = -2.0$, $\beta_1 = 0.004$ for group I, $\beta_0 = -14$, $\beta_1 = 0.13$ for group II and $\beta_0 = -2.3$, $\beta_1 = 0.02$ for group III. The value for γ_0 implies a yearly detection probability of $> 99.9\%$. The difference in AIC value to any model with constant true introduction rate equals 7.9,

providing strong evidence for a temporal increase in the true introduction rate (Table 3). The trend parameter β_1 differed significantly from zero for groups II and III (for both groups $P < 10^{-5}$, likelihood ratio test) but not for group I ($P = 0.52$, likelihood ratio test).

Table 3: Results of the five best models fitted to detection times

Parameters constrained to zero	Parameters shared between groups	Log-likelihood	Number parameters	AIC	Δ AIC
γ_1 and γ_2	γ_0, γ_1 and γ_2	-148.5	7	311	0
γ_1 and γ_2	None	-147.5	9	313	2
None	γ_0, γ_1 and γ_2	-148.5	9	315	4
β_1	None	-147.4	12	318.9	7.9
None	None	-148.1	15	326.1	15.1

CHAPTER IV DISCUSSION

We performed Cox regressions to determine which attributes of fishes present in the Red Sea are associated with the rate at which new alien species from the Red Sea are recorded in the Mediterranean (hazard rate). We also analyzed whether the true introduction rate changed over time. Our results showed that the highest hazard rate occurred among pelagic species, species living over soft-bottoms, species present in small families, and species recorded close to the Suez Canal. We also found that alien species could be separated into three groups, each displaying a different temporal trend in their true introduction rate. Two groups showed an increase in true introduction rate over time. The group that showed the strongest increase in introduction rate were solitary fishes living on hard bottoms.

Our analysis – and previous studies, e.g. (Belmaker *et al.*, 2013) – assumed that introductions of different species were independent of each other. This assumption can be justified since we used the date of first record in the Mediterranean as event time. Hence, our analysis focused on early stages of the introduction process, a stage that is less likely to be influenced by the presence of other species (Azzurro *et al.*, 2014).

A novel result of our study is that species belonging to small families were more prone to be introduced into the Mediterranean than species from large families. There are several possible reasons for this. Theoretical models of sympatric speciation (Doebeli & Dieckmann, 1999) and empirical analyses of herbivorous insects (Hardy & Otto, 2014) have shown that ecological specialization tends to be associated with higher diversification rates. Hence, species from highly diverse families might be more specialized and therefore less likely to colonize new habitats. Another possible explanation for the association between small family size and higher hazard rate could be that allopatric speciation creates a negative correlation between dispersal ability and family size. Members of families of good dispersers might have undergone allopatric speciation less often than members of families of poor dispersers and as a result families of good dispersers are less diverse than families of poor dispersers. Lessepsian migrants might predominantly come from families of good dispersers and therefore from smaller families. The correlations between predictor variables indicate that species from small families tend to occur away from the bottom (surface or midwater) and in large schools (Table 2). Hence, two traits that are associated with higher hazard rates are overrepresented in small families, suggesting an association between good dispersal and low within-family diversity. A full analysis of this association would require a phylogeny-based estimation of the influence of these two traits on diversification rate

(FitzJohn, Maddison, & Otto, 2009), which is beyond the scope of this study.

Regardless of the reason for the association between intra-family diversity and introduction risk, the fact that species from small families are more likely to pass into the Mediterranean provides a new explanation for Belmaker et al.'s (2013) observation that Lessepsian migrants show a higher trait evenness and divergence than randomly selected Red Sea species. The high trait evenness and divergence of Lessepsian migrants has previously been interpreted as evidence that migrants are filtered by competition (Belmaker *et al.*, 2013; Azzurro *et al.*, 2014). We provide the alternative explanation that Lessepsian migrants represent more families than a random sample from the source pool. More research is necessary to decide which of these explanations is more adequate.

Our analysis confirms the previously discovered associations between the hazard rate and the variables *SSTrange*, *SSTmax*, type of bottom, schooling level, and a species' occurrence in the water column (Belmaker et al., 2013; Golani, 1993b; Golani, 2010). The high hazard rate among soft-bottom fishes detected in our study matches the previous observation that Lessepsian species make up a large percentage among species that are common in sandy habitats in the northern Red Sea (Golani, 1993b).

Our results regarding the associations between the hazard rate and the variables *SSTrange* and *SSTmax* match the results of a previous study (Belmaker *et al.* 2013) but our study provides new interpretations for these associations. The association between hazard rate and *SSTrange* was not strong enough to overcome our false-discovery rate threshold. This could be because our set of sampling locations might differ from the ones used by Belmaker et al. (2013), or because we used a large number of variables and controlled for a false discovery rate. The association between high *SSTmax* and high

hazard rate was strong enough to pass the screening, but the variable *SSTmax* was not part of the best model when other, correlated variables were included. The variable *SSTmax* showed the strongest correlation with the variable “distance to the canal” which suggests a novel explanation of the effect of *SSTmax*. Since *SSTmax* is higher in the Red Sea than in most parts of the Indo-Pacific (Figure 5), species occurring at sampling locations in the Red Sea tend to have a higher *SSTmax*. Therefore, *SSTmax* might simply be a proxy for a species’ occurrence in the Red Sea sampling locations but not itself a predictor of the introduction probability. This interpretation of the effect of *SSTmax* is also supported by the fact that *SSTmax* is generally lower in the eastern Mediterranean than in the Red Sea (Figure 5). In contrast, Belmaker et al. (2013) interpreted the association between *SSTmax* and introduction probability as evidence that high maximum temperatures in parts of the eastern Mediterranean restrict the introduction of species that occur at lower temperatures in the Indo-Pacific. According to their interpretation, global warming will slow the invasion process from the Red Sea into the Mediterranean. Our interpretation of the effect of *SSTmax* does not suggest such an effect of global warming. More detailed data on the geographic distribution and thermal tolerance of Red Sea species are needed to disentangle the effects of *SSTmax* and geographic distance to the canal and to determine whether global warming will slow down Lessepsian migration as suggested by Belmaker et al. (2013) or facilitate it as suggested by other researchers (Lasram & Mouillot, 2009; Raitso et al., 2010).

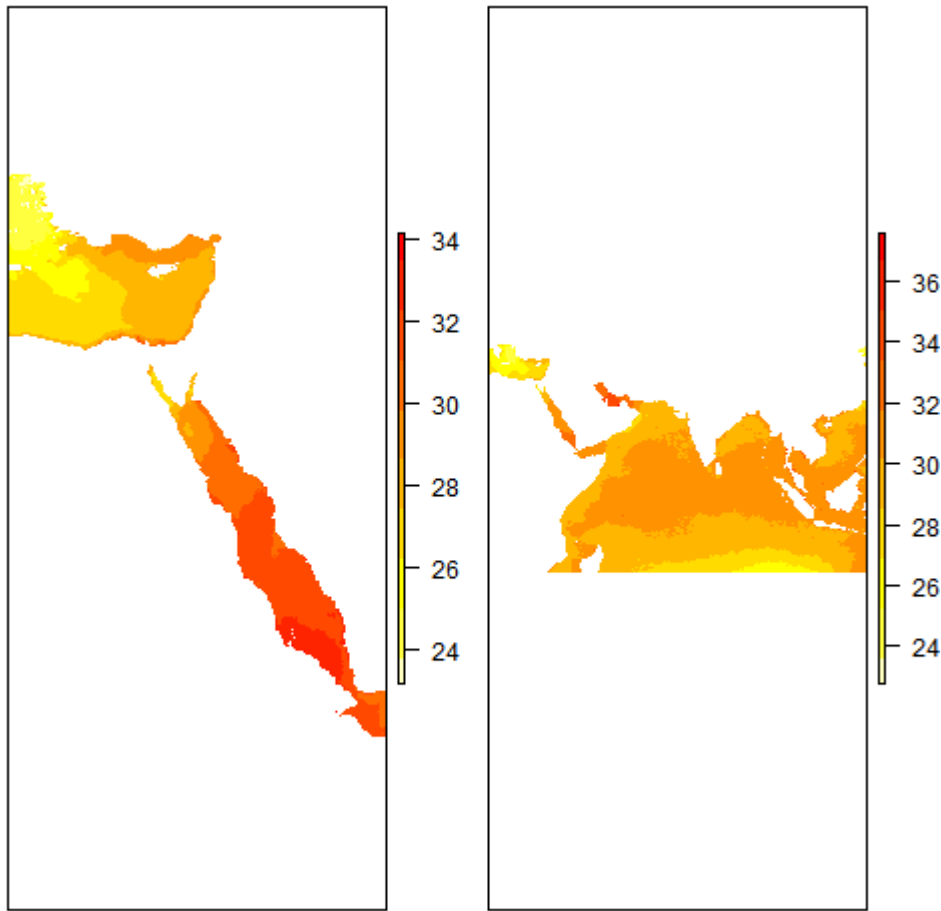


Figure 5: *SST*_{max} values [°C] in the Indo-Pacific and eastern Mediterranean. Data were obtained from <http://www.oracle.ugent.be/> and converted to a map using the statistical language R (R Core Team, 2013).

Our results show that the average hazard rate is higher among species living close to the surface than among species living midwater or close to the bottom (Figure 3B). This is in accordance with Belmaker *et al.*(2013). However, our analysis of introduction rate trends also shows that demersal species, while having the lowest average introduction rate, made up the majority of the alien species that were recorded in recent time (groups II and III in Figure 6). This is partly because there are more demersal than pelagic species in the source pool and partly because the introduction rate remained roughly constant over the last century for pelagic species (group I) but

increased over time among demersal species (groups II and III) (Figures 3F and 6). As a result, the current introduction rate is highest among demersal species. The current increase in introduction rate is highest among solitary hard-bottom species (group II) as nine out of the ten introduced solitary hard-bottom species have been recorded in the Mediterranean since 2002 (Figure 6).

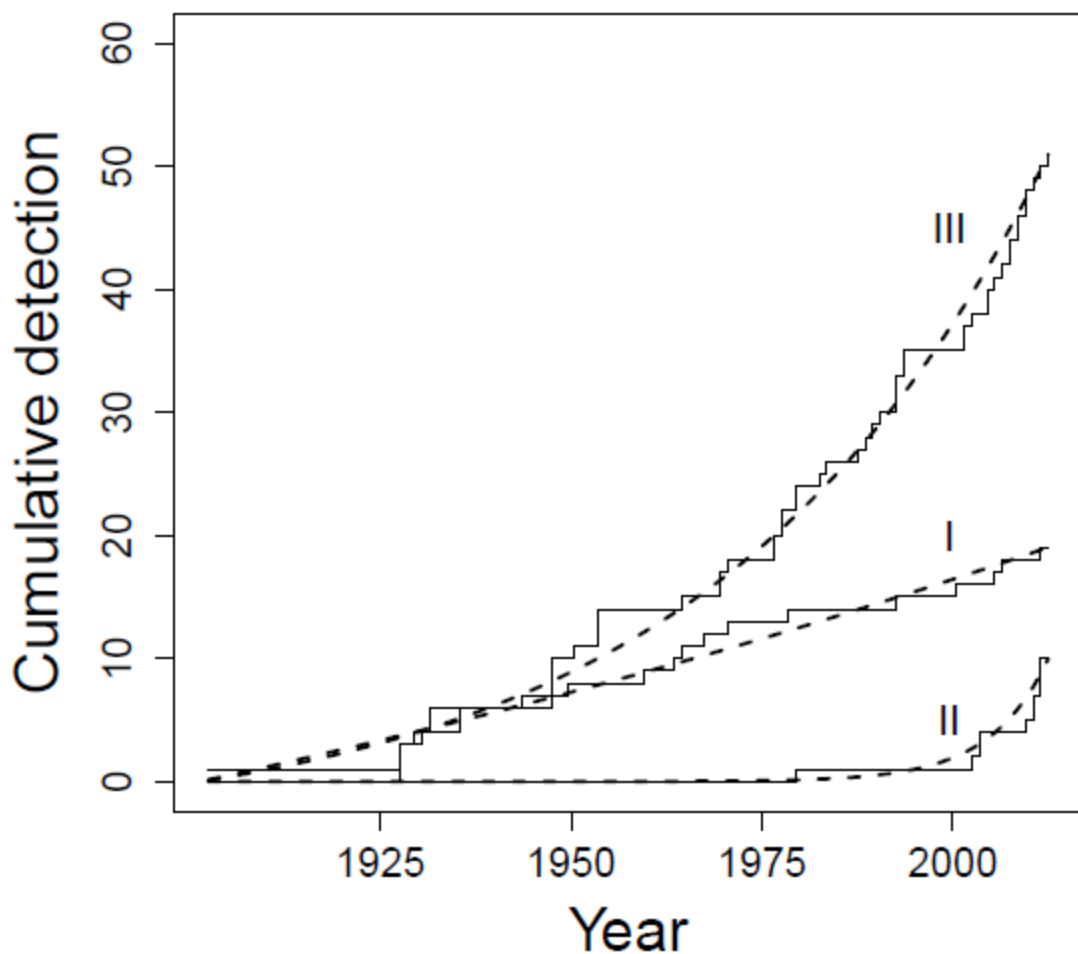


Figure 6: Observed (solid step lines) and fitted (dashed lines) cumulative number of detected introduced species for the three groups that have a different baseline hazard rate according to the proportionality test. The labels next to the lines indicate the groups (I-III). See text for description of groups. The fitted line corresponds to the highest ranked model (constant detection shared by all groups and increase in introduction rates).

The increase in true introduction rate among species of groups II and III is at odds with Belmaker et al. (2009), who analyzed temporal trends in true introduction rates of Lessepsian species and found no evidence for a temporal increase in the true introduction rate. Belmaker et al. (2009) used a different analysis method and a different dataset than our study and did not separate species into groups with different baseline hazard rates.

According to the highest ranked model in our study, the increase in the hazard rate is due to an increase in the true introduction rate rather than due to an improved detection. However, it is unclear to what degree our result is a consequence of the particular Estimated coefficients and P-values we used. The temporal change in records of introduced species is well approximated by the exponential function we used for the true introduction rate and as a result, the highest ranked model assumes an immediate detection of introduced species – an assumption that is certainly not true. The highest ranked model is therefore not necessarily an accurate description of the underlying processes but rather a benchmark to measure alternative models against. The highest ranked model performed substantially better than any model we fitted with constant true introduction rates. Hence, the models we fitted provide a strong evidence for an increase in the true introduction rate among demersal species.

Our estimation of temporal trends in introduction rates did not consider the effects of source pool depletion. The true introduction rate in our analysis is the total number of species introduced per time, i.e. the number of species in the source pool multiplied by the per-species introduction probability. Since we only considered first records, a species ceases to be part of the source pool once it has been recorded in the Mediterranean and hence each introduction event reduces the introduction rate.

Therefore, the per-species introduction probabilities must have increased even more than the increase in introduction rate shown in our analysis.

The ecological reason for the increase of the true introduction rate of demersal species (group III) over time is unclear. This increase could have been due to repeated expansions of the Suez Canal, the change in its salinity over time, or other unknown environmental changes within the canal. It could also be due to an increase in the susceptibility of the Mediterranean to the establishment of new species, as the invasibility of an environment can be influenced by an assortment of biotic and abiotic events and processes (Davis, 2011).

The detected sharp increase in the last decade of solitary species living on hard bottom (group II, Figure 6) might be results of aquarium release events. Species that are potentially used in aquariums constitute 80% of the species in group II (i.e. 8/10) and only around 18% of the species in group I and III (i.e. 12/68). It is therefore conceivable that the recent surge in the detection of group II species is due to the increase in the trade of tropical marine species in the Middle East, rather than to environmental changes. Genetic studies that can better locate the geographic source of newly introduced alien species are likely to shed more light on this hypothesis (Bariche *et al.*, 2015).

Regardless of the underlying reasons, the recent increase in the true introduction rate of demersal species should be a cause of concern. Introduced demersal species have the potential to drastically affect sensitive Mediterranean coastal ecosystems (Sala *et al.*, 2011). Our analysis treated the first Mediterranean record as event time and therefore focused on the early stage of the introduction process. The date of collection may lag years behind the date of introduction and it could take years for an

introduced species to become established (Galil, 2008a). Therefore, we have to assume that the full ecological cost of the recent surge in introductions of demersal species is not yet apparent. Furthermore, the concentration of recent records of newly introduced species with historically low introduction rates, indicates a shift in the nature of species introductions into the Mediterranean. It is important to understand the reason for this shift, particularly in light of the further expansion of the Suez Canal. If we do not understand and mitigate the ecological risks associated with the expansion of the Suez Canal, the integrity of a large part of the Mediterranean ecosystem could be in jeopardy.

APPENDIX CHAPTERS
CHAPTER I
APPENDIX TABLES

Table 4: List of bony fishes from the Red Sea according to Golani and Bogorodsky (2010) and their status in the study. Right censored: no Mediterranean record; introduced: reported in the Mediterranean Sea.

Species	Reason for exclusion	Classification
<i>Abalistes stellatus</i>	-	right censored
<i>Ablennes hians</i>	widely distributed species	excluded
<i>Abudefduf sexfasciatus</i>	-	right censored
<i>Abudefduf sordidus</i>	-	right censored
<i>Abudefduf vaigiensis</i>	-	introduced
<i>Acanthopagrus berda</i>	-	right censored
<i>Acanthopagrus bifasciatus</i>	-	right censored
<i>Acanthurus gahhm</i>	-	right censored
<i>Acanthurus mata</i>	-	right censored
<i>Acanthurus nigrofuscus</i>	-	right censored
<i>Acanthurus sohal</i>	-	right censored
<i>Acentrogobius nebulosus</i>	-	right censored
<i>Acentronura tentaculata</i>	-	right censored
<i>Acropoma japonicum</i>	-	right censored
<i>Aeoliscus punctulatus</i>	-	right censored
<i>Aesopia cornuta</i>	-	right censored
<i>Aethaloperca rogae</i>	-	right censored
<i>Albula glossodonta</i>	-	right censored
<i>Alectis ciliaris</i>	widely distributed species	excluded
<i>Alectis indica</i>	-	right censored
<i>Alepes djedaba</i>	-	introduced
<i>Alloblennius jugularis</i>	-	right censored
<i>Alloblennius pictus</i>	-	right censored
<i>Alticus kirkii</i>	-	right censored
<i>Aluterus monoceros</i>	widely distributed species	excluded
<i>Aluterus scriptus</i>	widely distributed species	excluded
<i>Amanses scopas</i>	-	right censored
<i>Ambassis dussumieri</i>	-	right censored
<i>Ambassis urotaenia</i>	-	right censored
<i>Amblyeleotris diagonalis</i>	-	right censored
<i>Amblyeleotris neglecta</i>	-	right censored

<i>Amblyeleotris steinitzi</i>	-	right censored
<i>Amblyeleotris sungami</i>	-	right censored
<i>Amblyeleotris triguttata</i>	-	right censored
<i>Amblyeleotris wheeleri</i>	-	right censored
<i>Amblygaster sirm</i>	-	right censored
<i>Amblyglyphidodon flavilatus</i>	-	right censored
<i>Amblyglyphidodon indicus</i>	-	right censored
<i>Amblygobius albimaculatus</i>	-	right censored
<i>Amblygobius esakiae</i>	-	right censored
<i>Amblygobius nocturnus</i>	-	right censored
<i>Amblygobius sewardii</i>	-	right censored
<i>Amphiprion bicinctus</i>	-	right censored
<i>Anampses caeruleopunctatus</i>	-	right censored
<i>Anampses lineatus</i>	-	right censored
<i>Anampses meleagrides</i>	-	right censored
<i>Anampses twistii</i>	-	right censored
<i>Antennablennius adenensis</i>	-	right censored
<i>Antennablennius australis</i>	-	right censored
<i>Antennablennius hypenetes</i>	-	right censored
<i>Antennarius commerson</i>	-	right censored
<i>Antennarius pictus</i>	-	right censored
<i>Antennarius striatus</i>	widely distributed species	excluded
<i>Antennatus coccineus</i>	-	right censored
<i>Antennatus nummifer</i>	-	right censored
<i>Antennatus rosaceus</i>	-	right censored
<i>Anyperodon leucogrammicus</i>	-	right censored
<i>Aphanius dispar</i>	Mediterranean record prior to opening of the Suez Canal (Kornfield & Nevo, 1976)	excluded
<i>Aphareus furca</i>	-	right censored
<i>Aphareus rutilans</i>	-	right censored
<i>Apistus carinatus</i>	-	right censored
<i>Apogon bryx</i>	-	right censored
<i>Apogon campbelli</i>	-	right censored
<i>Apogon coccineus</i>	-	right censored
<i>Apogon erythrosoma</i>	-	right censored
<i>Apogon isus</i>	-	right censored
<i>Apogon multitaeniatus</i>	-	right censored
<i>Apogon pselion</i>	-	right censored
<i>Apogon queketti</i>	-	introduced
<i>Apogon semiornatus</i>	-	right censored
<i>Apogon smithi</i>	-	introduced
<i>Apogon spilurus</i>	-	right censored
<i>Apogonichthyoides heptastigma</i>	-	right censored
<i>Apogonichthyoides pharaonis</i>	-	introduced

<i>Apogonichthyoides pseudotaeniatus</i>	-	right censored
<i>Apogonichthyoides taeniatus</i>	-	right censored
<i>Apogonichthyoides timorensis</i>	-	right censored
<i>Apogonichthys perdix</i>	-	right censored
<i>Apolemichthys xanthotis</i>	-	right censored
<i>Aprion virescens</i>	-	right censored
<i>Archamia bilineata</i>	-	right censored
<i>Archamia fucata</i>	-	right censored
<i>Archamia lineolata</i>	-	right censored
<i>Arcygobius baliurus</i>	-	right censored
<i>Argyrops filamentosus</i>	-	right censored
<i>Argyrops megalommatus</i>	-	right censored
<i>Argyrops spinifer</i>	-	right censored
<i>Argyrosomus regius</i>	Atlantic and/or Mediterranean species	excluded
<i>Ariomma brevimanum</i>	-	right censored
<i>Ariomma indicum</i>	-	right censored
<i>Ariosoma sanzoi</i>	-	right censored
<i>Arnoglossus macrolophus</i>	-	right censored
<i>Arnoglossus marisrubri</i>	-	right censored
<i>Arothron diadematus</i>	-	right censored
<i>Arothron hispidus</i>	-	right censored
<i>Arothron immaculatus</i>	-	right censored
<i>Arothron reticularis</i>	-	right censored
<i>Arothron stellatus</i>	-	right censored
<i>Aseraggodes sinusarabici</i>	-	right censored
<i>Aseraggodes steinitzi</i>	-	right censored
<i>Aspidontus dussumieri</i>	-	right censored
<i>Aspidontus tractus</i>	-	right censored
<i>Asterorhombus intermedius</i>	-	right censored
<i>Asterropteryx semipunctata</i>	-	right censored
<i>Astronesthes martensii</i>	deep sea species	excluded
<i>Ateleopus natalensis</i>	deep sea species	excluded
<i>Atherinomorus forskalii</i>	-	introduced
<i>Atherinomorus lacunosus</i>	-	right censored
<i>Atrobucca geniae</i>	-	right censored
<i>Atrosalarias fuscus</i>	-	right censored
<i>Atule mate</i>	-	right censored
<i>Aulacocephalus temminckii</i>	-	right censored
<i>Aurigequula fasciata</i>	-	right censored
<i>Auxis thazard</i>	widely distributed species	excluded
<i>Balistapus undulatus</i>	-	right censored
<i>Balistoides viridescens</i>	-	right censored
<i>Barchatus cirrhosus</i>	-	right censored
<i>Bathygobius cyclopterus</i>	-	right censored

<i>Bathygobius fuscus</i>	-	right censored
<i>Bembrops caudimacula</i>	deep sea species	excluded
<i>Benthoosema pterotum</i>	deep sea species	excluded
<i>Blenniella periophthalmus</i>	-	right censored
<i>Bodianus anthioides</i>	-	right censored
<i>Bodianus axillaris</i>	-	right censored
<i>Bodianus diana</i>	-	right censored
<i>Bodianus opercularis</i>	-	right censored
<i>Bodianus trilineatus</i>	-	right censored
<i>Bolbometopon muricatum</i>	-	right censored
<i>Bothus pantherinus</i>	-	right censored
<i>Brachaluteres fahaqa</i>	-	right censored
<i>Brachypterois serrulata</i>	-	right censored
<i>Brachysomophis cirrocheilos</i>	-	right censored
<i>Branchiostegus sawakinensis</i>	-	right censored
<i>Bregmaceros arabicus</i>	-	right censored
<i>Brosomphyciops pautzkei</i>	-	right censored
<i>Brotula multibarbata</i>	-	right censored
<i>Bryaninops natans</i>	-	right censored
<i>Bryaninops ridens</i>	-	right censored
<i>Bryaninops yongei</i>	-	right censored
<i>Bryx analicarens</i>	-	right censored
<i>Caesio caeruleaurea</i>	-	right censored
<i>Caesio lunaris</i>	-	right censored
<i>Caesio striata</i>	-	right censored
<i>Caesio suevica</i>	-	right censored
<i>Caesio varilineata</i>	-	right censored
<i>Caesio xanthonota</i>	-	right censored
<i>Callechelys catostoma</i>	-	right censored
<i>Callechelys marmorata</i>	-	right censored
<i>Callionymus bentuviai</i>	-	right censored
<i>Callionymus delicatulus</i>	-	right censored
<i>Callionymus erythraeus</i>	-	right censored
<i>Callionymus filamentosus</i>	-	introduced
<i>Callionymus flavus</i>	-	right censored
<i>Callionymus gardineri</i>	-	right censored
<i>Callionymus muscatensis</i>	-	right censored
<i>Callionymus oxycephalus</i>	-	right censored
<i>Callogobius amikami</i>	-	right censored
<i>Callogobius bifasciatus</i>	-	right censored
<i>Callogobius dori</i>	-	right censored
<i>Callogobius flavobrunneus</i>	-	right censored
<i>Callogobius maculipinnis</i>	-	right censored
<i>Calloplelesiops altivelis</i>	-	right censored

<i>Calotomus viridescens</i>	-	right censored
<i>Cantherhines pardalis</i>	-	right censored
<i>Canthidermis macrolepis</i>	-	right censored
<i>Canthigaster cyanospilota</i>	-	right censored
<i>Canthigaster margaritata</i>	-	right censored
<i>Canthigaster pygmaea</i>	-	right censored
<i>Carangoides armatus</i>	-	right censored
<i>Carangoides bajad</i>	-	right censored
<i>Carangoides chrysophrys</i>	-	right censored
<i>Carangoides coeruleopinnatus</i>	-	right censored
<i>Carangoides equula</i>	-	right censored
<i>Carangoides ferdau</i>	-	right censored
<i>Carangoides fulvoguttatus</i>	-	right censored
<i>Carangoides plagiotaenia</i>	-	right censored
<i>Caranx heberi</i>	-	right censored
<i>Caranx ignobilis</i>	-	right censored
<i>Caranx melampygyus</i>	-	right censored
<i>Caranx sexfasciatus</i>	-	right censored
<i>Carapus mourlani</i>	-	right censored
<i>Centropyge multispinis</i>	-	right censored
<i>Cephalopholis argus</i>	-	right censored
<i>Cephalopholis hemistiktos</i>	-	right censored
<i>Cephalopholis miniata</i>	-	right censored
<i>Cephalopholis oligosticta</i>	-	right censored
<i>Cephalopholis sexmaculata</i>	-	right censored
<i>Cercamia eremia</i>	-	right censored
<i>Cetoscarus bicolor</i>	-	right censored
<i>Chaetodon auriga</i>	-	right censored
<i>Chaetodon austriacus</i>	-	introduced
<i>Chaetodon fasciatus</i>	-	right censored
<i>Chaetodon larvatus</i>	-	introduced
<i>Chaetodon leucopleura</i>	-	right censored
<i>Chaetodon lineolatus</i>	-	right censored
<i>Chaetodon melannotus</i>	-	right censored
<i>Chaetodon melapterus</i>	-	right censored
<i>Chaetodon mesoleucos</i>	-	right censored
<i>Chaetodon paucifasciatus</i>	-	right censored
<i>Chaetodon pictus</i>	-	right censored
<i>Chaetodon semilarvatus</i>	-	right censored
<i>Chaetodon trifascialis</i>	-	right censored
<i>Champsodon capensis</i>	-	right censored
<i>Champsodon omanensis</i>	-	right censored
<i>Chanos chanos</i>	-	introduced
<i>Cheilinus abudjubbe</i>	-	right censored

<i>Cheilinus fasciatus</i>	-	right censored
<i>Cheilinus lunulatus</i>	-	right censored
<i>Cheilinus undulatus</i>	-	right censored
<i>Cheilio inermis</i>	-	right censored
<i>Cheilodipterus arabicus</i>	-	right censored
<i>Cheilodipterus lachneri</i>	-	right censored
<i>Cheilodipterus macrodon</i>	-	right censored
<i>Cheilodipterus novemstriatus</i>	-	introduced
<i>Cheilodipterus pygmaios</i>	-	right censored
<i>Cheilodipterus quinquelineatus</i>	-	right censored
<i>Cheilopogon cyanopterus</i>	-	right censored
<i>Cheimerius nufar</i>	-	right censored
<i>Chelidoperca pleurospilus</i>	-	right censored
<i>Chelon planiceps</i>	-	right censored
<i>Chelon subviridis</i>	-	right censored
<i>Chirocentrus dorab</i>	-	right censored
<i>Chirocentrus nudus</i>	-	right censored
<i>Chlidichthys auratus</i>	-	right censored
<i>Chlidichthys rubiceps</i>	-	right censored
<i>Chlorurus genazonatus</i>	-	right censored
<i>Chlorurus gibbus</i>	-	right censored
<i>Chlorurus sordidus</i>	-	right censored
<i>Choerodon robustus</i>	-	right censored
<i>Choeroichthys brachysoma</i>	-	right censored
<i>Choridactylus multibarbus</i>	-	right censored
<i>Chromis dimidiata</i>	-	right censored
<i>Chromis flavaxilla</i>	-	right censored
<i>Chromis pelloura</i>	-	right censored
<i>Chromis pembrae</i>	-	right censored
<i>Chromis trialpha</i>	-	right censored
<i>Chromis viridis</i>	-	right censored
<i>Chromis weberi</i>	-	right censored
<i>Chrysiptera annulata</i>	-	right censored
<i>Chrysiptera unimaculata</i>	-	right censored
<i>Cirrhilabrus blatteus</i>	-	right censored
<i>Cirrhilabrus rubriventralis</i>	-	right censored
<i>Cirrhimuraena playfairii</i>	-	right censored
<i>Cirrhitichthys oxycephalus</i>	-	right censored
<i>Cirrhitus pinnulatus</i>	-	right censored
<i>Cirripectes castaneus</i>	-	right censored
<i>Cirripectes filamentosus</i>	-	right censored
<i>Cociella punctata</i>	-	right censored
<i>Cocotropus steinitzi</i>	-	right censored
<i>Conger cinereus</i>	-	right censored

<i>Congresox talabonoides</i>	-	right censored
<i>Coris aygula</i>	-	right censored
<i>Coris caudimacula</i>	-	right censored
<i>Coris cuvieri</i>	-	right censored
<i>Coris formosa</i>	-	right censored
<i>Coris variegata</i>	-	right censored
<i>Coryogalops anomolus</i>	-	right censored
<i>Coryogalops ocheticus</i>	-	introduced
<i>Coryphaena hippurus</i>	widely distributed species	excluded
<i>Coryphopterus humeralis</i>	-	right censored
<i>Corythoichthys flavofasciatus</i>	-	right censored
<i>Corythoichthys nigripectus</i>	-	right censored
<i>Corythoichthys schultzi</i>	-	right censored
<i>Cosmocampus banneri</i>	-	right censored
<i>Cosmocampus maxweberi</i>	-	right censored
<i>Crenidens crenidens</i>	-	introduced
<i>Crenimugil crenilabis</i>	-	right censored
<i>Cryptocentroides arabicus</i>	-	right censored
<i>Cryptocentrus caeruleopunctatus</i>	-	right censored
<i>Cryptocentrus cryptocentrus</i>	-	right censored
<i>Cryptocentrus fasciatus</i>	-	right censored
<i>Cryptocentrus lutheri</i>	-	right censored
<i>Ctenochaetus striatus</i>	-	right censored
<i>Ctenogobiops crocineus</i>	-	right censored
<i>Ctenogobiops feroculus</i>	-	right censored
<i>Ctenogobiops maculosus</i>	-	right censored
<i>Cylichthys orbicularis</i>	-	right censored
<i>Cylichthys spilostylus</i>	-	introduced
<i>Cynoglossus acutirostris</i>	-	right censored
<i>Cynoglossus bilineatus</i>	-	right censored
<i>Cynoglossus dollfusi</i>	-	right censored
<i>Cynoglossus lachneri</i>	-	right censored
<i>Cynoglossus lingua</i>	-	right censored
<i>Cynoglossus pottii</i>	-	right censored
<i>Cynoglossus sinusarabici</i>	-	introduced
<i>Cypselurus hexazona</i>	-	right censored
<i>Dactyloptena orientalis</i>	-	right censored
<i>Dactyloptena peterseni</i>	-	right censored
<i>Dascyllus aruanus</i>	-	right censored
<i>Dascyllus marginatus</i>	-	right censored
<i>Dascyllus trimaculatus</i>	-	right censored
<i>Decapterus macarellus</i>	widely distributed species	excluded
<i>Decapterus macrosoma</i>	-	right censored
<i>Decapterus russelli</i>	-	introduced

<i>Dendrochirus brachypterus</i>	-	right censored
<i>Dendrochirus zebra</i>	-	right censored
<i>Dermatolepis striolata</i>	-	right censored
<i>Diagramma punctatum</i>	-	right censored
<i>Diaphus coeruleus</i>	deep sea species	excluded
<i>Dicentrarchus labrax</i>	Atlantic and/or Mediterranean species	excluded
<i>Dicentrarchus punctatus</i>	Atlantic and/or Mediterranean species	excluded
<i>Dinematichthys iluocoeteoides</i>	-	right censored
<i>Diodon hystrix</i>	widely distributed species	excluded
<i>Diodon liturosus</i>	-	right censored
<i>Diploconger polystigmatus</i>	-	right censored
<i>Diplodus noct</i>	-	right censored
<i>Diplogrammus gruveli</i>	-	right censored
<i>Diplogrammus infulatus</i>	-	right censored
<i>Diplogrammus randalli</i>	-	right censored
<i>Diploprion drachi</i>	-	right censored
<i>Discordipinna griessingeri</i>	-	right censored
<i>Doryrhamphus excisus abbreviatus</i>	-	right censored
<i>Drepane longimana</i>	-	right censored
<i>Dunckerocampus boylei</i>	-	right censored
<i>Dunckerocampus multiannulatus</i>	-	right censored
<i>Dussumieria elopsoides</i>	-	introduced
<i>Dysomma fuscoventralis</i>	deep sea species	excluded
<i>Echeneis naucrates</i>	widely distributed species	excluded
<i>Echidna nebulosa</i>	-	right censored
<i>Echidna polyzona</i>	-	right censored
<i>Ecsenius aroni</i>	-	right censored
<i>Ecsenius dentex</i>	-	right censored
<i>Ecsenius frontalis</i>	-	right censored
<i>Ecsenius gravieri</i>	-	right censored
<i>Ecsenius midas</i>	-	right censored
<i>Elagatis bipinnulata</i>	widely distributed species	excluded
<i>Ellochelon vaigiensis</i>	-	right censored
<i>Elops machnata</i>	-	right censored
<i>Encheliophis gracilis</i>	-	right censored
<i>Encheliophis homei</i>	-	right censored
<i>Enchelycore bayeri</i>	-	right censored
<i>Enchelycore schismatorhynchus</i>	-	right censored
<i>Enchelyurus kraussii</i>	-	right censored
<i>Enchelyurus petersi</i>	-	right censored
<i>Encrasicholina heteroloba</i>	-	right censored
<i>Encrasicholina punctifer</i>	-	right censored
<i>Engraulis encrasicolus</i>	Atlantic and/or Mediterranean species	excluded
<i>Engyprosopon grandisquama</i>	-	right censored

<i>Engyprosopon hureaui</i>	-	right censored
<i>Engyprosopon latifrons</i>	-	right censored
<i>Engyprosopon macrolepis</i>	-	right censored
<i>Enneapterygius abeli</i>	-	right censored
<i>Enneapterygius clarkae</i>	-	right censored
<i>Enneapterygius destai</i>	-	right censored
<i>Enneapterygius obscurus</i>	-	right censored
<i>Enneapterygius pallidus</i>	-	right censored
<i>Enneapterygius pusillus</i>	-	right censored
<i>Enneapterygius tutuilae</i>	-	right censored
<i>Enneapterygius ventermaculus</i>	-	right censored
<i>Epibulus insidiator</i>	-	right censored
<i>Epigonus marisrubri</i>	-	right censored
<i>Epinephelus areolatus</i>	-	right censored
<i>Epinephelus chlorostigma</i>	-	right censored
<i>Epinephelus coioides</i>	-	introduced
<i>Epinephelus epistictus</i>	-	right censored
<i>Epinephelus fasciatus</i>	-	introduced
<i>Epinephelus fuscoguttatus</i>	-	right censored
<i>Epinephelus lanceolatus</i>	-	right censored
<i>Epinephelus latifasciatus</i>	-	right censored
<i>Epinephelus malabaricus</i>	-	introduced
<i>Epinephelus morrhua</i>	-	right censored
<i>Epinephelus polyphkadion</i>	-	right censored
<i>Epinephelus radiatus</i>	-	right censored
<i>Epinephelus stoliczkae</i>	-	right censored
<i>Epinephelus summana</i>	-	right censored
<i>Epinephelus tauvina</i>	-	right censored
<i>Epinephelus tukula</i>	-	right censored
<i>Equulites klunzingeri</i>	-	introduced
<i>Etrumeus golanii</i>	-	introduced
<i>Eubleekeria splendens</i>	-	right censored
<i>Euleptorhamphus viridis</i>	-	right censored
<i>Eurypegasmus draconis</i>	-	right censored
<i>Euthynnus affinis</i>	-	right censored
<i>Eviota distigma</i>	-	right censored
<i>Eviota guttata</i>	-	right censored
<i>Eviota pardalota</i>	-	right censored
<i>Eviota prasina</i>	-	right censored
<i>Eviota sebreei</i>	-	right censored
<i>Eviota zebrina</i>	-	right censored
<i>Exallias brevis</i>	-	right censored
<i>Exyrias belissimus</i>	-	right censored
<i>Facciolella karreri</i>	deep sea species	excluded

<i>Facciolella saurecheloides</i>	deep sea species	excluded
<i>Favonigobius melanobranchus</i>	-	right censored
<i>Favonigobius reichei</i>	-	right censored
<i>Feia nympha</i>	-	right censored
<i>Fistularia commersonii</i>	-	introduced
<i>Fistularia petimba</i>	widely distributed species	excluded
<i>Foa fo</i>	-	right censored
<i>Forcipiger flavissimus</i>	-	right censored
<i>Fowleria aurita</i>	-	right censored
<i>Fowleria isostigma</i>	-	right censored
<i>Fowleria marmorata</i>	-	right censored
<i>Fowleria vaiulae</i>	-	right censored
<i>Fowleria variegata</i>	-	right censored
<i>Fusigobius longispinus</i>	-	right censored
<i>Fusigobius maximus</i>	-	right censored
<i>Fusigobius neophytus</i>	-	right censored
<i>Gazza minuta</i>	-	right censored
<i>Genicanthus caudovittatus</i>	-	right censored
<i>Gerres filamentosus</i>	-	right censored
<i>Gerres longirostris</i>	-	right censored
<i>Gerres macracanthus</i>	-	right censored
<i>Gerres oblongus</i>	-	right censored
<i>Gerres oyena</i>	-	right censored
<i>Gladiogobius rex</i>	-	right censored
<i>Glossogobius giuris</i>	-	right censored
<i>Gnathanodon speciosus</i>	-	right censored
<i>Gnatholepis anjerensis</i>	-	right censored
<i>Gobiodon citrinus</i>	-	right censored
<i>Gobiodon histrio</i>	-	right censored
<i>Gobiodon prolixus</i>	-	right censored
<i>Gobiodon reticulatus</i>	-	right censored
<i>Gobiodon rivulatus</i>	-	right censored
<i>Gobius cobitis</i>	Atlantic and/or Mediterranean species	excluded
<i>Gobius paganellus</i>	Atlantic and/or Mediterranean species	excluded
<i>Gomphosus caeruleus</i>	-	right censored
<i>Gorgasia sillneri</i>	-	right censored
<i>Grammatobothus krempfi</i>	-	right censored
<i>Grammatorcynus bilineatus</i>	-	right censored
<i>Grammistes sexlineatus</i>	-	right censored
<i>Grammonus robustus</i>	-	right censored
<i>Grammoplites suppositus</i>	-	right censored
<i>Gunnellichthys monostigma</i>	-	right censored
<i>Gymnapogon melanogaster</i>	-	right censored
<i>Gymnocaesio gymnoptera</i>	-	right censored

<i>Gymnocranius grandoculis</i>	-	right censored
<i>Gymnomuraena zebra</i>	-	right censored
<i>Gymnosarda unicolor</i>	-	right censored
<i>Gymnothorax angusticauda</i>	-	right censored
<i>Gymnothorax atollii</i>	-	right censored
<i>Gymnothorax baranesi</i>	-	right censored
<i>Gymnothorax buroensis</i>	-	right censored
<i>Gymnothorax elegans</i>	-	right censored
<i>Gymnothorax favagineus</i>	-	right censored
<i>Gymnothorax flavimarginatus</i>	-	right censored
<i>Gymnothorax griseus</i>	-	right censored
<i>Gymnothorax hepaticus</i>	-	right censored
<i>Gymnothorax javanicus</i>	-	right censored
<i>Gymnothorax johnsoni</i>	-	right censored
<i>Gymnothorax moluccensis</i>	-	right censored
<i>Gymnothorax nudivomer</i>	-	right censored
<i>Gymnothorax pictus</i>	-	right censored
<i>Gymnothorax pindae</i>	-	right censored
<i>Gymnothorax pseudoherrei</i>	-	right censored
<i>Gymnothorax punctatus</i>	-	right censored
<i>Gymnothorax randalli</i>	-	right censored
<i>Gymnothorax reticularis</i>	-	introduced
<i>Gymnothorax rueppelliae</i>	-	right censored
<i>Gymnothorax undulatus</i>	-	right censored
<i>Halicampus dunckeri</i>	-	right censored
<i>Halicampus macrorhynchus</i>	-	right censored
<i>Halicampus mataafae</i>	-	right censored
<i>Halichoeres hortulanus</i>	-	right censored
<i>Halichoeres iridis</i>	-	right censored
<i>Halichoeres marginatus</i>	-	right censored
<i>Halichoeres nebulosus</i>	-	right censored
<i>Halichoeres scapularis</i>	-	right censored
<i>Halichoeres zeylonicus</i>	-	right censored
<i>Haliophis guttatus</i>	-	right censored
<i>Harpadon erythraeus</i>	-	right censored
<i>Hazeus elati</i>	-	right censored
<i>Helcogramma obtusirostris</i>	-	right censored
<i>Helcogramma steinitzi</i>	-	right censored
<i>Hemigymnus fasciatus</i>	-	right censored
<i>Hemigymnus melapterus</i>	-	right censored
<i>Hemiramphus convexus</i>	-	right censored
<i>Hemiramphus far</i>	-	introduced
<i>Hemiramphus marginatus</i>	-	right censored
<i>Heniochus diphreutes</i>	-	right censored

<i>Heniochus intermedius</i>	-	introduced
<i>Herklotsichthys punctatus</i>	-	introduced
<i>Herklotsichthys quadrimaculatus</i>	-	right censored
<i>Heteroleotris bipunctata</i>	-	right censored
<i>Heteroleotris diademata</i>	-	right censored
<i>Heteroleotris vulgaris</i>	-	right censored
<i>Heteroconger balteatus</i>	-	right censored
<i>Hippichthys cyanospilos</i>	-	right censored
<i>Hippichthys spicifer</i>	-	right censored
<i>Hippocampus debelius</i>	-	right censored
<i>Hippocampus fuscus</i>	-	introduced
<i>Hippocampus jayakari</i>	-	right censored
<i>Hippocampus suzensis</i>	-	right censored
<i>Hipposcarus harid</i>	-	right censored
<i>Hirculops cornifer</i>	-	right censored
<i>Histiopterus typus</i>	-	right censored
<i>Histrion histrio</i>	-	right censored
<i>Hologymnosus annulatus</i>	-	right censored
<i>Hologymnosus doliatus</i>	-	right censored
<i>Hoplolatilus geo</i>	-	right censored
<i>Hoplolatilus oreni</i>	-	right censored
<i>Hoplostethus marisrubri</i>	deep sea species	excluded
<i>Hypoatherina temminckii</i>	-	right censored
<i>Hyporhamphus affinis</i>	-	introduced
<i>Hyporhamphus balinensis</i>	-	right censored
<i>Hyporhamphus gamberur</i>	-	right censored
<i>Iniistius baldwini</i>	-	right censored
<i>Iniistius bimaculatus</i>	-	right censored
<i>Iniistius pavo</i>	-	introduced
<i>Iniistius pentadactylus</i>	-	right censored
<i>Inimicus filamentosus</i>	-	right censored
<i>Istiblennius edentulus</i>	-	right censored
<i>Istiblennius flaviumbrinus</i>	-	right censored
<i>Istiblennius pox</i>	-	right censored
<i>Istiblennius rivulatus</i>	-	right censored
<i>Istiblennius unicolor</i>	-	right censored
<i>Istigobius decoratus</i>	-	right censored
<i>Istigobius ornatus</i>	-	right censored
<i>Istiophorus platypterus</i>	-	right censored
<i>Katsuwonus pelamis</i>	widely distributed species	excluded
<i>Koumansetta hectori</i>	-	right censored
<i>Kraemeria samoensis</i>	-	right censored
<i>Kuhlia mugil</i>	-	right censored
<i>Kyonemichthys rumengani</i>	-	right censored

<i>Kyphosus bigibbus</i>	-	right censored
<i>Kyphosus cinerascens</i>	-	right censored
<i>Kyphosus vaigiensis</i>	-	right censored
<i>Labroides dimidiatus</i>	-	right censored
<i>Lactoria cornuta</i>	-	right censored
<i>Lagocephalus lunaris</i>	-	right censored
<i>Lagocephalus scleratus</i>	-	introduced
<i>Lagocephalus spadiceus</i>	-	introduced
<i>Lagocephalus suezensis</i>	-	introduced
<i>Larabicus quadrilineatus</i>	-	right censored
<i>Leiognathus equulus</i>	-	right censored
<i>Leiognathus oblongus</i>	-	right censored
<i>Lepadichthys erythraeus</i>	-	right censored
<i>Lepadichthys lineatus</i>	-	right censored
<i>Lepidotrigla bispinosa</i>	-	right censored
<i>Lepidotrigla spiloptera</i>	-	right censored
<i>Leptoscarus vaigiensis</i>	-	right censored
<i>Lestidiops jayakari</i>	widely distributed and deep sea species	excluded
<i>Lestrolepis luetkeni</i>	-	right censored
<i>Lethrinus borbonicus</i>	-	right censored
<i>Lethrinus harak</i>	-	right censored
<i>Lethrinus lentjan</i>	-	right censored
<i>Lethrinus mahsena</i>	-	right censored
<i>Lethrinus microdon</i>	-	right censored
<i>Lethrinus nebulosus</i>	-	right censored
<i>Lethrinus obsoletus</i>	-	right censored
<i>Lethrinus olivaceus</i>	-	right censored
<i>Lethrinus variegatus</i>	-	right censored
<i>Lethrinus xanthochilus</i>	-	right censored
<i>Limnichthys nitidus</i>	-	right censored
<i>Liopropoma lunulatum</i>	-	right censored
<i>Liopropoma mitratum</i>	-	right censored
<i>Liopropoma susumi</i>	-	right censored
<i>Liparis fishelsoni</i>	-	right censored
<i>Lissocampus bannwarthi</i>	-	right censored
<i>Liza carinata</i>	-	introduced
<i>Lobotes surinamensis</i>	widely distributed species	excluded
<i>Lophiomus setigerus</i>	-	right censored
<i>Lotilia graciliosa</i>	-	right censored
<i>Luposicya lupus</i>	-	right censored
<i>Lutjanus argentimaculatus</i>	-	introduced
<i>Lutjanus bengalensis</i>	-	right censored
<i>Lutjanus bohar</i>	-	right censored
<i>Lutjanus coeruleolineatus</i>	-	right censored

<i>Lutjanus ehrenbergii</i>	-	right censored
<i>Lutjanus fulviflamma</i>	-	right censored
<i>Lutjanus fulvus</i>	-	right censored
<i>Lutjanus gibbus</i>	-	right censored
<i>Lutjanus kasmira</i>	-	right censored
<i>Lutjanus lutjanus</i>	-	right censored
<i>Lutjanus monostigma</i>	-	right censored
<i>Lutjanus rivulatus</i>	-	right censored
<i>Lutjanus russellii</i>	-	right censored
<i>Lutjanus sanguineus</i>	-	right censored
<i>Lutjanus sebae</i>	-	right censored
<i>Macolor niger</i>	-	right censored
<i>Macrodonotogobius wilburi</i>	-	right censored
<i>Macropharyngodon marisrubri</i>	-	right censored
<i>Malacanthus brevirostris</i>	-	right censored
<i>Malacanthus latovittatus</i>	-	right censored
<i>Masturus lanceolatus</i>	widely distributed species	excluded
<i>Mauroliticus mucronatus</i>	deep sea species	excluded
<i>Megalaspis cordyla</i>	-	right censored
<i>Megalops cyprinoides</i>	-	right censored
<i>Meiacanthus nigrolineatus</i>	-	right censored
<i>Microbrotula bentleyi</i>	-	right censored
<i>Micrognathus andersonii</i>	-	right censored
<i>Micrognathus brevirostris</i>	-	right censored
<i>brevirostris</i>		
<i>Mimoblennius cirrosus</i>	-	right censored
<i>Minilabrus striatus</i>	-	right censored
<i>Minous coccineus</i>	-	right censored
<i>Minous monodactylus</i>	-	right censored
<i>Mola mola</i>	widely distributed species	excluded
<i>Monocentris japonica</i>	-	right censored
<i>Monodactylus argenteus</i>	-	right censored
<i>Monotaxis grandoculis</i>	-	right censored
<i>Moolgarda cunnesius</i>	-	right censored
<i>Moolgarda seheli</i>	-	right censored
<i>Mugil cephalus</i>	widely distributed species	excluded
<i>Mulloidichthys flavolineatus</i>	-	right censored
<i>Mulloidichthys vanicolensis</i>	-	right censored
<i>Muraena helena</i>	Atlantic and/or Mediterranean species	excluded
<i>Muraenesox cinereus</i>	-	introduced
<i>Muraenichthys schultzei</i>	-	right censored
<i>Myrichthys colubrinus</i>	-	right censored
<i>Myrichthys maculosus</i>	-	right censored
<i>Myripristis chryseres</i>	-	right censored
<i>Myripristis murdjan</i>	-	right censored

<i>Myripristis xanthacra</i>	-	right censored
<i>Myrophis microchir</i>	-	right censored
<i>Naso annulatus</i>	-	right censored
<i>Naso brevirostris</i>	-	right censored
<i>Naso elegans</i>	-	right censored
<i>Naso hexacanthus</i>	-	right censored
<i>Naso unicornis</i>	-	right censored
<i>Naucrates ductor</i>	widely distributed species	excluded
<i>Neamia octospina</i>	-	right censored
<i>Nectamia annularis</i>	-	right censored
<i>Nectamia fusca</i>	-	right censored
<i>Nectamia zebrinus</i>	-	right censored
<i>Neenchelys microtretus</i>	-	right censored
<i>Nemateleotris decora</i>	-	right censored
<i>Nemipterus bipunctatus</i>	-	right censored
<i>Nemipterus japonicus</i>	-	right censored
<i>Nemipterus peronii</i>	-	right censored
<i>Nemipterus randalli</i>	-	introduced
<i>Nemipterus zysron</i>	-	right censored
<i>Neobythites stefanovi</i>	deep sea species	excluded
<i>Neocentropogon mesedai</i>	-	right censored
<i>Neoglyphidodon melas</i>	-	right censored
<i>Neomerinthe bathyperimensis</i>	-	right censored
<i>Neoniphon sammara</i>	-	right censored
<i>Neopomacentrus cyanomos</i>	-	right censored
<i>Neopomacentrus miryae</i>	-	right censored
<i>Neopomacentrus xanthurus</i>	-	right censored
<i>Netuma thalassina</i>	-	right censored
<i>Norfolkia brachylepis</i>	-	right censored
<i>Novaculichthys taeniourus</i>	-	right censored
<i>Novaculoides macrolepidotus</i>	-	right censored
<i>Obliquogobius turkayi</i>	-	right censored
<i>Odonus niger</i>	-	right censored
<i>Oedalechilus labiosus</i>	-	right censored
<i>Omobranchus fasciolatus</i>	-	right censored
<i>Omobranchus punctatus</i>	-	introduced
<i>Omobranchus steinitzi</i>	-	right censored
<i>Onigocia bimaculata</i>	-	right censored
<i>Ophichthus echeloides</i>	-	right censored
<i>Ophichthus erabo</i>	-	right censored
<i>Ophidion smithi</i>	deep sea species	excluded
<i>Opistognathus nigromarginatus</i>	-	right censored
<i>Oplopomus oplopomus</i>	-	right censored
<i>Ostichthys acanthorhinus</i>	-	right censored

<i>Ostichthys hypsipterygion</i>	-	right censored
<i>Ostorhinchus apogonoides</i>	-	right censored
<i>Ostorhinchus cookii</i>	-	right censored
<i>Ostorhinchus cyanosoma</i>	-	right censored
<i>Ostorhinchus fasciatus</i>	-	introduced
<i>Ostorhinchus fleurieu</i>	-	right censored
<i>Ostorhinchus gularis</i>	-	right censored
<i>Ostorhinchus nigrofasciatus</i>	-	right censored
<i>Ostorhinchus talboti</i>	-	right censored
<i>Ostracion cubicus</i>	-	introduced
<i>Ostracion cyanurus</i>	-	right censored
<i>Oxycheilinus arenatus</i>	-	right censored
<i>Oxycheilinus digramma</i>	-	right censored
<i>Oxycheilinus mentalis</i>	-	right censored
<i>Oxycheilinus orientalis</i>	-	right censored
<i>Oxycirrhites typus</i>	-	right censored
<i>Oxymonacanthus halli</i>	-	right censored
<i>Oxyurichthys petersi</i>	-	introduced
<i>Palutrus scapulopunctatus</i>	-	right censored
<i>Papilloculiceps longiceps</i>	-	introduced
<i>Parablennius cyclops</i>	-	right censored
<i>Parabothus budkeri</i>	-	right censored
<i>Paracaesio sordida</i>	-	right censored
<i>Paracheilinus octotaenia</i>	-	right censored
<i>Paracirrhites forsteri</i>	-	right censored
<i>Paragobiodon echinocephalus</i>	-	right censored
<i>Paragobiodon xanthosoma</i>	-	right censored
<i>Paragunnellichthys springeri</i>	-	right censored
<i>Paraluteres arqat</i>	-	right censored
<i>Paramonacanthus nematophorus</i>	-	right censored
<i>Paramonacanthus pusillus</i>	-	right censored
<i>Parapercis hexophtalma</i>	-	right censored
<i>Parapercis simulata</i>	-	right censored
<i>Parapercis somaliensis</i>	-	right censored
<i>Paraplagusia bilineata</i>	-	right censored
<i>Parapriacanthus ransonneti</i>	-	right censored
<i>Parascolopsis aspinosa</i>	-	right censored
<i>Parascolopsis baranesi</i>	-	right censored
<i>Parascolopsis eriomma</i>	-	right censored
<i>Parascorpaena aurita</i>	-	right censored
<i>Pardachirus marmoratus</i>	-	right censored
<i>Parexocoetus brachypterus</i>	-	right censored
<i>Parexocoetus mento</i>	-	introduced
<i>Parupeneus cyclostomus</i>	-	right censored

<i>Parupeneus forsskali</i>	-	introduced
<i>Parupeneus heptacanthus</i>	-	right censored
<i>Parupeneus macronemus</i>	-	right censored
<i>Parupeneus rubescens</i>	-	right censored
<i>Pectinochromis lubbocki</i>	-	right censored
<i>Pelates quadrilineatus</i>	-	introduced
<i>Pempheris rhomboidea</i>	-	introduced
<i>Pempheris schwenkii</i>	-	right censored
<i>Periophthalmus argentilineatus</i>	-	right censored
<i>Periophthalmus kalolo</i>	-	right censored
<i>Pervagor randalli</i>	-	right censored
<i>Petroscirtes ancylodon</i>	-	introduced
<i>Petroscirtes mitratus</i>	-	right censored
<i>Phaenomonas cooperae</i>	-	right censored
<i>Photoblepharon steinitzi</i>	deep sea species	excluded
<i>Photopectoralis bindus</i>	-	right censored
<i>Phoxocampus belcheri</i>	-	right censored
<i>Phyllophichthus xenodontus</i>	-	right censored
<i>Physiculus marisrubri</i>	-	right censored
<i>Pisodonophis cancrivorus</i>	-	right censored
<i>Plagiotremus rhinorhynchus</i>	-	right censored
<i>Plagiotremus tapeinosoma</i>	-	right censored
<i>Plagiotremus townsendi</i>	-	right censored
<i>Platax orbicularis</i>	-	right censored
<i>Platax teira</i>	-	introduced
<i>Platybelone argalus platura</i>	-	right censored
<i>Platycephalus indicus</i>	-	introduced
<i>Plectorhinchus albovittatus</i>	-	right censored
<i>Plectorhinchus flavomaculatus</i>	-	right censored
<i>Plectorhinchus gaterinus</i>	-	right censored
<i>Plectorhinchus gibbosus</i>	-	right censored
<i>Plectorhinchus schotaf</i>	-	right censored
<i>Plectorhinchus sordidus</i>	-	right censored
<i>Plectranthias klausewitzi</i>	-	right censored
<i>Plectranthias nanus</i>	-	right censored
<i>Plectranthias winniensis</i>	-	right censored
<i>Plectroglyphidodon lacrymatus</i>	-	right censored
<i>Plectroglyphidodon leucozonus</i>	-	right censored
<i>Plectropomus areolatus</i>	-	right censored
<i>Plectropomus pessuliferus</i>	-	right censored
<i>Plesiops coeruleolineatus</i>	-	right censored
<i>Plesiops mystaxus</i>	-	right censored
<i>Plesiops nigricans</i>	-	right censored
<i>Pleurosicya micheli</i>	-	right censored

<i>Pleurosicya mossambica</i>	-	right censored
<i>Pleurosicya plicata</i>	-	right censored
<i>Pleurosicya prognatha</i>	-	right censored
<i>Plotosus lineatus</i>	-	introduced
<i>Polysteganus coeruleopunctatus</i>	-	right censored
<i>Pomacanthus asfur</i>	-	right censored
<i>Pomacanthus imperator</i>	-	introduced
<i>Pomacanthus maculosus</i>	-	introduced
<i>Pomacentrus albicaudatus</i>	-	right censored
<i>Pomacentrus aquilus</i>	-	right censored
<i>Pomacentrus leptus</i>	-	right censored
<i>Pomacentrus sulfureus</i>	-	right censored
<i>Pomacentrus trichrourus</i>	-	right censored
<i>Pomacentrus trilineatus</i>	-	right censored
<i>Pomadasyys argenteus</i>	-	right censored
<i>Pomadasyys kaakan</i>	-	right censored
<i>Pomadasyys punctulatus</i>	-	right censored
<i>Pomadasyys stridens</i>	-	introduced
<i>Priacanthus blochii</i>	-	right censored
<i>Priacanthus hamrur</i>	-	right censored
<i>Priacanthus sagittarius</i>	-	introduced
<i>Priolepis cincta</i>	-	right censored
<i>Priolepis goldshmidtae</i>	-	right censored
<i>Priolepis randalli</i>	-	right censored
<i>Priolepis semidoliata</i>	-	right censored
<i>Pristiapogon exostigma</i>	-	right censored
<i>Pristiapogon fraenatus</i>	-	right censored
<i>Pristiapogon kallopterus</i>	-	right censored
<i>Pristigenys niphonia</i>	-	right censored
<i>Pristipomoides filamentosus</i>	-	right censored
<i>Pristipomoides multidentis</i>	-	right censored
<i>Pristipomoides sieboldii</i>	-	right censored
<i>Pristotis cyanostigma</i>	-	right censored
<i>Pristotis obtusirostris</i>	-	right censored
<i>Psettodes erumei</i>	-	right censored
<i>Pseudamia gelatinosa</i>	-	right censored
<i>Pseudanthias fasciatus</i>	-	right censored
<i>Pseudanthias heemstrai</i>	-	right censored
<i>Pseudanthias lunulatus</i>	-	right censored
<i>Pseudanthias squamipinnis</i>	-	right censored
<i>Pseudanthias taeniatus</i>	-	right censored
<i>Pseudobalistes flavimarginatus</i>	-	right censored
<i>Pseudobalistes fuscus</i>	-	right censored
<i>Pseudocheilinus evanidus</i>	-	right censored

<i>Pseudocheilinus hexataenia</i>	-	right censored
<i>Pseudochromis dixurus</i>	-	right censored
<i>Pseudochromis flavivertex</i>	-	right censored
<i>Pseudochromis fridmani</i>	-	right censored
<i>Pseudochromis nigrovittatus</i>	-	right censored
<i>Pseudochromis olivaceus</i>	-	right censored
<i>Pseudochromis pesi</i>	-	right censored
<i>Pseudochromis sankeyi</i>	-	right censored
<i>Pseudochromis springeri</i>	-	right censored
<i>Pseudodax moluccanus</i>	-	right censored
<i>Pseudogramma megamyctera</i>	-	right censored
<i>Pseudorhombus elevatus</i>	-	right censored
<i>Psilogobius randalli</i>	-	right censored
<i>Ptarmus gallus</i>	-	right censored
<i>Pteragogus cryptus</i>	-	right censored
<i>Pteragogus flagellifer</i>	-	right censored
<i>Pteragogus pelycus</i>	-	introduced
<i>Ptereleotris arabica</i>	-	right censored
<i>Ptereleotris evides</i>	-	right censored
<i>Ptereleotris heteroptera</i>	-	right censored
<i>Ptereleotris microlepis</i>	-	right censored
<i>Ptereleotris zebra</i>	-	right censored
<i>Pterocaesio chrysozona</i>	-	right censored
<i>Pterois miles</i>	-	introduced
<i>Pterois radiata</i>	-	right censored
<i>Pterygotrigla spirai</i>	-	right censored
<i>Pygoplites diacanthus</i>	-	right censored
<i>Rachycentron canadum</i>	widely distributed species	excluded
<i>Rastrelliger kanagurta</i>	-	introduced
<i>Remora albescens</i>	widely distributed species	excluded
<i>Remora brachyptera</i>	widely distributed species	excluded
<i>Remora remora</i>	widely distributed species	excluded
<i>Rhabdamia cypselurus</i>	-	right censored
<i>Rhabdamia nigrimentum</i>	-	right censored
<i>Rhabdamia spilota</i>	-	right censored
<i>Rhabdosargus haffara</i>	-	introduced
<i>Rhabdosargus sarba</i>	-	right censored
<i>Rhinecanthus assasi</i>	-	right censored
<i>Rhynchoconger trewavasae</i>	-	introduced
<i>Roa jayakari</i>	-	right censored
<i>Rogadius pristiger</i>	-	right censored
<i>Salarias fasciatus</i>	-	right censored
<i>Samaris cristatus</i>	-	right censored
<i>Samariscus inornatus</i>	-	right censored

<i>Sarda orientalis</i>	-	right censored
<i>Sardinella albella</i>	-	right censored
<i>Sardinella longiceps</i>	-	right censored
<i>Sargocentron caudimaculatum</i>	-	right censored
<i>Sargocentron diadema</i>	-	right censored
<i>Sargocentron ittodai</i>	-	right censored
<i>Sargocentron macrosquamis</i>	-	right censored
<i>Sargocentron marisrubri</i>	-	right censored
<i>Sargocentron punctatissimum</i>	-	right censored
<i>Sargocentron rubrum</i>	-	introduced
<i>Sargocentron spiniferum</i>	-	right censored
<i>Saurenhelys meteori</i>	deep sea species	excluded
<i>Saurida gracilis</i>	-	right censored
<i>Saurida macrolepis</i>	-	right censored
<i>Saurida tumbil</i>	-	right censored
<i>Scarus collana</i>	-	right censored
<i>Scarus ferrugineus</i>	-	right censored
<i>Scarus frenatus</i>	-	right censored
<i>Scarus fuscopurpureus</i>	-	right censored
<i>Scarus ghobban</i>	-	introduced
<i>Scarus niger</i>	-	right censored
<i>Scarus psittacus</i>	-	right censored
<i>Scarus rubroviolaceus</i>	-	right censored
<i>Scarus scaber</i>	-	right censored
<i>Scarus viridifucatus</i>	-	right censored
<i>Schindleria sp.</i>	unspecified species	excluded
<i>Scolecenchelys erythraeensis</i>	-	right censored
<i>Scolecenchelys gymnota</i>	-	right censored
<i>Scolecenchelys laticaudata</i>	-	right censored
<i>Scolopsis bimaculata</i>	-	right censored
<i>Scolopsis ghanam</i>	-	right censored
<i>Scolopsis taeniata</i>	-	right censored
<i>Scolopsis vosmeri</i>	-	right censored
<i>Scomber australasicus</i>	-	right censored
<i>Scomberoides commersonianus</i>	-	right censored
<i>Scomberoides lysan</i>	-	right censored
<i>Scomberomorus commerson</i>	-	introduced
<i>Scorpaenodes albaiensis</i>	-	right censored
<i>Scorpaenodes guamensis</i>	-	right censored
<i>Scorpaenodes hirsutus</i>	-	right censored
<i>Scorpaenodes parvipinnis</i>	-	right censored
<i>Scorpaenodes steinitzi</i>	-	right censored
<i>Scorpaenopsis barbata</i>	-	right censored
<i>Scorpaenopsis diabolus</i>	-	right censored

<i>Scorpaenopsis oxycephala</i>	-	right censored
<i>Scorpaenopsis possi</i>	-	right censored
<i>Scorpaenopsis vittapinna</i>	-	right censored
<i>Sebastapistes cyanostigma</i>	-	right censored
<i>Sebastapistes strongia</i>	-	right censored
<i>Secutor insidiator</i>	-	right censored
<i>Selar crumenophthalmus</i>	widely distributed species	excluded
<i>Seriola dumerili</i>	widely distributed species	excluded
<i>Seriolina nigrofasciata</i>	-	right censored
<i>Serranus cabrilla</i>	Atlantic and/or Mediterranean species	excluded
<i>Siganus argenteus</i>	-	right censored
<i>Siganus luridus</i>	-	introduced
<i>Siganus rivulatus</i>	-	introduced
<i>Siganus stellatus</i>	-	right censored
<i>Silhouettea aegyptia</i>	-	introduced
<i>Silhouettea chaimi</i>	-	right censored
<i>Silhouettea insinuans</i>	-	right censored
<i>Sillago sihama</i>	-	right censored
<i>Siokunichthys bentuviai</i>	-	right censored
<i>Siokunichthys herrei</i>	-	right censored
<i>Siphamia tubifer</i>	-	right censored
<i>Sirembo jerdoni</i>	deep sea species	excluded
<i>Skythrenchelys lentiginosa</i>	-	right censored
<i>Soleichthys dori</i>	-	right censored
<i>Solenostomus cyanopterus</i>	-	right censored
<i>Solenostomus paradoxus</i>	-	right censored
<i>Sorsogona prionota</i>	-	introduced
<i>Sparus aurata</i>	Atlantic and/or Mediterranean species	excluded
<i>Sphaeramia orbicularis</i>	-	right censored
<i>Sphyaena barracuda</i>	-	right censored
<i>Sphyaena chrysotaenia</i>	-	introduced
<i>Sphyaena forsteri</i>	-	right censored
<i>Sphyaena jello</i>	-	right censored
<i>Sphyaena obtusata</i>	-	introduced
<i>Sphyaena putnamae</i>	-	right censored
<i>Sphyaena qenie</i>	-	right censored
<i>Spratelloides delicatulus</i>	-	introduced
<i>Spratelloides gracilis</i>	-	right censored
<i>Stalix davidsheni</i>	-	right censored
<i>Stegastes nigricans</i>	-	right censored
<i>Stegastes punctatus</i>	-	right censored
<i>Stephanolepis diaspros</i>	-	introduced
<i>Stethojulis albovittata</i>	-	right censored
<i>Stethojulis interrupta</i>	-	right censored

<i>Stolephorus indicus</i>	-	right censored
<i>Stomias affinis</i>	deep sea species	excluded
<i>Strophidon sathete</i>	-	right censored
<i>Suezichthys caudavittatus</i>	-	right censored
<i>Suezichthys russelli</i>	-	right censored
<i>Sufflamen albicaudatum</i>	-	right censored
<i>Sufflamen fraenatum</i>	-	right censored
<i>Symphysanodon disii</i>	-	right censored
<i>Synagrops philippinensis</i>	-	right censored
<i>Synanceia nana</i>	-	right censored
<i>Synanceia verrucosa</i>	-	introduced
<i>Synchiropus sechellensis</i>	-	right censored
<i>Syngnathoides biaculeatus</i>	-	right censored
<i>Syngnathus macrophthalmus</i>	-	right censored
<i>Syngnathus safina</i>	-	right censored
<i>Synodus dermatogenys</i>	-	right censored
<i>Synodus hoshinonis</i>	-	right censored
<i>Synodus indicus</i>	-	right censored
<i>Synodus randalli</i>	-	right censored
<i>Synodus variegatus</i>	-	right censored
<i>Taractichthys steindachneri</i>	widely distributed species	excluded
<i>Teixeirichthys jordani</i>	-	right censored
<i>Tentoriceps cristatus</i>	-	right censored
<i>Terapon jarbua</i>	-	introduced
<i>Terapon puta</i>	-	introduced
<i>Terapon theraps</i>	-	right censored
<i>Tetrosomus gibbosus</i>	-	introduced
<i>Thalassoma lunare</i>	-	right censored
<i>Thalassoma purpurum</i>	-	right censored
<i>Thalassoma rueppellii</i>	-	right censored
<i>Thamnaconus modestoides</i>	-	right censored
<i>Thryssa baelama</i>	-	right censored
<i>Thunnus alalunga</i>	widely distributed species	excluded
<i>Thunnus albacares</i>	widely distributed species	excluded
<i>Thunnus tonggol</i>	-	right censored
<i>Thyrsitoides marleyi</i>	-	right censored
<i>Thysanophrys chiltonae</i>	-	right censored
<i>Tilapia zillii</i>	freshwater species	excluded
<i>Tomiyamichthys fourmanoiri</i>	-	right censored
<i>Tomiyamichthys latruncularius</i>	-	right censored
<i>Torquigener flavimaculosus</i>	-	introduced
<i>Trachinocephalus myops</i>	widely distributed species	excluded
<i>Trachinotus baillonii</i>	-	right censored
<i>Trachinotus blochii</i>	-	right censored

<i>Trachurus indicus</i>	-	right censored
<i>Trachyrhamphus bicoarctatus</i>	-	right censored
<i>Trachyrhamphus longirostris</i>	-	right censored
<i>Trichiurus auriga</i>	-	right censored
<i>Trichiurus lepturus</i>	widely distributed species	excluded
<i>Trichonotus nikii</i>	-	right censored
<i>Trimma avidori</i>	-	right censored
<i>Trimma barralli</i>	-	right censored
<i>Trimma filamentosum</i>	-	right censored
<i>Trimma fishelsoni</i>	-	right censored
<i>Trimma flammeum</i>	-	right censored
<i>Trimma flavicaudatum</i>	-	right censored
<i>Trimma mendelssohni</i>	-	right censored
<i>Trimma sheppardi</i>	-	right censored
<i>Trimma taylori</i>	-	right censored
<i>Trimma tevegae</i>	-	right censored
<i>Trimmatom nanus</i>	-	right censored
<i>Tylosurus acus melanotus</i>	-	right censored
<i>Tylosurus choram</i>	-	introduced
<i>Tylosurus crocodilus</i>	-	right censored
<i>Ulua mentalis</i>	-	right censored
<i>Upeneus davidaromi</i>	-	right censored
<i>Upeneus guttatus</i>	-	right censored
<i>Upeneus margarethae</i>	-	right censored
<i>Upeneus moluccensis</i>	-	introduced
<i>Upeneus pori</i>	-	introduced
<i>Upeneus suahelicus</i>	-	right censored
<i>Upeneus sulphureus</i>	-	right censored
<i>Upeneus tragula</i>	-	right censored
<i>Upeneus vittatus</i>	-	right censored
<i>Uranoscopus bauchotae</i>	-	right censored
<i>Uranoscopus dahlakensis</i>	-	right censored
<i>Uranoscopus dollfusi</i>	-	right censored
<i>Uranoscopus guttatus</i>	-	right censored
<i>Uranoscopus marisrubri</i>	-	right censored
<i>Uranoscopus scaber</i>	Atlantic and/or Mediterranean species	excluded
<i>Uranoscopus sulphureus</i>	-	right censored
<i>Uraspis helvola</i>	widely distributed species	excluded
<i>Uroconger erythraeus</i>	-	right censored
<i>Uroconger lepturus</i>	-	right censored
<i>Uropterygius concolor</i>	-	right censored
<i>Uropterygius genie</i>	-	right censored
<i>Uropterygius golanii</i>	-	right censored
<i>Uropterygius macrocephalus</i>	-	right censored

<i>Uropterygius micropterus</i>	-	right censored
<i>Uropterygius nagoensis</i>	-	right censored
<i>Uropterygius polyspilus</i>	-	right censored
<i>Valenciennea helsdingenii</i>	-	right censored
<i>Valenciennea puellaris</i>	-	right censored
<i>Valenciennea sexguttata</i>	-	right censored
<i>Valenciennea wardii</i>	-	right censored
<i>Vanderhorstia ambanoro</i>	-	right censored
<i>Vanderhorstia delagoae</i>	-	right censored
<i>Vanderhorstia mertensi</i>	-	right censored
<i>Vanderhorstia opercularis</i>	-	right censored
<i>Vanderhorstia ornatissima</i>	-	right censored
<i>Variola louti</i>	-	right censored
<i>Vinciguerria mabahiss</i>	deep sea species	excluded
<i>Wetmorella nigropinnata</i>	-	right censored
<i>Xenisthmus polyzonatus</i>	-	right censored
<i>Xestochilus nebulosus</i>	-	right censored
<i>Xiphasia setifer</i>	-	right censored
<i>Xiphias gladius</i>	widely distributed species	excluded
<i>Xyrichtys javanicus</i>	-	right censored
<i>Yirrkala tenuis</i>	-	right censored
<i>Zebrasoma desjardini</i>	-	right censored
<i>Zebrasoma xanthurum</i>	-	right censored
<i>Zoramia leptacantha</i>	-	right censored

Table 5: List of introduced bony fishes in the Mediterranean Sea from the Indo-Pacific area according to Golani et al. (2013) and their status in the study. Right censored: no Mediterranean record; introduced

Species	Classification	Reason of Classification	Place of the first record	Year of record	Reference of first record
<i>Abudefduf vaigiensis</i>	introduced	-	Italy	1959	Tardent (1959)
<i>Acanthopagrus bifasciatus</i>	right censored	Location of first record	Tunisia	2009	Iwatsuki & Heemstra (2011)
<i>Alepes djedaba</i>	introduced	-	Palestine	1927	Steinitz (1927)
<i>Apogon queketti</i>	introduced	-	Turkey	2004	Eryilmaz & Dalyan (2006)
<i>Apogon smithi</i>	introduced	-	Israel	2007	Golani et al. (2008)
<i>Apogonichthyoides pharaonis</i>	introduced	-	Palestine	1947	Haas & Steinitz (1947)
<i>Atherinomorus forskalii</i>	introduced	-	Egypt	1902	Tillier (1902)

<i>Callionymus filamentosus</i>	introduced	-	Israel	1953	Ben-Tuvia (1953)
<i>Chaetodon austriacus</i>	introduced	-	Israel	2011	Goren et al. (2011)
<i>Chaetodon larvatus</i>	introduced	-	Israel	2011	Salameh et al. (2011)
<i>Chanos chanos</i>	introduced	-	Turkey	2011	Özvarol & Gökoglu (2012)
<i>Cheilodipterus novemstriatus</i>	introduced	-	Israel	2010	Bariche & Azzurro (2013)
<i>Coryogalops ocheticus</i>	introduced	-	Egypt	1927	Norman (1927)
<i>Crenidens crenidens</i>	introduced	-	Egypt	1970	Lourie & Ben-Tuvia (1970)
<i>Cylichthys spilostylus</i>	introduced	-	Israel	1993	Golani (1993a)
<i>Cynoglossus sinusarabici</i>	introduced	-	Israel	1953	Ben-Tuvia (1953)
<i>Decapterus russelli</i>	introduced	-	Israel	2005	Golani (2006)
<i>Dussumieria elopoides</i>	introduced	-	Israel	1949	Lissner (1949)
<i>Epinephelus coioides</i>	introduced	-	Israel	1969	Ben-Tuvia & Lourie (1969)
<i>Epinephelus fasciatus</i>	introduced	-	Lebanon	2011	Bariche & Heemstra (2012)
<i>Epinephelus malabaricus</i>	introduced	-	Israel	1969	Ben-Tuvia & Lourie (1969)
<i>Equulites klunzingeri</i>	introduced	-	Syria	1931	Gruvel (1931)
<i>Etrumeus golanii</i>	introduced	-	Israel	1963	Whitehead (1963)
<i>Fistularia commersonii</i>	introduced	-	Israel	2000	Golani (2000)
<i>Gymnothorax reticularis</i>	introduced	-	Israel	2012	Stern & Goren (2013)
<i>Hemiramphus far</i>	introduced	-	Palestine	1927	Steinitz (1927)
<i>Heniochus intermedius</i>	introduced	-	Turkey	2002	Gökoglu et al. (2003)
<i>Herklotsichthys punctatus</i>	introduced	-	Palestine	1943	Bertin (1943)
<i>Hippocampus fuscus</i>	introduced	-	Israel	2001	Golani & Fine (2002)
<i>Hyporhamphus affinis</i>	introduced	-	Lebanon	1964	George et al. (1964)
<i>Iniistius pavo</i>	introduced	-	Greece	2004	Corsini et al. (2006)
<i>Lagocephalus sceleratus</i>	introduced	-	Turkey	2003	Golani & Levy (2005)
<i>Lagocephalus spadiceus</i>	introduced	-	Greece	1930	Sanzo (1930)
<i>Lagocephalus suezensis</i>	introduced	-	Lebanon	1977	Mouneimne (1979)
<i>Liza carinata</i>	introduced	-	Egypt	1929	Norman (1929)

<i>Lutjanus argentimaculatus</i>	introduced	-	Lebanon	1979	Mouneimne (1979)
<i>Muraenesox cinereus</i>	introduced	-	Israel	1982	Golani & Ben-Tuvia (1982)
<i>Nemipterus randalli</i>	introduced	-	Israel	2005	Golani & Sonin (2006)
<i>Omobranchus punctatus</i>	introduced	-	Israel	2003	Golani (2004)
<i>Ostracion cubicus</i>	introduced	-	Lebanon	2011	Bariche (2011)
<i>Ostorhinchus fasciatus</i>	introduced	-	Israel	2008	Goren et al. (2009)
<i>Oxyurichthys petersi</i>	introduced	-	Israel	1983	Ben-Tuvia (1983)
<i>Papilloculiceps longiceps</i>	introduced	-	Israel	1990	Golani & Ben-Tuvia (1990)
<i>Parexocoetus mento</i>	introduced	-	Palestine	1935	Bruun (1935)
<i>Parupeneus forsskali</i>	introduced	-	Lebanon	2006	Çinar et al. (2006)
<i>Pelates quadrilineatus</i>	introduced	-	Egypt	1977	Ben-Tuvia (1977)
<i>Pempheris rhomboidea</i>	introduced	-	Lebanon	1979	Mouneimne (1979)
<i>Petroscirtes ancyllodon</i>	introduced	-	Israel	1989	Goren & Galil (1989)
<i>Platax teira</i>	introduced	-	Turkey	2006	Bilecenoglu & Kaya (2006)
<i>Platycephalus indicus</i>	introduced	-	Israel	1953	Ben-Tuvia (1953)
<i>Plotosus lineatus</i>	introduced	-	Israel	2002	Golani (2002)
<i>Pomacanthus imperator</i>	introduced	-	Israel	2009	Golani et al. (2010)
<i>Pomacanthus maculosus</i>	introduced	-	Lebanon	2008	Bariche (2012)
<i>Pomadasys stridens</i>	introduced	-	Israel	1976	Torchio (1976)
<i>Priacanthus sagittarius</i>	introduced	-	Israel	2010	Goren et al. (2010)
<i>Pteragogus pelycus</i>	introduced	-	Israel	1992	Golani & Sonin (1992)
<i>Pterois miles</i>	introduced	-	Israel	1992	Golani & Sonin (1992)
<i>Rastrelliger kanagurta</i>	introduced	-	Israel	1970	Collette (1970)
<i>Rhabdosargus haffara</i>	introduced	-	Israel	1992	Golani (1992)
<i>Rhynchoconger trewavasae</i>	introduced	-	Israel	1993	Ben-Tuvia (1993)
<i>Sargocentron rubrum</i>	introduced	-	Palestine	1947	Haas & Steinitz (1947)
<i>Scarus ghobban</i>	introduced	-	Israel	2001	Goren & Aronov (2002)
<i>Scomberomorus commerson</i>	introduced	-	Palestine	1935	Hornell (1935)

<i>Siganus luridus</i>	introduced	-	Israel	1964	Ben-Tuvia (1964)
<i>Siganus rivulatus</i>	introduced	-	Palestine	1927	Steinitz (1927)
<i>Silhouettea aegyptia</i>	introduced	-	Egypt	1979	Ben-Tuvia & Golani (1979)
<i>Sorsogona prionota</i>	introduced	-	Israel	1947	Golani & Ben-Tuvia (1990)
<i>Sphyraena chrysotaenia</i>	introduced	-	Palestine	1931	Spicer (1931)
<i>Sphyraena obtusata</i>	introduced	-	Israel	1992	Golani (1992)
<i>Spratelloides delicatulus</i>	introduced	-	Israel	1978	Ben-Tuvia (1978)
<i>Stephanolepis diaspros</i>	introduced	-	Palestine	1927	Steinitz (1927)
<i>Synanceia verrucosa</i>	introduced	-	Israel	2010	Edelist et al. (2011)
<i>Terapon jarbua</i>	introduced	-	Israel	2009	Golani & Appelbaum-Golani (2010)
<i>Terapon puta</i>	introduced	-	Egypt	1976	Ben-Tuvia (1976)
<i>Terapon theraps</i>	right censored	Location of first record	Slovenia	2007	Lipej et al. (2008)
<i>Tetrosomus gibbosus</i>	introduced	-	Israel	1988	Spanier & Goren (1988)
<i>Torquigener flavimaculosus</i>	introduced	-	Israel	1987	Golani (1987)
<i>Tylosurus choram</i>	introduced	-	Israel	1967	Parin (1967)
<i>Upeneus moluccensis</i>	introduced	-	Palestine	1947	Haas & Steinitz (1947)
<i>Upeneus pori</i>	introduced	-	Turkey	1950	Kosswig (1950)

Table 6: Traits of Red Sea fish species that were analysed. *P*-value according to the likelihood ratio test; ABH: Adjusted Benjamini-Hochberg correction. NA: no data. The asterisk refers to *adjusted P < 0.05*.

Variable	Short Description	<i>P</i>	Adjusted <i>P</i>	Type of Variable	Nb of Cat	Categories
MinDistToCanal	Straight line distance from the closest location of the recorded species to the Suez Canal	0.00004	0.0021*	numerical	-	-
NrSpPerFamily_RS	Number of species per family	0.00006	0.0041*	numerical	-	-
Type.of.Bottom.1	Preferred bottom beneath each species	0.00008	0.0062*	categorical/ nominal	5	soft, hard, both, none (pelagic), NA
DemersPelag	Habitat of the species in relation to the bottom	0.00012	0.0082*	ordinal	5	1 = surface, 2 = midwater, 3 = close to bottom, 4 = on the bottom, NA
Schooling.Ordinal	The way fish species aggregate	0.00133	0.0103*	ordinal	8	1 = 1-2, 1.5 = 1-2 & 3-10, 2 = 3-10, 2.5 = 3-10 & 11-100, 3 = 11-100, 3.5 = 11-100 & >100, 4 = >100, NA

SSTmax	Monthly maximum sea surface temperature recorded for the observed species	0.00396	0.0123*	numerical	-	-
Special.Habitats	Whether a species exists in estuaries, mangroves, bays, harbour, brakish water or river	0.02509	0.01440	binary	2	yes, no info
SSTrange	Mean value of the yearly sea surface temperature range of the observed species	0.04213	0.01640	numerical	-	-
Eggs	Way of suspension of the eggs	0.06057	0.01850	categorical/ nominal	3	benthic, pelagic, NA
Transport	Whether the species is capable of attaching to moving bodies	0.07791	0.02050	binary	2	yes, no info
RepGuild1	Strategies to parental care	0.08249	0.02260	categorical/ nominal	4	bearers, guarders, nonguarders, NA
FeedingType	Most common diet of the fish species	0.08967	0.02460	categorical/ nominal	6	carnivore, detritivore, herbivore, omnivore, piscivore, NA
Vulnerability	"Level of catchability"	0.09123	0.02670	numerical	-	-
Length	Maximum Length (TL)	0.14395	0.02870	numerical	-	-

Fertilization	Way of exchanging gametes	0.20463	0.03080	categorical/ nominal	4	external, in brood pouch or similar structure, internal (oviduct), NA
BodyShapeI	Body shape lateral view	0.32746	0.03280	categorical/ nominal	6	eel-like, elongated, fusiform, short & deep, other, NA
Resilience	Ability of the fish species to recover from fishing pressure	0.35957	0.03490	ordinal	5	1 = Very low, 2 = Low, 3 = Medium, 4 = High, NA
CShape	Shape of the caudal fin	0.40992	0.03690	categorical/ nominal	5	forked, truncate, pointed, other, NA
Vertical.Migration	Diel vertical movement with depth	0.42379	0.03900	binary	2	yes, no info
CaringParent	Defines which parent is the caring parent	0.44508	0.04100	categorical/ nominal	4	maternal, paternal, none, NA
Habitat.1	Mode of living	0.48348	0.04310	categorical/ nominal	4	benthic, pelagic, benthopelagic, NA

ReproMode	Reproduction mode of the species	0.48360	0.04520	categorical/ 5 nominal		dioecism, protandry, protogyny, true hermaphroditism, NA
MaxDepth	Maximum depth the species was recorded	0.49117	0.04720	numerical	-	-
Food.items	Common food items in stomach contents	0.53244	0.04930	categorical/ 13 nominal		benthic invertebrates, fish, benthic algae, seaweed, zooplankton, cephalopods, seagrass, detritus, phytoplankton, scavenger, parasites, other, NA
Territoriality	Whether a species is territorial or not	0.54717	0.05130	binary	2	yes, no info
FoodTroph	Trophic level of the species	0.54905	0.05340	numerical	-	-
BodyShapeII	Body shape cross section	0.64633	0.05540	categorical/ 7 nominal		angular, circular, compressed, flattened, oval, other, NA

Herbivory2	Very general description of the diet of fish species	0.69037	0.05750	categorical/ 4 nominal	mainly animals (troph.2.8 and up), mainly plants/detritus (troph.2-2.19), plants/detritus + animals (troph.2.2-2.79), NA
PD50	Phylogenetic diversity index (PD50)	0.72791	0.05950	numerical - -	
PosOfMouth	Position of the mouth	0.75573	0.06160	categorical/ 4 nominal	inferior, superior, terminal, NA
MinDepth	Minimum depth the species was recorded	0.77135	0.06360	numerical - -	
StockDefs	Distributions of each fish species	0.83853	0.06570	categorical/ 6 nominal	Indo Pacific, Indo West Pacific, Indian, Red Sea, Western Indian, Western Pacific
Activity	Peak time of activity	0.94090	0.06770	categorical/ 4 nominal	diurnal, nocturnal, both, NA

CHAPTER II WORK FLOW

A. Work flow diagram:

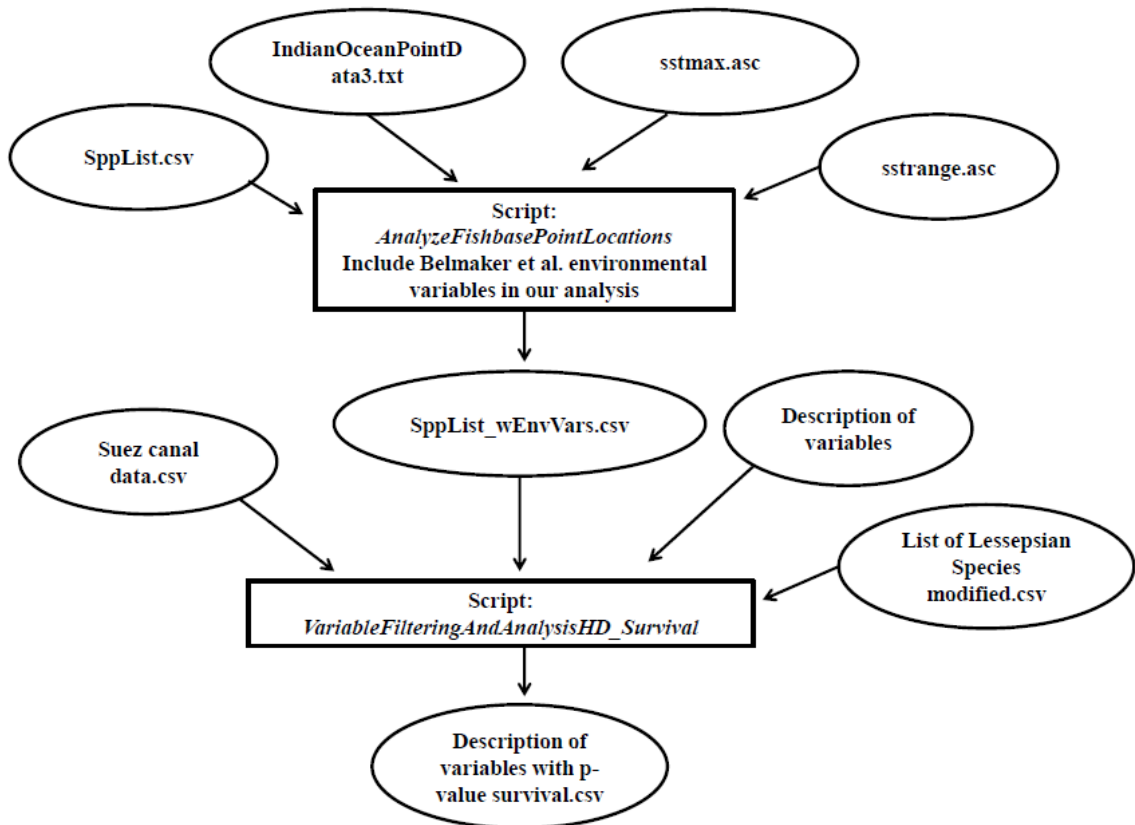


Figure 7: Work flow diagram for the analysis steps

B. Files used in the analysis:

Table 7: A short description of the files that were used in the analysis.

File name	Short description
SppList.csv	Species list of Red Sea fish species with the information that is ready to enter the analysis i.e.: Risk Set.
IndianOceanPointData3.txt	Sampling location data for species obtained from Fishbase.

sstmax.asc	Monthly maximum sea surface temperature for each of the sampling locations and it was obtained from the Bio-ORACLE database.
sstrange.asc	Yearly range of sea surface temperature for each of the sampling locations and it was obtained from the Bio-ORACLE database.
SppList_wEnvVars.csv	It is the same list as the SppList.csv but with the environmental variable (Minimum distance to the canal, SSTmax and SSTRange) included as predictor variables.
Suez canal data.csv	A sheet downloaded from Fishbase that states the depth of the canal at different years.
Description of variables	A description of the variables which were included in the screening analysis with a short description and what their categories are.
List of Lessepsian Species modified.csv	List of lessepsian species that were used in the analysis.
Description of variables with p-value survival.csv	Description of variables table with the corresponding p values of the screening analysis.

CHAPTER III R SCRIPTS CODE

The content of the R scripts that were used in our analysis are found below.

A. AnalyzeFishbasePointLocations script:

```
# The following script reads in Fishbase point locations and calculates values  
  
# that are tied to locations such as SSTmax, SSTrange, Salinity  
  
# Source start script  
  
source("C:/Masters project/Scripts/_StartScript.r")  
  
# Load packages  
  
library(geosphere)  
  
library(maps)  
  
library(raster)  
  
# Read in location data (obtained from Fishbase)  
  
IndianOceanPoints <- read.delim("C:/Masters project/Data/Raw  
Data/IndianOceanPointData3.txt",  
  
  quote = "", encoding = "UTF-8", as.is = T)  
  
# Read sea surface temperature data  
  
SSTmax <- raster("C:/Masters project/Data/Raw Data/BioOracle/sstmax.asc")
```

```

SSTrange <- raster("C:/Masters project/Data/Raw Data/BioOracle/ssstrange.asc")

# Read in data file

FishData <- read.csv("C:/Masters project/Data/Processed Data/SppList.csv",

                    as.is = T)

# Make species names consistent between the data sets

FishDataSp <- gsub(" ", "", FishData$Species)

IOSpecies <- gsub(" ", "", IndianOceanPoints$Species)

FishDataSp[is.na(FishDataSp)] <- "Unknown"

# Loop through all species and get the maximum temperature values

EnvValsPerSp <- sapply(FishDataSp, function(Sp){

  LatLongs <- IndianOceanPoints[IOSpecies == Sp, c("Longitude", "Latitude")]

  SSTm <- extract(SSTmax, LatLongs)

  SSTr <- extract(SSTrange, LatLongs)

  c(SSTmax = max(SSTm, na.rm = T), SSTrange = mean(SSTr, na.rm = T))

})

EnvValsPerSp[EnvValsPerSp == -Inf] <- NA

EnvValsPerSp[EnvValsPerSp == Inf] <- NA

EnvValsPerSp <- as.data.frame(t(EnvValsPerSp))

```

```

FishData <- cbind(FishData, EnvValsPerSp[,c("SSTmax", "SSTrange")])

# Determine the location of the Suez Canal and plot it for confirmation

CanalCoords <- c(32.3,30.8)

map(xlim = c(30,50), ylim = c(22, 35))

points(CanalCoords[1], CanalCoords[2], col = "red")

# Plot temperature map

tiff(filename = "Manuscript/TempMapSmallScale.tif")

plot(SSTmax, xlim = c(25,45), ylim = c(10, 40), xaxt = "n", yaxt = "n",

      bty = "n")

dev.off()

tiff(filename = "Manuscript/TempMapLargeScale.tif")

plot(SSTmax, xlim = c(20,120), ylim = c(-20, 40), xaxt = "n", yaxt = "n",

      bty = "n")

dev.off()

tiff(filename = "Manuscript/TempMapCombined.tif")

par(mfrow = c(1, 2), mar = c(1, 1, 1, 1))

plot(SSTmax, xlim = c(25,45), ylim = c(10, 40), xaxt = "n", yaxt = "n",

      bty = "n", col = heat.colors(10)[10:1])

```

```

plot(SSTmax, xlim = c(20,120), ylim = c(-20, 40), xaxt = "n", yaxt = "n",

      bty = "n", col = heat.colors(10)[10:1])

dev.off()

# Loop through all species and determine whether the species has locations
# in the Red Sea

DistanceSuez <- sapply(FishDataSp, function(Sp){

  idxSp <- IOSpecies == Sp

  if (sum(idxSp) > 0){

    LatLongs <- IndianOceanPoints[IOSpecies == Sp, c("Longitude", "Latitude")]

    Dists <- distVincentyEllipsoid(CanalCoords, LatLongs) / 1000

    min(Dists, na.rm = T)

  } else {NA}

})

FishData$MinDistToCanal <- DistanceSuez

# Write data to file

write.csv(FishData, "C:/Masters project/Data/Processed Data/SppList_wEnvVars.csv",

          row.names = F)

```


B. VariableFilteringAndAnalysis_Survival script:

```
# This script filters all the variables that are potential predictor for  
  
# Lessepsian migration.It tests predictor variables separately and keeps the  
  
# significant ones while controlling for the false discovery rate.  
  
# After filtering it performs a logistic regression with filtered variables  
  
# Source start script  
  
source("C:/Masters project/Scripts/_StartScript.r")  
  
library("ape")  
  
#####  
  
#           #  
  
#  Read data      #  
  
#           #  
  
#####  
  
# Read in data file  
  
Data <- read.csv("C:/Masters project/Data/Processed Data/SppList_wEnvVars.csv",  
  
                as.is = T)  
  
# Replace a species name that was misclassified
```

```

Data$Species[Data$Species == "Pempheris mangula"] <- "Pempheris rhomboidea"

# Read in appendix tables

AppendixA1 <- read.csv("C:/Masters project/Data/Raw Data/Appendix Table A1 2015-
08-11.csv",
                      as.is = T)

AppendixA2 <- read.csv("C:/Masters project/Data/Raw Data/Appendix Table A2 2015-
08-11.csv",
                      as.is = T)

AppendixA3 <- read.csv("C:/Masters project/Data/Raw Data/Appendix Table A3 2015-
08-11.csv",
                      as.is = T)

# Determine which species are not excluded

A1Included <- AppendixA1[AppendixA1$Classification != "excluded", ]

# Read suex canal data

CanalData <- read.csv("Data/Raw Data/Suez canal data.csv")

# Read table with potential aquarium species

AquariumSp <- read.csv("Data/Raw Data/Potential aquarium species.csv",
                      as.is = T)

```

```
#####

#                               #

# Pre-process data             #

#                               #

#####

# Auxiliary function to remove empty spaces after species name

StandardSpNames <- function(SpNameVector) {

  sapply(SpNameVector, function(x){

    SplitSp <- strsplit(x, '[:blank:]')[[1]]

    SplitSp <- SplitSp[SplitSp != ""]

    paste(SplitSp, collapse = " ")

  })

}

# Remove empty spaces after species names

Data$Species    <- StandardSpNames(Data$Species)

A1Included$Species <- StandardSpNames(A1Included$Species)

AppendixA2$Species <- StandardSpNames(AppendixA2$Species)

AquariumSp$Species <- StandardSpNames(AquariumSp$Species)
```

```

# Check whether there are any species that are in the appendix but not in

# SppList or vice versa

SpInAppendix1NotSppList <- setdiff(A1Included$Species, Data$Species)

SpInSppListNotAppendix1 <- setdiff(Data$Species, A1Included$Species)

SpInAppendix2NotSppList <- setdiff(AppendixA2$Species, Data$Species)

if (length(SpInAppendix1NotSppList) > 0){

  stop("The following species are in appendix A1 but not in SppList: \n",

       paste(SpInAppendix1NotSppList, collapse = "\n"))

}

if (length(SpInSppListNotAppendix1) > 0){

  stop("The following species are in SppList but not appendix A1: \n",

       paste(SpInSppListNotAppendix1, collapse = "\n"))

}

if (length(SpInAppendix2NotSppList) > 0){

  stop("The following species are in appendix A2 but not in SppList: \n",

       paste(SpInAppendix2NotSppList, collapse = "\n"))

}

# Check that classification is consistent between appendix table

```

```

AppendixA2$Classification <- tolower(AppendixA2$Classification)

SpMatch <- match(AppendixA2$Species, A1Included$Species)

NotInA2 <- !A1Included$Species %in% AppendixA2$Species

if (any(AppendixA2$Classification != A1Included$Classification[SpMatch])){

  stop("Classification not consistent between appendix tables")

}

if (any(A1Included$Classification[NotInA2] == "introduced")){

  stop("The following species are labeled as introduced in A1 but

    do not appear in A2:\n", A1Included$Species[NotInA2 &
A1Included$Classification == "introduced"])

}

which(AppendixA2$Classification != A1Included$Classification[SpMatch])

# Update type of bottom for aquarium species

for (i in which(!is.na(AquariumSp$Type.of.Bottom.1))){

  idxSp <- which(Data$Species == AquariumSp$Species[i])

  TypeB <- AquariumSp$Type.of.Bottom.1[i]

  if (TypeB != "?"){

    cat("Replacing type of bottom for", AquariumSp$Species[i], "\n")
  }
}

```

```

cat(TypeB, "instead of", Data$Type.of.Bottom.1[idxSp], "\n")

Data$Type.of.Bottom.1[idxSp] <- TypeB

}

}

# Merge data and check that the definition of Lessepsian migration is equal

# between the datasets

Data <- merge(Data, A1Included)

Lesseps <- Data$Lessepsian == 1

Introduced <- Data$Classification == "introduced"

if (sum(Lesseps & !Introduced) > 0){

  warning("The following species are Lessepsian according to SppList\n",

    "but not according to the Appendix table A1:\n",

    paste(Data$Species[Lesseps & !Introduced], collapse = "\n"))

}

if (sum(!Lesseps & Introduced) > 0){

  warning("The following species are Lessepsian according to Appendix table A1\n",

    "but not according to the SppList:\n",

    paste(Data$Species[!Lesseps & Introduced], collapse = "\n"))

```

```

}

# Update Lessepsian column according to Appendix Table A1

Data$Lessepsian      <- 0

Data$Lessepsian[Introduced] <- 1

# Merge data from Appendix Table A2

Data <- merge(Data, AppendixA2, by = "Species", all.x = T)

sum(!is.na(Data$Year.of.record))

#####

#           #

#  Modify covariates      #

#           #

#####

#####

# Create survival object

#####

# Define a time 0 and censoring time (MaxTime)

Time0 <- 1869

MaxTime <- 2013

```

```

# Add event column for survival analysis

Data$Event <- Introduced

# Replace non-existing introduction time with current year

Data$Year.of.record[is.na(Data$Year.of.record)] <- MaxTime

# Define a survival object

SurvObj <- Surv(time = Data$Year.of.record - Time0,

                event = Data$Event)

# Estimate hazard

HazEst <- muhaz(times = Data$Year.of.record - Time0,

                delta = Data$Event, max.time = MaxTime - Time0)

plot(HazEst$haz.est)

plot(HazEst, ylab = "Migration Rate", xlab = "Follow-Up Time")

dev.copy2pdf(file = "Figures/HazardRateEstimate.pdf", width = 7, height = 5)

#####

# Count species per family

#####

# This analysis calculates the number of Red-Sea-species per family since

# it will be considered as a covariate in our regression analysis later

```



```

# Sum the number of species per family

FamilyCountRedSea <- aggregate(rep(1, nrow(Data)),

                               by = list(Family = Data$Family), FUN = sum)

# Match family to Red Sea data

MatchRS <- match(Data$Family, FamilyCountRedSea$Family)

Data$Family[is.na(MatchRS)]

# Append additional data columns to the data table RedSeaFish

Data$NrSpPerFamily_RS <- FamilyCountRedSea[MatchRS,2]

#####

# Only retain length measurements that are based on TL

#####

Data$Length[Data$LTypeMaxM != "TL"] <- NA

#####

# Recode NA as "No Info" to create binary variables and make Resilience to an ordinal
var

#####

# A vector of variables that have either a single value or NA

BinaryVars <- c("Territoriality", "Vertical.Migration", "Special.Habitats",

```

```

"Transport")

# Loop through variables and turn them into binary variables by changing "NA"

# into "No Info"

for(x in BinaryVars){

  NAentries <- is.na(Data[,x])

  Data[NAentries, x] <- "No Info"

}

# Change Resilience to an ordinal variable

Data$Resilience[Data$Resilience=="Very low"] <- 1

Data$Resilience[Data$Resilience=="Low"] <- 2

Data$Resilience[Data$Resilience=="Medium"] <- 3

Data$Resilience[Data$Resilience=="High"] <- 4

# Change "soft-hard" Type.of.bottom to "both"

Data$Type.of.Bottom.1[Data$Type.of.Bottom.1 == "soft - hard"] <- "both"

#####

# #

# Variable Filtering #

# #

```

```
#####

#####

# Analysis of variable "Food.items."

#####

# This variable has categories that are not mutually exclusive. Therefore a

# different indicator variable was created for each variable level - however,

# in terms of screening it is treated as a single variable

# Calculate p-value based on likelihood-ratio test

surv.Food.items <- coxph(SurvObj ~ Food.items..Adults..invertebrates +

  Food.items..Adults..seaweed + Food.items..Adults..fish +

  Food.items..Adults..NA + Food.items..Adults. +

  Food.items..Adults.Specialization + cluster(Family), data = Data)

SumCPH.Food.items <- summary(surv.Food.items )

pLR.Food.items <- SumCPH.Food.items$logtest["pvalue"]

# Generate a p-value table

PTab.Food.items <- data.frame(Variable = "Food.items", p.value = pLR.Food.items )

#####

# Analysis of all other variables
```

```

#####

# Define list of all variables that are not covariates

NotCoVars <- c("Species", "Family", "SpecCode", "StockCode", "Lessepsian",

               "Schooling", "Golani", "Species.number", "Added.Species",

               "Event", "Year.of.record", "LTypeMaxM", "Classification",

               "Classification.x")

# Get all covariates for analysis by removing variable names that are not

# covariates and Food.items since it was analyzed above

Vars <- colnames(Data)[!colnames(Data) %in% NotCoVars]

Vars <- Vars[!grep("Food.items", Vars)]

# Calculate the proportion of entries that are not NA and keep only the ones

# with more than 20% not NA

PropNotNA <- sapply(Vars, function(x) sum(!is.na(Data[,x])) / nrow(Data))

NrLevels <- sapply(Vars, function(x) length(unique(Data[!is.na(Data[,x]),x])))

Vars <- Vars[PropNotNA > 0.2 & NrLevels > 1]

# Loop through variables and calculate likelihood-ratio test per variable

PVals <- sapply(Vars, function(i){

               # Calculate p-value based on likelihood-ratio test

```

```

FunCall <- paste("coxph(SurvObj ~", i, "+ cluster(Family), data = Data)")

surv <- eval(parse(text = FunCall))

SumCPH <- summary(surv)

p    <- SumCPH$logtest["pvalue"]

})

# Create a table without the variables with mutually exclusive categories

PTabOther <- data.frame(Variable = Vars, p.value = PVals)

# Append variables with mutually exclusive categories and their p values to PTabOther

PTab <- rbind(PTabOther, PTab.Food.items)

cat("*****", nrow(PTab), "covariates screened *****\n\n")

#####

# False Discovery Rate

#####

# Set allowable false discovery rate

q <- 0.05

# Get vector of all p-values

AllPs <- PTab[, "p.value"]

# Determine rank and order of p-values

```

```

m      <- nrow(PTab)

PValOrder <- order(PTab[,"p.value"])

PValRank <- rank(PTab[,"p.value"])

# Step 1: Order P-values

PTabOrdered <- PTab[PValOrder, ]

# Step 2: first screening

NrPass1 <- sum(PTabOrdered[,"p.value"] <= (1:m) * q/ m)

cat("***** ", NrPass1, "p-values passed first screening with a q of", q,

    "***** \n\n")

# Step 3: calculate slopes

Slopes <- (1 - PTabOrdered[,"p.value"]) / (m + 1 - (1:m))

# Step 4: determine first slope for which Slopes[i] < Slopes[i - 1] and use it

# to estimate m0

FirstNeg <- min(which((Slopes[-1] - Slopes[-length(Slopes[-1])]) < 0))

Sj <- Slopes[FirstNeg + 1]

m0 <- min(m, 1 / Sj + 1)

# Step 5: determine largest p value that passes threshold

LargestK <- max(which(PTabOrdered[,"p.value"] <= (1:m) * q / m0))

```

```

PTabPassed <- PTabOrdered[1:LargestK, ]

LargestKBH <- max(which(PTabOrdered[, "p.value"] <= (1:m) * q / m))

# Plot ordered p values vs fitted line

par(mfrow = c(1,1), mar = c(4,5,2,1))

plot((LargestK + 1):(m + 1), c(PTabOrdered$p.value[(LargestK + 1):m], 1),

      xlab = expression(paste("Rank of ", italic(P), "-value")),

      ylab = expression(paste(italic(P), "-value")),

      xlim = c(1, m + 1), ylim = c(0, 1))

points(1:LargestK, PTabOrdered$p.value[1:LargestK], pch = 16)

lines(c(0, m + 1), c(1 - Sj * (m + 1), 1))

dev.copy2pdf(file = "Figures/ABHscreeningSurvival.pdf")

# Create a table for new p values of variables according to BH

PTabOrdered$ABH <- round((1:m) * q / m0, digits = 4)

PTabOrdered$BH <- round((1:m) * q / m, digits = 4)

PTabOrdered$BH <- PTabOrdered$p.value * m / (1:m)

PadjBH <- p.adjust(PTabOrdered$p.value, method = "BH")

par(mfrow = c(1, 1))

plot(PTabOrdered$BH, PadjBH, xlim = c(0, 0.5), ylim = c(0, 0.5))

```

```

lines(c(0,1), c(0,1))

PTabOrdered$ABH2 <- PTabOrdered$p.value * m0 / (1:m)

hist(PTabOrdered$p.value, breaks = seq(0,1, 0.05))

#####

# Append P.values, BH and ABH to "Description of variables"

#####

# Read in the table

DescriptionTable <- AppendixA3

# Match the analyzed variables to the variables in the descriptiontable

VarMatch <- match(PTabOrdered$Variable, DescriptionTable$Variable)

MergedTable <- merge(PTabOrdered, DescriptionTable, all = T)

# Re-order the table according to p-values

MergedTable <- MergedTable[order(MergedTable$p.value),]

# Check the differences between variables of the table and the

# analyzed variables

VarsNotAnalyzed <- setdiff(DescriptionTable$Variable, Vars)

if (length(VarsNotAnalyzed) > 0){

  warning("Variables described but not analyzed: \n",

```



```

    paste(VarsNotAnalyzed, collapse = "\n"))

}

VarsNotDescribed <- setdiff(Vars, DescriptionTable$Variable)

if (length(VarsNotDescribed) > 0){

  warning("Variables analyzed but not described: \n",

    paste(VarsNotDescribed, collapse = "\n"))

}

# Create vectors with stars to attach to significant BH and ABH values

ABHStars <- c(rep("*", LargestK), rep("", nrow(MergedTable) - LargestK))

BHStars <- c(rep("*", LargestKBH), rep("", nrow(MergedTable) - LargestKBH))

MergedTable$ABH <- paste(MergedTable$ABH, ABHStars, sep = "")

MergedTable$BH <- paste(MergedTable$BH, BHStars, sep = "")

# Save Table

write.csv(MergedTable,

  "C:/Masters project/Manuscript/Appendix table A3.csv",

  row.names = F)

#####

#           #

```

```

# Survival analysis with filtered variables #

# #

#####

#####

# Determine missing values among filtered variables

#####

# Get filtered variables and produce a status message

FilteredVars <- PTabOrdered$Variable[1:LargestK]

cat("***** Variables that passed screening: ***** \n",

    paste(FilteredVars, collapse = "\n"), "\n\n")

# Get the number of NAs per variable and keep only the ones that have values for

# more than 60% of the observations

idxFilteredVars <- match(FilteredVars, colnames(Data))

PropNas <- sapply(idxFilteredVars,

                 function(x) sum(is.na(Data[,x])) / nrow(Data))

idxVarNA <- PropNas >= 0.3

PredictVarsNoNA <- FilteredVars[!idxVarNA]

cat("***** Variables with enough entries: ***** \n",

```

```

paste(FilteredVars[!idxVarNA], collapse = "\n"), "\n\n")

cat("***** Variables with not enough entries: ***** \n",

paste(FilteredVars[idxVarNA], collapse = "\n"), "\n\n")

#####

# Replace missing values by means

#####

# Loop through variables with more than 30% NA, perform anova to determine

# whether values are structured by family and then replace NA by means

for (Var in FilteredVars[idxVarNA]){

cat("Replacing NAs by means for", Var, "\n")

VarName <- paste("Data$", Var, sep = "")

Vals <- eval(parse(text = VarName))

P <- anova(lm(Vals ~ Data$Family))$Pr(>F)[1]

Fval <- anova(lm(Vals ~ Data$Family))$F value'[1]

if (Fval > 2){

# cat("Using family means since P=", P, "\n\n")

cat("Using family means since F=", Fval, "\n\n")

NewVar <- ReplaceNAByGroupMean(Vals, Data$Family)

```

```

} else {

  NewVar <- ReplaceNAByGroupMean(Vals)

#   cat("Using grand means since P=", P, "\n\n")

  cat("Using grand means since F=", Fval, "\n\n")

}

NewVarName <- paste(Var, ".Mean4NA", sep = "")

Data <- cbind(Data, NewVar)

colnames(Data)[colnames(Data) == "NewVar"] <- NewVarName

}

# Create final predictor variables by appending variable schooling with NAs

# replaced by mean schooling.

FinalPredictVars <- c(as.character(FilteredVars[!idxVarNA]),

                      paste(FilteredVars[idxVarNA], "Mean4NA", sep = "."))

# Get index of rows that are not NA in any predictor variable

NotNAMat <- sapply(FinalPredictVars, function(x) !is.na(Data[,x]))

idxNotNARows <- rowMeans(NotNAMat) == 1

#####

# Test proportionality assumption and define strata

```

```
#####

# Auxilliary function to create a matrix of p-values for pairwise proportionality

CoxZphMatrix <- function(Covariate) {

  FactorLevels <- unique(Covariate)

  pVals <- rep(NA, length(FactorLevels))

  names(pVals) <- paste("NewCovariate", FactorLevels, sep = "")

  sapply(FactorLevels, function(x){

    NewCovariate <- Covariate

    NewCovariate[NewCovariate == x] <- 0

    SurvFit_cph <- coxph(SurvObj ~ NewCovariate + cluster(Family), data = Data)

    ZphResults <- cox.zph(SurvFit_cph)

    pValsLocal <- ZphResults$table[, "p"]

    if (length(pValsLocal) > 1){

      pValsLocal <- pValsLocal[names(pValsLocal) != "GLOBAL"]

      pVals[names(pValsLocal)] <- pValsLocal

    } else {

      pVals[names(pVals) != paste("NewCovariate", x, sep = "")] <- pValsLocal

    }

  })
}
```

```

    pVals

  })

}

# Auxilliary function to merge factor levels that don't differ significantly

# to coxzph

MergeLevels_Coxzph <- function(Covariate) {

  # Initialize maximum P-value and

  ZphMat <- CoxZphMatrix(Covariate)

  MaxP <- max(ZphMat, na.rm = T)

  NrLevels <- length(unique(Covariate[!is.na(Covariate)]))

  # As long as there are groups that don't differ (MaxP > 0.5) merge groups

  while (MaxP > 0.05 & NrLevels > 2){

    MergeFact <- colnames(ZphMat)[arrayInd(which.max(ZphMat),

      .dim = dim(ZphMat))]

    cat("Merging levels", MergeFact, "\n")

    Covariate[which(Covariate == MergeFact[1])] <- MergeFact[2]

    Covariate[which(Covariate == MergeFact[2])] <- paste(MergeFact, collapse = "+")

    NrLevels <- length(unique(Covariate[!is.na(Covariate)]))
  }
}

```

```

ZphMat <- CoxZphMatrix(Covariate)

MaxP <- max(ZphMat, na.rm = T)

}

list(NewGroups = Covariate, ZphMat = ZphMat)

}

# Create regression formula

PredictVars <- paste(FinalPredictVars, collapse = " + ")

FunCall_cph_zph <- paste("coxph(SurvObj ~", PredictVars,

                        "+ cluster(Family), data = Data)")

# Check for violation of the proportionality assumption

SurvFit_cph_zph <- eval(parse(text = FunCall_cph_zph))

cox.zph(SurvFit_cph_zph)

# Turn schooling into a factor and test proportionality of each factor level

Data$Schooling.Factor <- as.character(round(Data$Schooling.Ordinal.Mean4NA))

Merge_ToB <- MergeLevels_Coxzph(Data$Type.of.Bottom.1)

Merge_Scl <- MergeLevels_Coxzph(Data$Schooling.Factor)

# Combine merged groups and merge

```

```

CombinedCov <- paste(Merge_ToB$NewGroups, Merge_Scl$NewGroups, sep =
".and.")

MergeCombo <- MergeLevels_Coxzph(CombinedCov)

unique(MergeCombo$NewGroups)

# Define strata to refit best model with strata

Data$Strata <- MergeCombo$NewGroups

#####

# Find best combination of predictor variables

#####

# Fit effect of schooling in a separate run

SurvMFit.Schooling <-

  coxph(SurvObj ~ Schooling.Ordinal + cluster(Family) + strata(Strata),

    data = Data)

summary(SurvMFit.Schooling)

cox.zph(SurvMFit.Schooling)

# Build all possible models with final predictor variables

cat("\n\n***** Model selection with random effects ... ")

ModelEval <- BestModel_AllCombos_Survival(SurvObj = SurvObj,

```



```

PredictVars = FinalPredictVars,

AdditionalTerms = "cluster(Family) + strata(Strata)",

Data = Data)

cat(" DONE! ***** \n\n")

# Select the best model and save it

BestModel <- ModelEval$BestModel

summary(BestModel)

save(file = "Data/Processed Data/ModelEvalResultsSurvival.RData",

list = c("ModelEval", "Data", "Time0"))

write.csv(summary(BestModel)$coefficients[,c("coef", "Pr(>|z|)"],

"Manuscript/Table1.csv")

#####

# Goodness of Fit for the Best Model

#####

# Get predictor variables from equation

PredVars <- ModelEval$PredictVarsBestModel

# Create vector of predictor variables

```

```

PredVarsVect <- strsplit(PredVars, split = "\\+")[1]

PredVarsVect <- gsub(" ", "", PredVarsVect)

# Create a table of predictor variables for fitted relative hazard rates

PredictData <- rep(NA, nrow(Data))

for (Var in PredVarsVect) {

  VarType <- is(Data[,Var])[1]

  if (VarType %in% c("integer", "numeric")){

    PredictData <- cbind(PredictData, Data[,Var])

    colnames(PredictData)[ncol(PredictData)] <- Var

  } else {

    PredictData <- cbind(PredictData,

                        1*CreateIndicatorVars(Data[,Var], Var))

  }

}

# Get estimated fixed effects according to best model and set NA values to 0

FixedEffects <- BestModel$coefficients

FixedEffects[is.na(FixedEffects)] <- 0

# Reorder columns of PredictData_NotNA so that they match fixed effects

```

```

ColMatch <- match(names(FixedEffects), colnames(PredictData))

PredictData <- PredictData[, ColMatch]

# Get indicators of entries with all data not NA

NotNA <- apply(PredictData, 1, function(x) all(!is.na(x)))

PredictData_NotNA <- PredictData[NotNA, ]

Data_NotNA <- Data[NotNA, ]

# Calculate predicted relative hazard rate

PredRelHaz <- exp(PredictData_NotNA %*% FixedEffects)

# Add quantile groups to data table

Data_NotNA$RelHazQuantGroup <- QuantileGroups(PredRelHaz,

                                               Probs = seq(1/8, 1, 1/8))

# Perform cox

# Define a survival object

SurvObj_NotNA <- Surv(time = Data_NotNA$Year.of.record - Time0,

                     event = Data_NotNA$Event)

# Create regression formula

FunCall_cph <- paste("coxph(SurvObj_NotNA ~", PredVars,

```

```

"+ RelHazQuantGroup + cluster(Family) + strata(Strata), data =
Data_NotNA)")

# Perform survival analysis

SurvFit_cph <- eval(parse(text = FunCall_cph))

summary(SurvFit_cph)

#####

# Create numeric type of bottom

#####

# Type.of.Bottom.1 is a categorical variable where the category "no bottom" have been
# proven to be a considered as a stratifying variable. Therefore, we transformt this
# variable into an ordinal variable excluding "no bottom" category

Data$Type.of.Bottom <- Data$Type.of.Bottom.1

Data$Type.of.Bottom[Data$Type.of.Bottom == "soft"] <- 1

Data$Type.of.Bottom[Data$Type.of.Bottom == "soft - hard"] <- 2

Data$Type.of.Bottom[Data$Type.of.Bottom == "hard"] <- 3

Data$Type.of.Bottom[Data$Type.of.Bottom == "no bottom"] <- NA

Data$Type.of.Bottom <- as.numeric(Data$Type.of.Bottom)

# Save data with new strata column

```

```

write.csv(Data, "C:/Masters project/Data/Processed
Data/SppList_wEnvVars_Strata.csv")

#####

# Pairwise correlation between filtered variables

#####

# Create a vector of numeric predictor variables

PredVarsVectNum <- as.character(FilteredVars)

PredVarsVectNum[PredVarsVectNum == "Type.of.Bottom.1"] <- "Type.of.Bottom"

# Create all pairwise combinations of predictor variables

PredVarsCombo <- combn(PredVarsVectNum, 2)

# Initialize correlation matrix and fill in entries

CorrMat <- matrix(nrow = length(PredVarsVectNum),

                  ncol = length(PredVarsVectNum),

                  dimnames = list(PredVarsVectNum, PredVarsVectNum))

for (i in 1:ncol(PredVarsCombo)){

  Test <- cor.test(Data[,PredVarsCombo[1, i]], Data[,PredVarsCombo[2, i]],

                  method = "kendall")

  P <- round(Test$p.value, 4)

```

```

Cor <- round(Test$estimate, 2)

Entry <- paste(Cor, " (", P, ")", sep = "")

Entry <- Cor

CorrMat[PredVarsCombo[1, i], PredVarsCombo[2, i]] <- Entry

}

# Write correlation matrix as csv file

write.csv(CorrMat, file = "Manuscript/PredictVarCorrs.csv")

#####

#           #

#       Plots       #

#           #

#####

# Define time labels for the plots below

TimeLabels <- seq(1875, 2000, 25)

#####

# Multipanel plots to show effects of significant covariates

#####

# Set up plot parameters

```

```

par(mfrow = c(3, 2), mar = c(0.5, 3, 3, 2) + .1,

    oma = c(2.5, 2.5, 1.5, 1.5))

Lcex = 0.9

YI = 0.3

##### Schooling variable not significant anymore after stratification, therefore no
plotting

### Plot for schooling levels

## Calculate proportion of migrants per schooling level

SFit <- survfit(SurvObj ~ round(Schooling.Ordinal), data = Data)

LegendLabels <- rep(NA, length(names(SFit$strata)))

LegendLabels[grep("=1", names(SFit$strata))] <- "1-2"

LegendLabels[grep("=2", names(SFit$strata))] <- "3-10"

LegendLabels[grep("=3", names(SFit$strata))] <- "10-100"

LegendLabels[grep("=4", names(SFit$strata))] <- ">100"

nL <- length(SFit$strata)

plot(SFit, fun = "log", lty = 1:nL, xaxt = "n", ylab = "", xlab = "",

     main = "A", ylim = c(0.6, 1), lwd = 1.75)

axis(1, at = TimeLabels - Time0, labels = TimeLabels)

```

```

legend("bottomleft", lty = 0:nL, title = "Schooling size",

      legend = c("", LegendLabels), cex = Lcex, bty = "n", y.intersp = YI, lwd = 1.75,

      title.adj = 0)

# Plot for DemersPelag levels

# Calculate proportion per demersal-pelagic gradient

SFit <- survfit(SurvObj ~ DemersPelag, data = Data)

nL <- length(SFit$strata)

LegendLabels <- rep(NA, length(names(SFit$strata)))

LegendLabels[grep("=1", names(SFit$strata))] <- "surface"

LegendLabels[grep("=2", names(SFit$strata))] <- "water column"

LegendLabels[grep("=3", names(SFit$strata))] <- "close to bottom"

LegendLabels[grep("=4", names(SFit$strata))] <- "on bottom"

plot(SFit, fun = "log", lty = 1:nL, xaxt = "n", ylab = "", xlab = "",

      main = "B", ylim = c(0.6, 1), lwd = 1.75)

axis(1, at = TimeLabels - Time0, labels = TimeLabels)

O <- c(4:1)

legend("bottomleft", lty = c(0,c(1:nL)[O]), title = "Demersal - pelagic",

      legend = c("", LegendLabels[O]), cex = Lcex, bty = "n",

```



```

x.intersp = 1, title.adj = 0, y.intersp = YI, lwd = 1.75)

# Plot for Type of bottom 1

# Calculate proportion of migrants per Type of bottom 1 level

SFit <- survfit(SurvObj ~ Type.of.Bottom.1, data = Data)

nL <- length(SFit$strata)

LegendLabels <- sapply(names(SFit$strata),

                        function(x) strsplit(x, "=")[[1]][2])

plot(SFit, fun = "log", lty = 1:nL, xaxt = "n", ylab = "", xlab = "",

      main = "C", ylim = c(0.8, 1), lwd = 1.75)

axis(1, at = TimeLabels - Time0, labels = TimeLabels)

O <- c(4, 1, 2, 3)

legend("bottomleft", lty = c(0,c(1:nL)[O]), title = "Type of bottom",

      legend = c("", LegendLabels[O]), cex = Lcex, bty = "n",

      x.intersp = 1, title.adj = 0, y.intersp = YI, lwd = 1.75)

# Plot for Nr of Species per family

# Turn nr of species per family in factor with 4 levels

Data$NrSpLevels <- cut(Data$NrSpPerFamily_RS, breaks = c(0, 10, 20, 120 ))

```

```

# Calculate proportion of migrants per species per family level

SFit <- survfit(SurvObj ~ NrSpLevels, data = Data)

nL <- length(SFit$strata)

LegendLabels <- sapply(names(SFit$strata), function(x) {

  Range <- strsplit(x, "\\(")[[1]][2]

  RangeSplit <- strsplit(Range, ",")[1]

  R1 <- as.numeric(RangeSplit[1]) + 1

  paste(R1, gsub("]", "", RangeSplit[2]), sep = "-")

})

plot(SFit, fun = "log", lty = 1:nL, xaxt = "n", ylab = "", xlab = "",

      main = "D", ylim = c(0.85, 1), lwd = 1.75)

axis(1, at = TimeLabels - Time0, labels = TimeLabels)

legend("bottomleft", lty = 0:nL, title = "Nr. species/family",

      legend = c("", LegendLabels), cex = Lcex, bty = "n",

      x.intersp = 1, title.adj = 0, y.intersp = YI, lwd = 1.75)

# Plot for distance from Canal

# Turn nr of species per family in factor with 4 levels

Data$MinDistLevels <- cut(Data$MinDistToCanal.Mean4NA, breaks =

```

```

c(0, 500, 2000, 4000, 15000 ))

# Calculate proportion of migrants per species per distance class

SFit <- survfit(SurvObj ~ MinDistLevels, data = Data)

nL <- length(SFit$strata)

LegendLabels <- sapply(names(SFit$strata), function(x) {

  Range <- strsplit(x, "\\(")[[1]][2]

  RangeSplit <- strsplit(Range, ",")[1]

  R1 <- as.numeric(RangeSplit[1]) + 1

  R2 <- gsub("]", "", RangeSplit[2])

  R2 <- as.numeric(R2)

  paste(R1, R2, sep = "-")

})

plot(SFit, fun = "log", lty = 1:nL, xaxt = "n", ylab = "", xlab = "",

      main = "E", ylim = c(0.85, 1), lwd = 1.75)

axis(1, at = TimeLabels - Time0, labels = TimeLabels)

legend("bottomleft", lty = 0:nL, title = "Distance [km]",

      legend = c("", LegendLabels), cex = Lcex, bty = "n",

      x.intersp = 1, title.adj = 0, y.intersp = YI, lwd = 1.75)

```

```

# Calculate proportion of migrants per species per distance class

SFit <- survfit(SurvObj ~ Strata, data = Data)

nL <- length(SFit$strata)

LegendLabels <- rep(NA, length(names(SFit$strata)))

LegendLabels[grep("no bottom", names(SFit$strata))] <- "I"

LegendLabels[grep("both", names(SFit$strata))] <- "III"

LegendLabels[grep("=hard.and.1", names(SFit$strata))] <- "II"

plot(SFit, fun = "log", lty = 1:nL, xaxt = "n", ylab = "", xlab = "",

      main = "F", ylim = c(0.85, 1), lwd = 1.75)

axis(1, at = TimeLabels - Time0, labels = TimeLabels)

O <- c(3:1)

legend("bottomleft", lty = c(0, c(1:nL)[O]), title = "Group",

      legend = c("", LegendLabels[O]), cex = Lcex, bty = "n",

      x.intersp = 1, title.adj = 0, y.intersp = YI, lwd = 1.75)

# Add axes labels to the margins

mtext("Year", side = 1, line = 1, outer = T)

mtext("Proportion without record in Mediterranean", side = 2, line = 1, outer = T)

# Copy plot to pdf device

```

```
dev.copy2pdf(file = "Manuscript/Figure 2.pdf", width = 7,  
             height = 7)
```

C. PenalizedRidgeRegression script:

```
#####
```

```
# Penalized Ridge regression analysis
```

```
#####
```

```
# Penalized package is used in this script to build a model that predicts well without
```

```
# collinearity. The ridge regression analysis is an alternative way of dealing with the
```

```
# weakly-fitted model in order to decrease its variance and obtain better estimates.
```

```
# It includes some bias to our model and through ridge regression we will have a trade-  
off
```

```
# between variability and bias.
```

```
par(mfrow=c(1,1))
```

```
# Source start script
```

```
source("C:/Masters project/Scripts/_StartScript.r")
```

```
# Source variable filtering script
```

```

source("C:/Masters project/Scripts/VariableFilteringAndAnalysis_Survival.r")

# Get index of rows that are not NA in any predictor variable

FinalPredictVars <- PredVarsVect

NotNAMat <- sapply(FinalPredictVars, function(x) !is.na(Data[,x]))

idxNotNARows <- which(rowMeans(NotNAMat) == 1)

DataNoNA <- Data[idxNotNARows,]

##### Ridge Regression using penalized package

## Profiling cross-validated log likelihood

# Create new SurvObj

PRSurvObj <- Surv(time = DataNoNA$Year.of.record - Time0,

                 event = DataNoNA$Event)

fit1 <- profL1(PRSurvObj ~ MinDistToCanal + NrSpPerFamily_RS +Type.of.Bottom.1
+
                 DemersPelag + Schooling.Ordinal.Mean4NA,

                 data=DataNoNA, fold=10,

                 minlambda1=0.01, maxlambda1 = 50, plot=TRUE)

fit2 <- profL2(PRSurvObj ~ MinDistToCanal + NrSpPerFamily_RS +Type.of.Bottom.1
+
                 DemersPelag + Schooling.Ordinal.Mean4NA,

```

```

data=DataNoNA, fold=fit1$fold,

minlambda2 = 0.01, maxlambda2 = 50)

par(mfrow = c(1,1))

plot(fit2$lambda, fit2$cvl, type="l", ylab = "Cross Validated Likelihood",

xlab = "Lambda2", main = "Profiling CVL vs Lambda2")

dev.copy2pdf(file = "Figures/Profiling CVL vs Lambda2.pdf", width = 7, height = 5)

Plotpath_modified_no_colors(fit2$fullfit, XLab = expression(Lambda[2]), standardize
= TRUE)

dev.copy2pdf(file = "Figures/Variation of coefficients with respect to Lambda2 -- No
Colors.pdf",

width = 7, height = 5)

## Optimum lambda 2

opt <- optL2(PRSurvObj ~ MinDistToCanal + NrSpPerFamily_RS +Type.of.Bottom.1
+

DemersPelag + Schooling.Ordinal.Mean4NA,

data=DataNoNA, fold = 5)

coefficients(opt$fullfit)

Lambda2Opt <- opt$lambda

# Penalized Fit

```

```

Penalized_Fit <- penalized(PRSurvObj ~ MinDistToCanal + NrSpPerFamily_RS
+Type.of.Bottom.1 +

      DemersPelag + Schooling.Ordinal.Mean4NA,

      data=DataNoNA, lambda2=Lambda2Opt)

loglik(Penalized_Fit)

coefficients(Penalized_Fit)

```

D. ML_SolowCostello script:

```

## The script below estimates parameters of the introduction process according
## to the method by Solow & Costello 2004, Ecology

# Source start script and load packages

source("C:/Masters project/Scripts/_StartScript.r")

library(boot)

#####

#                                     #

#       Read data                       #

#                                     #

```



```

#####

# Read suez canal data

CanalData <- read.csv("Data/Raw Data/Suez canal data.csv")

# Read in whole species list from Golani and Bogorodski 2010 (Red Sea risk set)

SppList <- read.csv("C:/Masters project/Data/Processed
Data/SppList_wEnvVars_Strata.csv",

                as.is = T)

# Merge data with time data and keep only relevant columns

SppList <- SppList[,c("Year.of.record", "Lessepsian", "Strata")]

#####

#                                     #

#   Generate input data               #

#                                     #

#####

#####

# Auxilliary function

#####

# Function to generate species counts per time interval

```

```

SpPerInterval <- function(Stratum, YearIntervals) {

  idxIntroduced <- !is.na(SppList$Year.of.record)

  idxStratum <- SppList$Strata == Stratum

  YearData <- SppList$Year.of.record[which(idxIntroduced & idxStratum)]

  sapply(1:(length(YearIntervals) - 1), function(x){

    sum(YearData >= YearIntervals[x] & YearData < YearIntervals[x + 1])

  })

}

#####

# Input data based on Golani and Bogorodski 2010

#####

# Create a vector of years

YearInterval <- 1

Years <- seq(min(SppList$Year.of.record, na.rm = T), 2013,

            YearInterval)

# Get all the strata

UniqueStrata <- unique(SppList$Strata)

# Data for demersal hard-bottom species

```

```

yt_NoBottom <- SpPerInterval(UniqueStrata[2], Years)

yt_SoftBottom <- SpPerInterval(UniqueStrata[1], Years)

yt_HardBottom <- SpPerInterval(UniqueStrata[3], Years)

#####

#                                     #

#   General ikelihood functions       #

#                                     #

#####

#####

# Basic functions

#####

# Function to calculate the lambda for one data set and one set of parameters

Lambda <- function(nt, g0, g1, g2, b0, b1){

  tvect <- seq_len(nt)

  ts <- outer(tvect, tvect, "-")

  tsneg <- ts < 0

  ts[tsneg] <- 0

  Pi_LinTerm <- g0 + g1 * tvect + g2 * ts

```

```

Pi_st    <- boot::inv.logit(Pi_LinTerm)

Pi_st[tsneg] <- 0

P_st     <- Pi_st

for (i in 2:nt){

  P_st[i,i:1] <- c(1, cumprod(1 - Pi_st[i, i:2])) * Pi_st[i, i:1]

}

mu    <- exp(b0 + b1 * tvect)

P_st %*% mu

}

# Function to calculate the likelihood for one data set and one set of parameters

LogL_local <- function(yt, g0, g1, g2, b0, b1){

  nt <- length(yt)

  lambda <- Lambda(nt, g0, g1, g2, b0, b1)

  sum(yt * log(lambda) - lambda)

}

# Log-likelihood for all three data sets

LogL <- function(g0_1, g1_1, g2_1, b0_1, b1_1,

                g0_2, g1_2, g2_2, b0_2, b1_2,

```

```

    g0_3, g1_3, g2_3, b0_3, b1_3){

LogL_local(yt_NoBottom, g0_1, g1_1, g2_1, b0_1, b1_1) +

    LogL_local(yt_SoftBottom, g0_2, g1_2, g2_2, b0_2, b1_2) +

    LogL_local(yt_HardBottom, g0_3, g1_3, g2_3, b0_3, b1_3)

}

#####

#                                     #

#  Functions to estimate particular models      #

#                                     #

#####

#####

# Function for single data set

#####

# Optimize parameters for a single data set

MaxL_SingleData <- function(yt, StartPars, FixedPars, Maxit = 500){

    ArgList <- vector("list", length(StartPars) + 1)

    names(ArgList) <- c("yt", names(StartPars))

    ArgList$yt <- yt

```

```

StartPar_Subset <- StartPars[!names(StartPars) %in% names(FixedPars)]

optim(par = StartPar_Subset,

      fn = function(x){

        StartPars[names(x)] <- x

        ArgList[2:length(ArgList)] <- StartPars

        -do.call(LogL_local, ArgList)

      },

      control = list(maxit = Maxit))

}

# Combine optimization of parameters of separate single data set

CombineMaxL_SingleData <- function(StartPar_full, FixedPars, Maxit = 500){

  yList <- list(yt_NoBottom = yt_NoBottom, yt_SoftBottom = yt_SoftBottom,

              yt_HardBottom = yt_HardBottom)

  OptList <- lapply(1:3, function(x){

    Suffix <- paste("_", x, sep = "")

    StartPars <- StartPar_full[grep(Suffix, names(StartPar_full))]

    names(StartPars) <- substr(names(StartPars), 1, 2)

    MaxL_SingleData(yList[[x]], StartPars, FixedPars, Maxit)
  })
}

```

```

    })

    names(OptList) <- names(yList)

    OptList

  }

#####

# Function for 3 data sets combined

#####

# Function to maximizes likelihood for a given values of starting parameters

# Input:

# FixedPars: named vector of fixed parameters (not optimized)

# SharedPars: names of parameters shared between groups

MaxL_CombinedData <- function(StartPar_full, FixedPars = NULL,

                               SharedPars = NULL,

                               Maxit = 500){

  # Check whether some parameters are specified as fixed and shared

  if (length(intersect(names(FixedPars), SharedPars)) > 0){

    warning("Some parameters are specified as shared and fixed. \n",

            "Fixed parameters are always assumed to be shared.\n")
  }

```

```

SharedPars <- setdiff(SharedPars, names(FixedPars))

}

# Create a vector of parameter names that are fixed and fill in StartPar_full

FixedNames <- NULL

for (n in names(FixedPars)){

  MatchNames <- grep(n, names(StartPar_full), value = T)

  StartPar_full[MatchNames] <- FixedPars[n]

  FixedNames <- c(FixedNames, MatchNames)

}

# Create a vector of parameters to be estimated (not fixed)

NotFixed <- !names(StartPar_full) %in% FixedNames

StartPar_Subset <- StartPar_full[NotFixed]

# Create entries and a map for parameters shared between datasets

SharedListMap <- lapply(SharedPars, function(x){

  grep(x, names(StartPar_Subset))

})

if (length(SharedListMap) > 0){

  SharedParVals <- sapply(SharedListMap, function(x)StartPar_Subset[x[1]])

```



```

StartPar_Subset <- StartPar_Subset[-unlist(SharedListMap)]

names(SharedParVals) <- SharedPars

StartPar_Subset  <- c(SharedParVals, StartPar_Subset)

}

ParMap_full  <- vector("list", length(StartPar_Subset))

names(ParMap_full) <- names(StartPar_Subset)

for (pn in names(StartPar_Subset)){

  ParMap_full[[pn]] <- grep(pn, names(StartPar_full))

}

# Create a list with arguments for the full likelihood model

ArgList  <- as.list(StartPar_full)

optim(par = StartPar_Subset,

      fn = function(x){

        for (n in names(x)){

          ArgList[ParMap_full[[n]]] <- x[n]

        }

        -do.call(LogL, ArgList)

      },

```

```

    control = list(maxit = Maxit))

}

#####

# Functions to summarize results

#####

# Get optimization result from comparing single sample and multi sample data

BestOptim <- function(OptimSingle, OptimMulti){

  NrPars <- length(OptimSingle$par)

  ParRows <- (NrPars + 1):(2 * NrPars)

  LLRow <- 2 * NrPars + 1

  minCol <- which.min(OptimMulti[LLRow,])

  LLmin <- OptimMulti[LLRow, minCol]

  names(LLmin) <- NULL

  if (LLmin < OptimSingle$value){

    list(par = OptimMulti[ParRows, minCol], value = LLmin)

  } else {OptimSingle}

}

# Function to extract AIC from optim object

```

```

AICfromOptim <- function(Opt){

  c(k = length(Opt$par),

    AIC = 2 * (length(Opt$par) + Opt$value))

}

#####

#                               #

#   Likelihood maximization     #

#                               #

#####

#####

# Create parameter start values and options

#####

# Create starting values for b0

b0Start1 <- log(sum(yt_NoBottom) / length(yt_NoBottom))

b0Start2 <- log(sum(yt_SoftBottom) / length(yt_SoftBottom))

b0Start3 <- log(sum(yt_HardBottom) / length(yt_HardBottom))

# Create starting values for g0

Startg0 <- function(yt) {

```

```

t2 <- min(which(cumsum(yt) >= 2))

logit(4 / t2^2 / sum(yt) * length(yt))

}

g0Start1 <- Startg0(yt_NoBottom)

g0Start2 <- Startg0(yt_SoftBottom)

g0Start3 <- Startg0(yt_HardBottom)

inv.logit(g0Start1)

StartPar_full <- c(g0_1 = 0, g1_1 = 0, g2_1 = 0, b0_1 = b0Start1, b1_1 = 0,

g0_2 = 0, g1_2 = 0, g2_2 = 0, b0_2 = b0Start2, b1_2 = 0,

g0_3 = 0, g1_3 = 0, g2_3 = 0, b0_3 = b0Start3, b1_3 = 0)

# Create a list with options of which parameters to fix

FixedParsOptions <- list(None = NULL, Detect = c(g1 = 0, g2 = 0),

Intro = c(b1 = 0), Both = c(b1 = 0, g1 = 0, g2 = 0))

# Create a list with options of which parameters are shared

SharedParsOptions <- list(Detect = c("g0", "g1", "g2"),

Intro = c("b0", "b1"),

Both = c("b0", "b1", "g0", "g1", "g2"))

#####

```

```

# Maximize likelihood

#####

# Intialize list of optimization output and other parameters

NrCombos <- length(FixedParsOptions) * (1 + length(SharedParsOptions))

OptList <- vector("list", NrCombos)

ResultTable <- data.frame(FixedPars = rep(NA, NrCombos),

                          SharedPars = rep(NA, NrCombos),

                          LogLik = rep(NA, NrCombos),

                          Convergence = rep(NA, NrCombos),

                          NrPars = rep(NA, NrCombos),

                          AIC = rep(NA, NrCombos))

Counter <- 1

# Find maximum likelihood for each combination

for (j in 1:length(FixedParsOptions)){

  # Determine fixed parameters and produce status message

  FixedP <- FixedParsOptions[[j]]

  cat("Maximum likelihood calculation", Counter, "of", length(OptList), "\n")

  cat("Fixed parameters:", names(FixedP), "\n")
}

```

```

cat("Shared parameters: none\n\n")

# Perform optimization and calculate AIC

Opt <- CombineMaxL_SingleData(StartPar_full, FixedP, Maxit = 1000)

OptList[[Counter]] <- Opt

AICandK <- rowSums(sapply(Opt, function(x) AICfromOptim(x)))

# Fill in entries in result table

if (!is.null(FixedP)){

  FixedNames <- paste(names(FixedP), collapse = "+")

} else {

  FixedNames <- "none"

}

ResultTable$FixedPars[Counter] <- FixedNames

ResultTable$SharedPars[Counter] <- "none"

ResultTable$LogLik[Counter] <- - sum(sapply(Opt, function(x) x$value))

ResultTable$Convergence[Counter] <- max(sapply(Opt, function(x) x$convergence))

ResultTable$NrPars[Counter] <- AICandK["k"]

ResultTable$AIC[Counter] <- AICandK["AIC"]

Counter <- Counter + 1

```

```

}

# Find maximum likelihood for each combination

for (i in 1:length(SharedParsOptions)){

  SharedP <- SharedParsOptions[[i]]

  for (j in 1:length(FixedParsOptions)){

    # Determine fixed parameters and produce status message

    FixedP <- FixedParsOptions[[j]]

    cat("Maximum likelihood calculation", Counter, "of", length(OptList), "\n")

    cat("Fixed parameters:", names(FixedP), "\n")

    cat("Shared parameters:", SharedP, "\n\n")

    # Perform optimization and calculate AIC

    Opt <- MaxL_CombinedData(StartPar_full, FixedPars = FixedP,

      SharedPars = SharedP, Maxit = 1000)

    OptList[[Counter]] <- Opt

    AICandK <- AICfromOptim(Opt)

    # Fill in entries in result table

    if (!is.null(FixedP)){

      FixedNames <- paste(names(FixedP), collapse = "+")

```

```

} else {

  FixedNames <- "none"

}

ResultTable$FixedPars[Counter] <- FixedNames

ResultTable$SharedPars[Counter] <- paste(SharedP, collapse = "+")

ResultTable$LogLik[Counter] <- - Opt$value

ResultTable$Convergence[Counter] <- Opt$convergence

ResultTable$NrPars[Counter] <- AICandK["k"]

ResultTable$AIC[Counter] <- AICandK["AIC"]

Counter <- Counter + 1

}

}

# Results of model with lowest AIC

BestModelResults <- OptList[[which.min(ResultTable$AIC)]]

#####

# Likelihood ratio test

#####

# Estimate parameters for b1_1 = 0, b1_2 = 0, and b1_3 = 0

```



```

M__b11 <- optim(

par = StartPar_full[c("g0_1", "b0_1", "b0_2", "b0_3", "b1_2", "b1_3")],

fn = function(x){

- LogL(x["g0_1"], 0, 0, x["b0_1"], 0,

      x["g0_1"], 0, 0, x["b0_2"], x["b1_2"],

      x["g0_1"], 0, 0, x["b0_3"], x["b1_3"])

}, control = list(maxit = 1000))

```

```

M__b12 <- optim(

par = StartPar_full[c("g0_1", "b0_1", "b0_2", "b0_3", "b1_1", "b1_3")],

fn = function(x){

- LogL(x["g0_1"], 0, 0, x["b0_1"], x["b1_1"],

      x["g0_1"], 0, 0, x["b0_2"], 0,

      x["g0_1"], 0, 0, x["b0_3"], x["b1_3"])

}, control = list(maxit = 1000))

```

```

M__b13 <- optim(

par = StartPar_full[c("g0_1", "b0_1", "b0_2", "b0_3", "b1_1", "b1_2")],

fn = function(x){

- LogL(x["g0_1"], 0, 0, x["b0_1"], x["b1_1"],

```

```

x["g0_1"], 0, 0, x["b0_2"], x["b1_2"],

x["g0_1"], 0, 0, x["b0_3"], 0)

}, control = list(maxit = 1000))

# Perform likelihood ratio tests:

1 - pchisq(2*(M__b11$value - BestModelResults$value), 1)

1 - pchisq(2*(M__b12$value - BestModelResults$value), 1)

1 - pchisq(2*(M__b13$value - BestModelResults$value), 1)

# Write result into manuscript folder

ResultTable$DeltaAIC <- ResultTable$AIC - min(ResultTable$AIC)

ResultTable$LogLik <- round(ResultTable$LogLik, 1)

ResultTable$AIC <- round(ResultTable$AIC, 1)

ResultTable$DeltaAIC <- round(ResultTable$DeltaAIC, 1)

AICOrder <- order(ResultTable$AIC)

write.csv(ResultTable[AICOrder, ], "Manuscript/Results_timeModels.csv", row.names =
F)

# Save results

save(list = c("OptList", "ResultTable", "SppList", "yt_NoBottom",

"yt_SoftBottom", "yt_HardBottom"),

```

```

file = "Data/Processed data/ML_SolowCostelloResults.RData")

#####

#           #

#       Plots       #

#           #

#####

#####

# Plot functions

#####

# Function to plot detection over time

DetectionPlot <- function(Pars){

  DefaulPars <- c(g0 = 0, g1 = 0, g2 = 0, b0 = 0, b1 = 0)

  names(Pars) <- substr(names(Pars), 1, 2)

  DefaulPars[names(Pars)] <- Pars

  tvect <- 0:110

  Cols <- rainbow(11)

  ts  <- 0:11

  Pi_LinTerm <- DefaulPars["g0"] + DefaulPars["g1"] * tvect +

```

```

DefaultPars["g2"] * ts[1]

Pi_st <- boot::inv.logit(Pi_LinTerm)

plot(tvect, Pi_st, type = "l", xlab = expression(italic("t")),

     ylab = expression(italic(pi[st])), col = Cols[1], ylim = c(0, 1),

     xlim = c(-25, 111))

for (i in 2:11){

  Pi_LinTerm <- Pars["g0"] + Pars["g1"] * tvect + Pars["g2"] * ts[i]

  Pi_st <- boot::inv.logit(Pi_LinTerm)

  lines(tvect, Pi_st,col = Cols[i])

}

legend("topleft", legend = paste("t-s =", ts), lty = 1, col = Cols, cex = 0.5)

}

# Function to plot cumulative lambda, along with observed detections

Pars <- BestModelResults$par

CumulLambdaPlot <- function(Pars){

  Pars <- BestModelResults$par

  DefaultPars <- rep(0, 15)

  names(DefaultPars) <- sapply(1:3,

```

```

function(x) paste(c("g0", "g1", "g2", "b0", "b1"), x, sep = "_")

SharedPars <- Pars[!grep("_", names(Pars))]

SharedParsRep <- rep(SharedPars, each = 3)

RepNames <- sapply(names(SharedPars), function(x) paste(x, 1:3, sep = "_"))

names(SharedParsRep) <- RepNames

Pars <- c(SharedParsRep, Pars[grep("_", names(Pars))])

DefaultPars[names(Pars)] <- Pars

tvect <- seq_along(yt_NoBottom)

# Determine years for tickmarks

TickYears <- seq(1925, 2000, 25)

TickPos <- which((tvect + 1902) %in% TickYears) + 0.5

lambda1 <- Lambda(length(tvect), DefaultPars["g0_1"], DefaultPars["g1_1"],
  DefaultPars["g2_1"], DefaultPars["b0_1"],
  DefaultPars["b1_1"])

lambda2 <- Lambda(length(tvect), DefaultPars["g0_2"], DefaultPars["g1_2"],
  DefaultPars["g2_2"], DefaultPars["b0_2"],
  DefaultPars["b1_2"])

lambda3 <- Lambda(length(tvect), DefaultPars["g0_3"], DefaultPars["g1_3"],

```

```

DefaultPars["g2_3"], DefaultPars["b0_3"],

DefaultPars["b1_3"])

plot(tvect, cumsum(yt_NoBottom), type = "s", xlab = "Year",

ylab = "Cumulative detection",

# ylab = expression(paste("Cumulative detection, ", italic(lambda[t])),

ylim = c(0, 60), xaxt = "n", cex = 1.5, cex.lab = 1.5)

lines(tvect, cumsum(lambda1), lty = 2, lwd = 2)

lines(tvect, cumsum(yt_SoftBottom), type = "s")

lines(tvect, cumsum(lambda2), lty = 2, lwd = 2)

lines(tvect, cumsum(yt_HardBottom), type = "s")

lines(tvect, cumsum(lambda3), lty = 2, lwd = 2)

text(x = rep(98, 3), y = c(5, 20, 45), c("II", "I", "III"))

axis(1, at = TickPos, labels = TickYears)

}

# Function to plot lambda

LambdaPlot <- function(Pars){

names(Pars) <- substr(names(Pars), 1, 2)

tvect <- 0:110

```

```

lambda <- Lambda(length(tvect), Pars["g0"], Pars["g1"], Pars["g2"],
                Pars["b0"], Pars["b1"])

plot(tvect, lambda, type = "l", xlab = expression(italic("t")),
     ylab = expression(italic(lambda[t])))
}

#####

# Plots for parameter estimates

#####

# Plot detection for different parameters of the full model

DetectionPlot(BestModelResults$par)

# Plot cumulative detection

par(mfrow = c(1,1), mar = c(5, 5, 4, 1) + 0.1)

CumulLambdaPlot(BestModelResults$par)

dev.copy2pdf(file = "Figures/FittedSolowCostelloModel.pdf", height = 7,
            width = 7)

# Extrapolation plot

Pars <- BestModelResults$par

ts <- 0:200

```

```

ys1 <- cumsum(exp(Pars["b0_1"] + Pars["b1_1"] * ts))

ys2 <- cumsum(exp(Pars["b0_2"] + Pars["b1_2"] * ts))

ys3 <- cumsum(exp(Pars["b0_3"] + Pars["b1_3"] * ts))

min(which(ys3 > ys1)) + 1902

min(which(ys3 > ys2)) + 1902

plot(ts, ys1, type = "l", ylim = c(0, 100), xlim = c(100, 140))

lines(ts, ys2)

lines(ts, ys3)

exp(7.2)/(1+ exp(7.2))

yt_HardBottom

exp(Pars["b0_1"] + Pars["b1_1"] * 111)

exp(Pars["b0_1"] + Pars["b1_1"] * 111)

exp(Pars["b0_1"] + Pars["b1_1"] * 111)

```

E. Functions:

1. BestModel_AllCombos_Survival function:

General description:


```
# The following function takes a vector of predictor variables, creates all
# combinations of these variables, runs coxph for each combination
# and returns the model with the lowest AIC.

# Arguments:

# SurvObj: a survival object.

# PredictVars: character vector of predictor variables.

# AdditionalTerms: character vector of additional terms.

# FitFun: character string specifying the function used for fitting

#   glm, glmer

# Data: data to be used in model

# family: (see glmer)

# Output:

# FittedModels: list of all fitted models

# AICs: vector of AIC values

# idxBestModel: index of best model

# PredictorsBestModel: predictor variables of best model

# BestModel: best fitted models

BestModel_AllCombos_Survival <- function(SurvObj, PredictVars,
```

```

        AdditionalTerms = NULL,

        Data = NULL) {

# Create a combination of all predictor variables

VarCombos <- c(PredictVars,

               unlist(lapply(2:length(PredictVars), function(m){

                   CombMat <- combn(PredictVars, m)

                   apply(CombMat, 2, FUN = function(x) paste(x, collapse= " + "))

               })))

# Loop through all combinations of predictor variables and fit models

FittedModels <- lapply(VarCombos, function(x){

  if(is.null(AdditionalTerms)){

    FunCall <- paste("coxph(SurvObj ~", x, ", data = Data)")

  } else {

    FunCall <- paste("coxph(SurvObj ~", x, " + ", AdditionalTerms, ", data = Data)")

  }

  eval(parse(text = FunCall))

#  glmer(Formula, family = family, data = Data)

})

```

```

# Extract AIC

AICs <- sapply(FittedModels, function(x) extractAIC(x))

AICs <- AICs[2,]

# Get index of model with lowest AIC (best model)

idxBestModel <- which.min(AICs)

# Return AICs, index of best model, predictor variable combination of best
# model, best model and all fitted models

list(AICs = AICs, idxBestModel = idxBestModel,

      PredictVarsBestModel = VarCombos[idxBestModel],

      BestModel = FittedModels[[idxBestModel]],

      FittedModels = FittedModels)

} # End of function

```

2. CreateIndicatorVars function:

```

# General description:

# The following function takes a categorical variable and creates a set of

# indicatorvariables - one for each factor laevel.

# Arguments:

```

```

# Values: a vector of values.

# VariableName: character string indicating the name of the variable

# Output:

# BooleanMatrix, rows correspond to original entries in CompositeVariable and
# columns corresponding to unique levels of CategoricalVariable

CreateIndicatorVars <- function(Values, VariableName = NULL) {

  # Create a vector of unique values

  UniqueValues <- unique(Values)

  BooleanMatrix <- sapply(UniqueValues, function(x) {

    Values == x

  })

  colnames(BooleanMatrix) <- paste(VariableName, UniqueValues, sep = "")

  # Return BooleanMatrix

  return(BooleanMatrix)

} # End of function

```

3. Plotpath_modified_no_colors function:

```

# This is a modified version of the function plotpath that allows specification of

```

```

# the x-axis label

Plotpath_modified_no_colors <-function (object, labelsiz = 0.6, standardize = FALSE,

                                XLab = NULL,...)

{

if (length(object) > 0) {

    betas <- sapply(object, coefficients, "p")

}

if (standardize) {

    weights <- weights(object[[1]])

    if (length(weights) > nrow(betas))

        weights <- weights[-seq_len(length(weights) - nrow(betas))]

    betas <- betas * matrix(weights, nrow = nrow(betas),

                            ncol = ncol(betas))

}

remove <- apply(betas, 1, function(bet) all(bet == 0))

if (all(remove))

    stop("all coefficients are zero for all values of lambda in this object")

lambda <- sapply(object, function(object) object@lambda1[1])

```

```

label <- "lambda1"

if (all(lambda == lambda[1])) {

  lambda <- sapply(object, function(object) object@lambda2)

  label <- "lambda2"

}

labwidth <- ifelse(labelsizesize > 0, max(strwidth(rownames(betas[!remove,
                                                                    ]), "inches", labelsizesize)), 0)

# Allow for the specification of a label

if (!is.null(XLab)) label <- XLab

margins <- par("mai")

par(mai = c(margins[1:3], max(margins[4], labwidth * 1.4)))

matplot(lambda, t(betas[!remove, , drop = FALSE]), type = "l",

          ylab = "Coefficient", xlab = label, col = "black", lty = c(1:sum(!remove)),

          xlim = rev(range(lambda)), ...)

if (labelsizesize > 0 && !is.null(rownames(betas))) {

  take <- which(!remove)

  for (i in 1:sum(!remove)) {

    j <- take[i]

```

```

axis(4, at = betas[j, ncol(betas)], labels = rownames(betas)[j],

      las = 1, cex.axis = labelsizes, col.axis = "black")

}

}

par(mai = margins)

return(invisible(NULL))

}

```

4. QuantileGroups function:

```

# General description:

# The following function reads in a vector of values, groups them into

# quantiles and creates a vector of factor values, indicating for each input

# value which quantile group it belongs to

# Arguments:

# InputValues: vector of numeric values.

# Probs: vector of cumulative proportions to group the InputValues

# Min: theoretical

# Output:

```

```

# Groups: vector of factor values (same length as vector InputValues),

#   indicating the quantile group each element of InputValues belongs to

QuantileGroups <- function(InputValues, Probs = seq(0.1, 1, 0.1)) {

  Quantiles <- quantile(InputValues, probs = Probs)

  Groups   <- cut(InputValues, c(min(InputValues), Quantiles))

  return(Groups)

} # End of function

```

5. ReplaceNAByGroupMean function:

```

# General description:

#   The following function takes a vector of data and groups and replaces

#   missing values in data vector by group-specific means

# Arguments:

#   Values: a vector containing data.

#   Groups: a vector containing groups, same length as Values

# Output:

#   ValuesMean4NA: Values with NAs replaced

ReplaceNAByGroupMean <- function(Values, Groups = rep(1, length(Values))) {

```



```

# Check that both vectors have the same length

if (length(Values) != length(Groups)){

  stop("Length of value and group vector have to be the same\n")

}

# Loop through groups and replace NA by group mean

ValuesMean4NA <- Values

AllGroups <- unique(Groups)

for (CurrentGroup in AllGroups){

  CurrentRows <- which(Groups == CurrentGroup)

  MeanVal <- mean(Values[CurrentRows], na.rm = T)

  NARows <- CurrentRows[is.na(ValuesMean4NA[CurrentRows])]

  ValuesMean4NA[NARows] <- MeanVal

}

# Replace all the remaining missing values by grand mean

GrandMean <- mean(Values, na.rm = T)

ValuesMean4NA[is.na(ValuesMean4NA)] <- GrandMean

ValuesMean4NA} # End of function

```

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