

Estimating the rate of biological introductions: Lessepsian fishes in the Mediterranean

JONATHAN BELMAKER,^{1,2,4} ERAN BROKOVICH,^{1,3} VICTOR CHINA,^{1,2} DANIEL GOLANI,³ AND MOSHE KIFLAWI^{1,2}

¹*Interuniversity Institute of Marine Sciences, Eilat, Israel*

²*Department of Life Sciences, Ben-Gurion University, Be'er Sheva, Israel*

³*Department of Evolution, Systematics and Ecology, Hebrew University, Jerusalem, Israel*

Abstract. Sampling issues preclude the direct use of the discovery rate of exotic species as a robust estimate of their rate of introduction. Recently, a method was advanced that allows maximum-likelihood estimation of both the observational probability and the introduction rate from the discovery record. Here, we propose an alternative approach that utilizes the discovery record of native species to control for sampling effort. Implemented in a Bayesian framework using Markov chain Monte Carlo simulations, the approach provides estimates of the rate of introduction of the exotic species, and of additional parameters such as the size of the species pool from which they are drawn. We illustrate the approach using Red Sea fishes recorded in the eastern Mediterranean, after crossing the Suez Canal, and show that the two approaches may lead to different conclusions. The analytical framework is highly flexible and could provide a basis for easy modification to other systems for which first-sighting data on native and introduced species are available.

Key words: *colonization; coral reef fishes; hierarchical Bayes; invasion; nonindigenous species; state-space modeling.*

INTRODUCTION

Biological introductions are one of the central causes of the current global biodiversity crisis, and entail high economic and social costs (Pimentel et al. 2000). Much effort has been devoted to understanding specific species attributes related to introduction and invasion success, with varying success (e.g., Golani 1993, Goodwin et al. 1999, Sutherland 2004, Lambdon and Hulme 2006). Broad-scale approaches aim to overlook heterogeneity among species and concentrate on the large-scale dynamics of introduction and invasion. Once introduction patterns are clear, it is easier to add species traits to form a predictive modeling framework. Such a context-specific model offers more flexibility and realism in assessing invasiveness compared to the mere identification of potentially damaging species (Lambdon and Hulme 2006). Establishing the magnitude of biological invasions is therefore the first step in controlling alien species (Bax et al. 2001), and realistic introduction patterns can be used by decision makers to define priorities and set prevention measures.

Sampling issues preclude the use of the rate with which new alien species are described as an estimate of introduction rates (Costello and Solow 2003, Solow and Costello 2004). Only the very common species with the most adverse effect are easily detected, while rarer invaders may be overlooked. Similarly, well-studied taxa will be sooner identified than poorly known taxa (Bax et al. 2001). Consequently, the number of known immigrants is always likely to underestimate the true number. In addition, an accelerating cumulative number of introduced species does not imply an accelerating introduction rate. Small absolute population size, population growth (Costello and Solow 2003), or extinction (Wonham and Pachevsky 2006) of introduced species may all result in an accelerating rate of new records even with a constant introduction rate and sampling effort. Nevertheless, this issue is still often neglected by studies that continue to use sighting rates as surrogate for introduction rates (e.g., Boudouresque and Verlaque 2002, Holeck et al. 2004).

Recently, Solow and Costello (2004) presented a method for inferring the rate of species introduction from the discovery record of new migrants (hereafter the SC model; see Appendix A). The method models both the discovery and the introduction process, thereby

Manuscript received 26 November 2007; revised 14 July 2008; accepted 21 July 2008. Corresponding Editor: E. Sala.

⁴E-mail: jbelmaker@ucsd.edu

enabling the statistical separation of the two effects. Here, we develop a method that utilizes the discovery record of native species to control for sampling effort. The added information allows us not only to estimate the introduction rate while relaxing assumptions regarding temporal trends in sampling intensities; but also to estimate additional parameters. One such parameter is the species-pool size of potential invaders, which may be of critical importance in predicting future impacts of species introductions.

Since the opening of the Suez Canal in 1869, species have been able to migrate between the Red Sea and the Eastern Mediterranean (hereafter Med). This migration of predominantly Red Sea species into the Med, a process known as “Lessepsian migration” (Por 1971), resulted in a large increase in the size of the species pool of Eastern Med fishes (Golani et al. 2002); with increasingly strong impact on the local environment. More than half of the known Lessepsian fish species have established large populations in the Med (Golani et al. 2006). Lessepsian migrants are also of economical importance as 50–90% of fish biomass in this region can be attributed to introduced fishes (Goren and Galil 2005). Nevertheless, no attempt has been made so far to give a reliable estimate of the rate of migration, and how it may be changing over time. The importance of resolving sampling biases in this system is highlighted by the fact that native Eastern Med species, which number should be relatively stable through time, are being continuously recorded (Golani 1996). The currently known number of fish species from the Red Sea is 1248, of which 502 are known from the Gulf of Suez—the potential launching pad for Lessepsian migrants (Golani 1999). These numbers form an upper bracket for the number of future potential Lessepsian introductions. However, the actual fraction of this pool that can potentially invade is unknown.

Using data on the fishes collected along Israel’s coastline over the past 80 years, we provide estimates of the current number of established Lessepsian fish in the Eastern Med, their rate of increase and the number of potential migrants in the Red Sea. We examine two hypotheses regarding the rate of Lessepsian fish immigration into the Mediterranean: one with the per-species probability of entering the Med, hereafter the immigration probability, held constant and the other in which immigration probability varies monotonically over time. Note that under this terminology “immigration probability” refers to a species’ probability (per unit time) of crossing into the Med, while “introduction rate” refers to the number (per unit time) of species that enter the Med for the first time. For reasons derived of the nature of the documentation record, we limit our analysis to migrant species that established viable Med populations, and do not consider “unsuccessful introductions.”

The model

Let R be the pool of Red Sea species that can (potentially) migrate into the eastern Med, which in turn is inhabited by a total of M native species. Next, consider the number of migrant species that have established a Med population after a series of t time intervals of a set duration. At the end of the t th interval, the proportion of native species in the total Eastern Med ichthyofauna is

$$\rho_t = \frac{M}{M + S_0 + \sum_{t=1}^t L_t} \tag{1}$$

where L_t is the number of migrant species that have established a population in the Med for the first time during the t th interval. The coincident proportion of the total number of migrant species established in the Med (for the first time) during the last (t)th interval is

$$\tau_t = \frac{L_t}{S_0 + \sum_{t=1}^t L_t} \tag{2}$$

(i.e., $1 - \tau_t$ of the migrants was established by $t - 1$). S_0 is the number of migrant species established in the Med by the onset of the first interval.

Next, define the sampling effort x_t as the total number of species that have been sampled in the Med during the t th interval. Assuming that a species’ probability of being sampled does not change with time and is independent of whether it is native or a migrant, and that species are correctly identified when first sampled, the expected number of new Med species which have been recorded in this interval is

$$\Delta S_{M_t} = x_t \times \rho_t \times \left(1 - \frac{S_{M_{t-1}}}{M}\right) \tag{3}$$

where $S_{M_{t-1}}$ is the number of Med species known at the end of the previous interval (i.e., the term in parenthesis is the probability that a native species was unknown from at the end of the previous interval). Similarly, the expected number of new migrant species that have been recorded in the t th interval is

$$\Delta S_{R_t} = x_t \times (1 - \rho_t) \times \left[(1 - \tau_t) \left(1 - \frac{S_{R_{t-1}}}{S_0 + \sum_{t=1}^t L_t}\right) + \tau_t \right]. \tag{4}$$

The left term of the sum in Eq. 4 is the proportion of migrant (Red Sea) species established in the Med by the $t - 1$ interval, unknown at the end of that interval.

Eqs. 3 and 4 assume that all of the species introduced into the Med during the t th interval do so at the interval’s onset: a reasonable approximation if intervals

are relatively short. As ΔS_M and ΔS_R can be calculated for any series of equally sized intervals that cut across the 80-year record of sampling in the Med, we can use a Bayesian framework to estimate the parameters appearing in Eqs. 3 and 4; as well as the uncertainty associated with these estimates. Bayesian models are increasingly being used in community ecology (Ellison 2004) and conservation biology (Wade 2000) for the relative ease with which they can accommodate complex models with multiple sources of uncertainty (Clark 2005).

Process model

The process model pertains to the successful introduction of Red Sea species into the Med, and the rate at which it proceeds. We considered the number of Red Sea species that cross the canal during the t th time interval as a random variable drawn from the following Poisson distribution:

$$L_t \sim \text{Poisson}(u_t \times R_{pt}) \tag{5}$$

where R_{pt} is the number of potential migrants that have not yet been established in the Med at the onset of the t th interval,

$$R_{pt} = R - S_0 - \sum_{t=1}^{t-1} L_t. \tag{6}$$

The parameter u_t is the probability with which each of the R Red Sea species enters and becomes established in the Med during t th interval, i.e., it is the main focus of the study. Eq. 5 is the Poisson approximation of the binomial that we adopted due to programming limitation associated with direct use of the binomial. To test for the possibility of a monotonic dependence of u on time elapsed since 1927 (the beginning of the time series, and the point from which intervals are counted) we set

$$\log\left(\frac{u_t}{1 - u_t}\right) = \beta_0 + \beta_1 \times t \tag{7}$$

where β_0 and β_1 are unknown parameters (note that a positive/negative β_1 implies an increasing/decreasing probability, whereas $\beta_1 = 0$ implies a constant probability). The equation may be expanded to include any covariates that may affect u (e.g., number of ships or volume of ballast water).

Data model

The data model is the model for the relationship between the actual data and the latent state variables and incorporates observational error. In our case, the numbers of native and migrant species recorded during the t th time interval were considered random variables drawn from the following binomial distributions, respectively:

$$\Delta S_{Mt} \sim \text{Binomial}\left[x_t, p_t \left(1 - \frac{S_{Mt-1}}{M}\right)\right] \tag{8}$$

$$\Delta S_{Rt} \sim \text{Binomial}\left[x_t, (1 - p_t) \times \left((1 - \tau_t) \left[1 - \frac{S_{Rt-1}}{S_0 + \sum_{t=1}^{t-1} L_t}\right] + \tau_t\right)\right]. \tag{9}$$

Parameter model

The number of species sampled during each time interval was drawn from a log normal distribution such that $\log(x_t) \sim \text{Normal}(\theta, \sigma^2)$; with the mean and precision drawn from the vague priors, $\theta \sim \text{uniform}(-2.3, 7.6)$ and $\sigma^2 \sim \text{uniform}(0, 100)$, respectively. We also considered models in which x_t was drawn from other distributions, however this did not have a sizeable effect on the parameter estimates. Vague prior distributions were set for both M and R ; truncated, in turn, around the number of native species currently known from the Israeli coastline and the Med as a whole, $M \sim \text{uniform}(350, 550)$, and around the currently known richness of migrant species and the species pool in the Gulf of Suez, $R \sim \text{uniform}(60, 600)$. Vague priors were used for the remaining parameters: $S_0 \sim \text{uniform}(1, R)$, $\beta_1 \sim \text{normal}(0, 1000)$, and $\beta_0 \sim \text{normal}(0, 1000)$.

Assuming that u is constant through time, the accumulation of migrant species up to the time of the first report (1927) forms a geometric series of length z intervals; starting at a point in time after 1869 in which dispersal through the canal became possible ($u > 0$):

$$\begin{aligned} S_0 &= \sum_{t=1}^{t=z} R \times u \times (1 - u)^{t-1} \tag{10} \\ &= \frac{R \times u \times [1 - (1 - u)^z]}{1 - (1 - u)} \\ &= R \times [1 - (1 - u)^z]. \end{aligned}$$

We can estimate this point in time by solving for z :

$$z = \frac{\ln\left(1 - \frac{S_0}{R}\right)}{\ln(1 - u)} - 1 \tag{11}$$

(i.e., we can estimate how soon after the opening of the canal did the first Red Sea species become established in the Med).

METHODS

Data

Israel's Med coastline has been subject to intensive and continuous ichthyological surveys for over 80 years (e.g., Por 1971, Diamant et al. 1986, Golani 1996, 2005),

and, for that reason, we limit our analysis to species reports pertaining to this area. Importantly, the coastline is close enough to the Suez Canal's entry into the Med to guarantee early colonization; but far enough to ensure that new records are likely to represent established populations rather than accidental observations. The latter makes it unnecessary to incorporate species survival rates into the model (e.g., Wonham and Pachepsky 2006). The complete and updated (to 2006) list of Med fish species recorded along Israel's coastline over the past 80 years was obtained from Golani (2005). To reduce variation caused by single years with no new records of either Lessepsian and/or native species, most likely due to low sampling effort, we pooled the data at two-year intervals.

Implementation of the model

The various models were fitted using Markov chain Monte Carlo techniques (MCMC), implemented in the computer package WinBUGS (Spiegelhalter et al. 2004). The code can be found in Appendix B. Convergence diagnostics were performed using Bayesian Output Analysis program (BOA; Smith 2005), and included the Brooks-Gelman-Rubin statistic (using two chains with dissimilar initial values [Brooks and Gelman 1998]) and the Cramer-von-Mises statistic (Heidelberger and Welch 1983). After a burn-in period of 5000 iterations, all parameters demonstrated convergence, and the value of the posterior distributions was estimated from 30,000 additional iterations of one chain of the MCMC simulation. To complement our analysis, we used "data cloning" ($k = 240$ clones) to obtain maximum likelihood (ML) parameter estimates which are invariant to the priors used (Lele et al. 2007).

Model selection

To compare our two hypotheses of u 's dependence on time, we used the deviance information criterion (DIC; Spiegelhalter et al. 2002). The DIC is conceptually similar to the Akaike information criterion (Hilborn and Mangel 1997), allowing to choose the best model after penalizing for increased complexity. A difference of more than two in DIC values implies that a particular model is considerably superior over the other. Due to programming limitation, the above model does not allow the calculation of DIC values. Therefore, we replaced Eq. 5 with the normal approximation of the binomial:

$$L_t \sim \text{normal}\{[u_t \times R_{pr}], [u_t \times (1 - u_t) \times R_{pr}]\}. \quad (12)$$

To avoid negative values of L_t , the distribution was censored to be larger or equal to zero. The parameter posterior distributions using the model containing Eq. 12 were very similar to those obtained from the model containing Eq. 5.

Relaxing the assumption of equal detectability

The model presented above assumes that native and introduced species are of similar detectability, and that detectability does not change with time. To examine the consequences of relaxing this assumption we replaced Eq. 1 with the following:

$$\rho_t = \frac{M}{\left[M + h \left(S_0 + \sum_{i=1}^t L_i \right) \right]} \quad (13)$$

where h is a parameter that defines how much harder ($h < 1$) or easier ($h > 1$) it is to detect migrants relative to native species. We considered two scenarios: first, where h is constant over time, and secondly with it increasing monotonically according to $h = \exp(c \times t)$. Exploring, in turn, a range of values of h and c , we followed the consequent changes in the posterior distributions of u and R .

Species traits

Our model assumes that all Lessepsian migrant species have an equal probability of being sampled (i.e., that the probability does not change with time). To test this assumption, we examined the relationship between the year of first record and a suite of species-specific traits that may be linked with detection probability. Lessepsian species were assigned ordinal trait values based on Golani et al. (2002); Golani et al. (2006) and expert opinion (D. Golani, *personal observation*). These included: size (1, small [total length, TL ≤ 10 cm]; 2, medium [$10 < \text{TL} \leq 50$ cm]; 3, large [TL > 50 cm]); depth (1, 0–20 m; 2, 0–250 m; 3, 0–>250 m; 4, >250 m); prevalence in fishery (1, no/very rare; 2, medium; 3, common/very common); the number of closely related species, both taxonomically and ecologically (1, many close species; 2, some close species; 3, no close species); and conspicuous color and shape that would facilitate identification as exotic in the Mediterranean (1, hard to identify, similar to indigenous species; 2, medium difficulty of identification; 3, easy to identify as exotic). We used multivariate ordinal regression analysis (implemented in Mplus [Muthén and Muthén 2007]) to model the relationship; evaluating its significance using the χ^2 goodness-of-fit test (i.e., observed vs. expected years). Unfortunately, we lack the data needed to repeat the analysis for the native species.

RESULTS

Regression analysis of the documentation record of fish species along the Israeli coastline (Fig. 1A) found that the increase with time of native richness is best described by a linear function (whole-model $R^2 = 0.95$, $P < 0.0001$; $\beta_1 = 20.3$, $P < 0.0001$; $\beta_2 = -0.45$, not significant); whereas that of migrants is best described by an accelerating second-degree polynomial (whole-

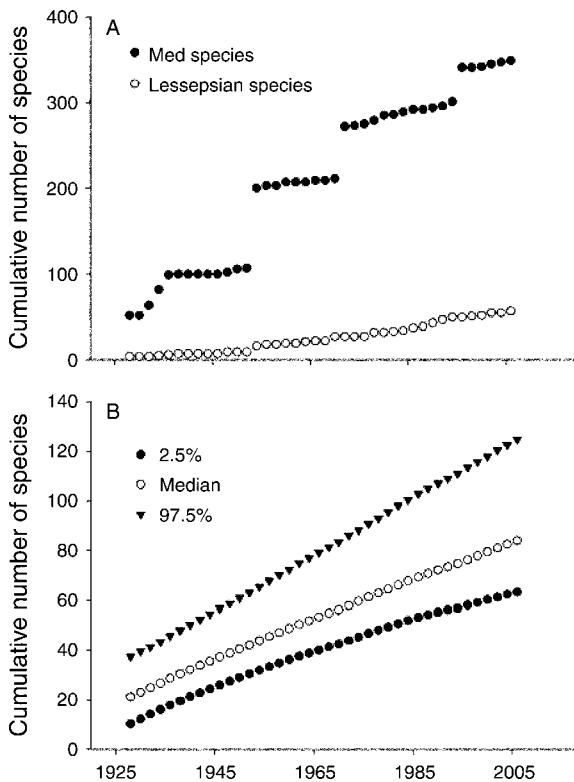


FIG. 1. (A) The cumulative number of indigenous Med and Lessepsian fish species observed in Israeli waters. Observations correspond to two-year intervals. (B) The cumulative number of Lessepsian species predicted by the temporal invariant immigration probability model. The median and 95% credible intervals (spanning 2.5% to 97.5%) are shown.

model $R^2 = 0.99$, $P < 0.0001$; $\beta_1 = 3.65$, $P < 0.0001$; $\beta_2 = 0.13$, $P < 0.001$). Importantly, this high fit to the data is obtained despite large, step-like increases in richness which followed known major ichthyological surveys.

Of the two models of the probability of being successfully introduced into the Med, u , the one assuming temporal invariance received a lower DIC value and is thus better supported by the data (DIC = 340.9 vs. DIC = 343.4, Δ DIC = 2.4). The 95% credible intervals for the effect of time in the more complex model, β_1 , included zero (Appendix C), again suggesting that the immigration probability into the Med remained constant; at least since 1927.

Concentrating on the simpler model we find that the estimated number of species successfully introduced into the Med decreased with time (Fig. 1B). The mode pool size of potential migrants (R), which corresponds to its best estimate, is 170; albeit the credible intervals are large (Fig. 2A, Appendix C). The parameter z has a mode of eight intervals, implying that the best estimate of the year before which the probability of crossing the canal was zero is 1911 (1927, the year of the first record, minus 8×2 yr; Fig. 2C). This coincides with the time the

salinity of the bitter lakes was sufficiently reduced to cease being a barrier to dispersal (Por 1971).

Allowing for unequal detectability of indigenous and introduced species did not alter our conclusion of a constant immigration probability (u), as the 95% credible intervals for the effect of time in the more complex model, β_1 , always included zero. Increasing the disparity in detectability in favor of the exotic species (i.e., higher values of h and c) produced lower estimates

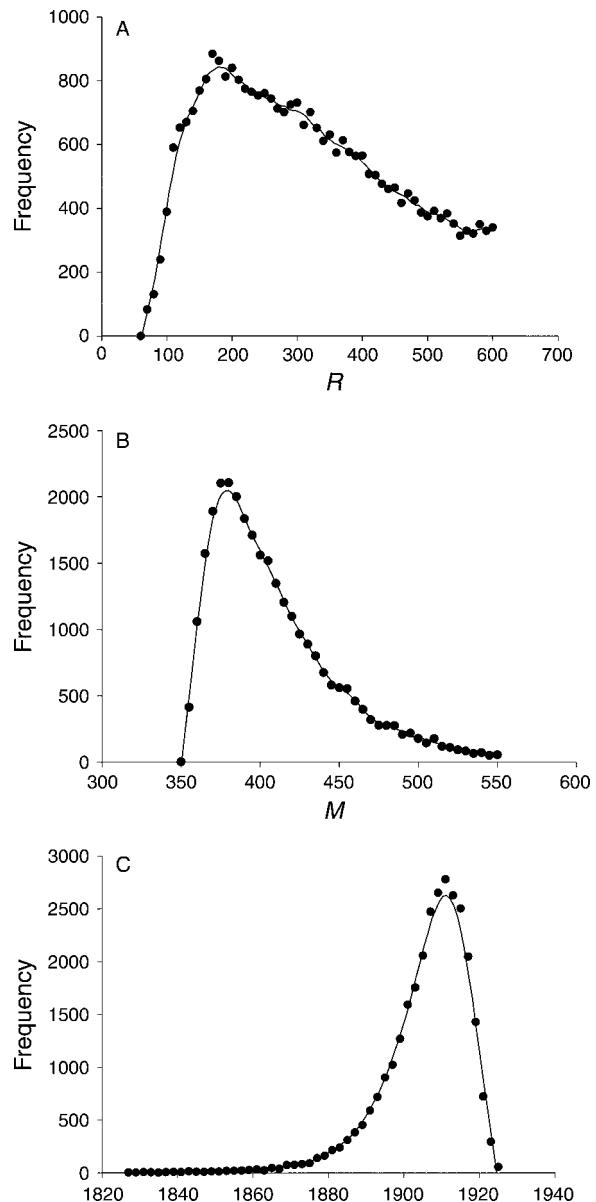


FIG. 2. Complete posterior distributions predicted by the constant immigration probability model for (A) the pool of potential Red Sea migrants, R ; (B) the total number of indigenous Mediterranean species, M ; and (C) the year in which dispersal through the canal became possible.

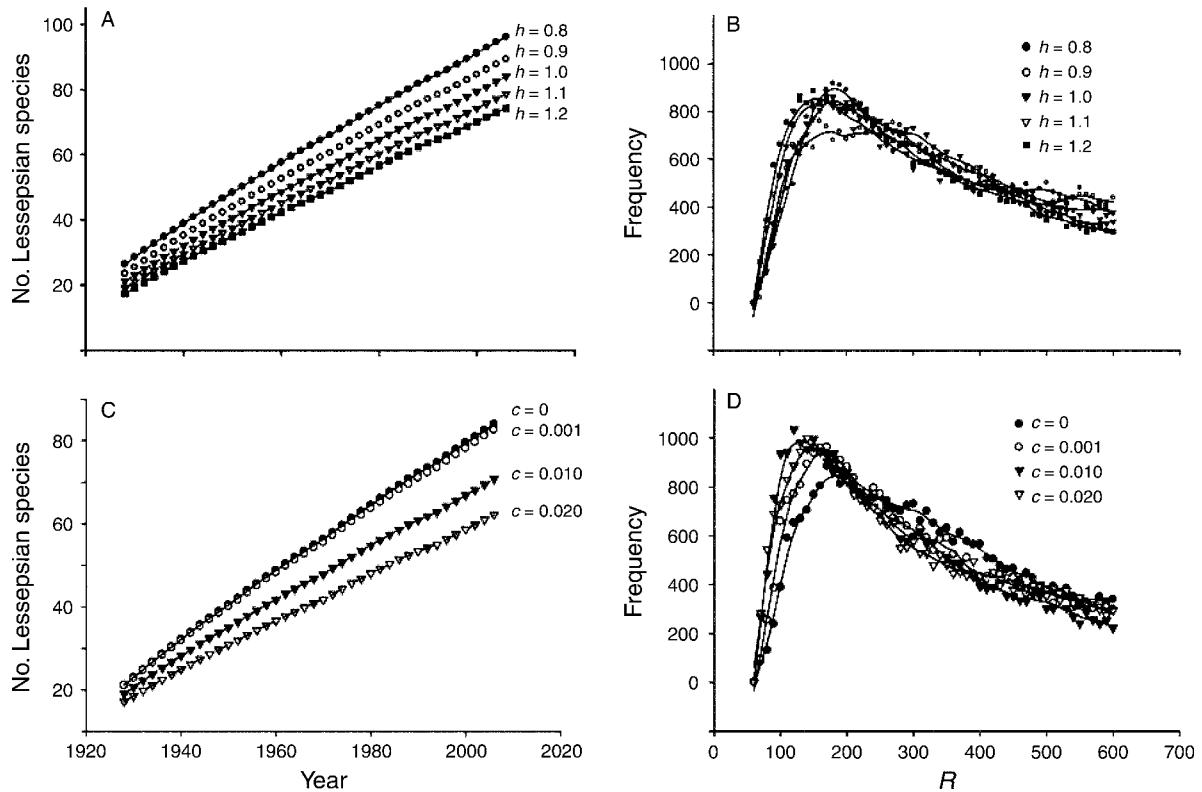


FIG. 3. Relaxing the assumption of equal detectability by setting $h \neq 1$ (where h is a parameter that defines how much harder [$h < 1$] or easier [$h > 1$] it is to detect migrants relative to native species) results in a range of estimates for (A) the cumulative number of Lessepsian species, but similar estimates of (B) the pool size of potential migrants, R . Allowing h itself to increase with time results in sequentially lower estimates of (C) the cumulative number of Lessepsian species as well as (D) a decreasing estimate of R .

of u , with a consequently lower successful introduction rate (Fig. 3A, C). The corresponding affect on the posterior distribution of the pool-size of potential immigrant species (R) was minimal (Fig. 3B, D).

ML estimates were similar to the mode of the posterior distribution for most parameters (Appendix C). An exception was the ML estimate of R in the temporally invariant model, which was consistently located at the upper limit of the prior. The value of u was correspondingly low; as the product of R and u must remain similar for all other parameters to be equal.

The regression model relating species traits to year of first record provided a poor fit to the data ($\chi^2 = 101$, $df = 10$, $P < 0.001$), suggesting no reason to question our assumption of equiprobable detectability across migrant species.

DISCUSSION

Our analysis suggests that Red Sea species have been becoming established in the Med with a constant probability (u), for at least the past 80 years. With migrants expected to be drawn from a species pool of fixed size (R), this implies that the actual number of new species established in the Med per year, i.e., the

introduction rate, has been declining continuously ever since. This conclusion contrasts with the accelerating introduction rate suggested by the discovery record (Fig. 1A); highlighting the need to control for sampling biases when estimating introduction rates (Costello and Solow 2003, Solow and Costello 2004, Wonham and Pачep-sky 2006).

Applying the SC model to our data, we find maximum support for a model invoking a constant introduction rate; estimated at 0.71 species/yr (Appendix A). This value is very close to the average annual successful introduction rate obtained from our simple model in which u is constant through time (0.72 species/yr). Nevertheless, the conclusions drawn from these two models are qualitatively different. While the SC model suggests a constant annual introduction rate, our approach would suggest that the number of new species entering the eastern Mediterranean per year is declining according to

$$\frac{\partial[R \times u \times (1 - u)^{t-1}]}{\partial t} = \frac{\ln(1 - u) \times R \times u}{(1 - u)^{t-1}}$$

The difference leading to this discrepancy is borne of an upper limit we impose on the pool size of potential

migrant species, R ; and which we estimate at 170. This estimate was insensitive to our prior on R , and we obtained similar values even when the prior was set to be much higher than biologically feasible (much larger than the total number of species in the Red Sea). Hence, our modeling approach represents a significant step forward, as it predicts the magnitude and dynamics of future introductions. Currently, 502 fish species are known from the Gulf of Suez (Golani 1999), of which only 67 are known to have crossed into the Med (Golani et al. 2008). This leaves an expected 100 species which await their chance to cross (and/or to be recorded), unless the system undergoes a major change. While we cannot determine why the majority of the species in the Gulf of Suez are not “destined” to enter the Med, it seems likely that fishes that are closely associated with coral reefs will not be able to survive in the coral-deprived waters of the Med. Clearly, estimation of the pool size of exotic species would be complicated (as would that of the introduction rate) in cases of multiple sources that feed the target at different rates.

ML parameter estimates obtained via data cloning are completely invariant to the choice of priors (Lele et al. 2007). Consequently, the comparison of ML and Bayesian estimates can indicate whether the estimates are dominated by the data or the prior. In our case, both analysis returned similar estimates for most of the parameters. A discrepancy arose only with respect to two parameters, which are problematic by definition. Simultaneous estimation of the successful introduction rate (u) and the pool size of potential migrant species (R) is inherently problematic since, for a given time interval, an infinite combination of u and R_{pt} can reproduce the data upon which the estimation is based; i.e., the number of new migrant species recorded during the interval. The range of potential combinations is clearly limited by having to simultaneously consider several dependent time intervals; but multiple solutions may still be possible. The upper limit placed on the otherwise vague prior of R allows, so it seems, the Bayesian model to locate a reasonable local maximum; while the ML model keeps searching for a global maximum which is located well outside the reasonable range (at least in the temporally invariant model). Moreover, the ML estimates should converge on the Bayesian the closer the number of migrant species is to the size of the species pool from which they are drawn (i.e., in systems close to saturation); as an infinitely large R will become progressively less likely. As the choice between a ML and Bayesian approach is a matter of philosophical perspective and pragmatism (Clark 2005), it would seem that, in this case, pragmatism should prevail and support the use of priors.

Our model's underlying assumption of constant and equal detectability for native and exotic species may be often violated and, as in the case analyzed here, difficult

to test comprehensively. While we show that the detectability of exotics did not change significantly over time, we were unable to compare it to that of the native species. Hence, for example, if the detectability of native species was to decline with time, our model will necessarily underestimate the sampling effort, and overestimate the introduction rate. Fortunately, the model's sensitivity to such deviations from the assumption can be easily evaluated. In the example of the Lessepsian migrants, relatively lower detectability of natives does not change the main conclusion of a constant immigration probability and subsequent declining introduction rate; nor does it change the conclusion that the pool of potential invaders is much smaller than the total number of species in the Gulf of Suez.

It is possible that what we call immigration probability has little to do with immigration through the canal; and is much more a function of the rate of population expansion in the Med (i.e., the probability of reaching the Israeli coast within a given time interval). While we are unable to identify the exact process which regulates the appearance of Red Sea species along the Israeli coast, the distinction need not affect our inferences regarding the dynamics followed by this process. Thus, a monotonic decrease in u with time would be expected if species differed in their capacity to cross the Suez Canal and/or expand their range within the Med; with better suited species crossing/proliferating earlier/faster. A temporally invariant u on the other hand implies that migration/proliferation is relatively independent of species traits. In other words, those Red Sea species which inhabit the Israeli coastline would appear to constitute a random draw from the pool of potential migrants, which themselves are a nonrandom subsample of the species found in the Gulf of Suez.

The need to estimate the rate of an underlying process from sample data that contains observation error is frequently encountered in ecology (e.g., Calder et al. 2003, Clark 2003, Wikle 2003). Solow and Costello (2004) approach the problem by focusing on the discovery record of introduced species to obtain maximum likelihood estimates for both the parameters of the introduction and discovery processes. We adopt a somewhat different approach whereby we model the expected change, over time, in the number of newly recorded native and introduced species to control for the (estimated) sampling effort while estimating the introduction rate. Parameter estimation is based on the joint consideration of information from two data sets (the discovery record of native and introduced species) and is easily achieved using MCMC simulations.

Our model should be considered a basis for modification, according to the system under consideration. Such modification may include temporal trends in sampling effort (Solow and Costello 2004), post-introduction extinctions (Wonham and Pachepsky

2006), and among-species variation in introduction and extinction rates (Wonham and Pachepsky 2006). The framework of Bayesian MCMC simulation offers the flexibility to implement such modifications. We expect that our approach will have broad implications to estimating introduction rates, and associated parameter, in other systems where first sighting data on native and introduced species is available.

ACKNOWLEDGMENT

This study was supported by a grant from the Kreitman Foundation to J. Belmaker.

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APPENDIX A

The SC model (*Ecological Archives* E090-074-A1).

APPENDIX B

Parameter estimates (*Ecological Archives* E090-074-A2).

SUPPLEMENT

The WinBUGS code (*Ecological Archives* E090-074-S1).