ANALYSIS

Reassessing the costs of biological invasion: *Mnemiopsis leidyi* in the Black sea

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Abstract

Invasions of ecosystems by exotic species have been the focus of a growing body of research in applied biology and ecology, but relatively little attention has been paid to their economic consequences. Even where economic estimates have been made these often make ad hoc assumptions about the biological relationships of interest and lack grounding in economic theory. This paper develops an integrated ecological-economic approach to assess the economic consequences of invasion for a commercially harvested endemic species whose population dynamics are altered by the invader. As a case study, the Black Sea anchovy fishery represents an interesting example of such a situation. In the early 1980s, the comb jelly *Mnemiopsis leidyi* invaded the Black Sea, eventually becoming established and experiencing a population explosion with dire consequences for the commercial anchovy fishery. In modeling the population dynamics of the Black Sea anchovy (*Engraulis encrasicolus*), the influence of *Mnemiopsis* is incorporated as a structural change in the anchovy stock-recruitment relationship. Then the economic loss associated with this structural change is assessed, using a discrete, dynamic bioeconomic model. It is shown that *Mnemiopsis* had a dramatic effect on the potential sustainable harvest from an optimally managed anchovy fishery but these losses were at least an order of magnitude lower than estimates cited elsewhere.

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1. Introduction

Interest in the unwanted economic consequences of species introductions has been increasing, in part because of a recent estimate of the costs of such invasions imposed on the economy of the US (Pimentel et al., 2000). Yet there exists little formal economic analysis of the costs imposed by species invasions.1 A number of issues arise in attempting to add to the limited knowledge on this issue. How should a

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1 For exceptions, see the collection of papers in the *American Journal of Agricultural Economics*, (Number 5, 2002) and Perrings et al. (2000).
species invasion be characterized in terms of its ecological and economic dimensions? Can historical invasions be subjected to proper empirical analysis grounded in theory, or will the problem remain one of primarily theoretical interest supplemented with occasional ad hoc calculations of economic impacts? Are existing methodologies adequate for quantifying the social costs imposed by invasions or are more specialized techniques required? This paper addresses such questions using as an example a well known marine invasion that has had a large impact: the introduction of the comb jelly *Mnemiopsis leidyi* into the Black Sea. This invasion makes a good case study since initial estimates of its economic impact on the fisheries of the Black Sea have been published in the scientific literature (Travis, 1993). These estimates make a useful reference point for the more formal analysis developed in this paper.

Invasions represent a problem with both economic and ecological dimensions. The economic cost associated with a historical biological invasion has several components. In addition to direct impacts on human welfare (i.e. they are arguments in the utility function), invasions are likely to affect human welfare indirectly via disruptions in the population dynamics of valuable indigenous species. Valuation of these latter effects can be accomplished using the production function or related approaches (Knowler, 2002). Additionally, any costs of control should be included to provide a full accounting of the social costs of invasion.

The characteristics of the invasion of the Black Sea analyzed in this paper motivate the particular modeling approach adopted here. For example, the direct impact on utility and the costs of controlling the invader once it became established were not included in the model, since these have not been significant factors in the case study application. Instead, a bioeconomic modeling approach was used to capture the indirect influence of the invader (*M. leidyi*) on a commercially harvested species, the Black Sea anchovy (*Engraulis encrasicolus*). A bioeconomic model can employ the tools of welfare measurement when there is a change in an environmental input into a production activity (Freeman, 1993). However, applying this approach requires that the underlying biological and ecological relationships be specified explicitly.

In biological and ecological terms, an invasion constitutes an ecosystem surprise or shock, potentially leading to nonlinear, discontinuous and other complex dynamic behavior (Holling, 1986). Applied modeling of such events faces challenges, not least because of the limitations of conventional modeling techniques that rely on continuous variables for most biological (and economic) applications. Moreover, the sudden appearance of a foreign species in an ecosystem cannot be characterized readily by existing predator–prey or similar models, as these presuppose some degree of continuity in the ambient environment, allowing the researcher to concentrate on the interrelationship between predator and prey without worrying about other relationships. In contrast, the entry of an exotic species may set off numerous responses among a wide range of species, disrupting preexisting ecosystem functioning and creating feedbacks that cannot be captured by the relatively narrowly focused predator–prey model.

For the present, empirical researchers may need to be satisfied with characterizing prior and post states and examining the long run implications of an invasion in economic terms. This observation implies an analysis of steady states (assuming these exist), with the economic costs of invasion measured as the difference in economic welfare under the pre- and post-invasion states (Barbier, 2001). When taking this approach, the shift from one state to another can be conceived as a structural change in the biological relationships characterizing the initial state of the ecosystem. For example, the introduction of an exotic comb jelly may alter the population dynamics of a species that it preys upon and/or competes with and this could be captured as a structural change in the parameters of the stock-recruitment relationship of the prey. Structural change models are widely used in economics (see Maddala and Kim, 1998), but this paper applies such a model to the biological relationship between an invading species and a commercially important fish species.

An important attribute of the model is its assumption of optimal management of the Black Sea anchovy fishery, which contrasts with the historic condition of de facto open access.\(^2\) Moreover, since anchovy is an

\[^2\text{It might be argued that the situation comes closer to what Homans and Wilen (1997) refer to as regulated open access, since the Turkish authorities imposed some restrictions in the form of minimum catch size but it is not known how well these were enforced.}\]
internationally traded fish product, demand is liable to be highly or even perfectly elastic. The implications of this situation for assessing the costs of invasion are clear: the actual welfare losses from invasion of the Black Sea may have been quite small, despite large economic impacts in the fishing industry. The approach to measuring economic welfare loss taken in this paper argues that the invasion foreclosed on the opportunity to obtain welfare benefits from the fishery in the future, assuming that eventually it was managed more efficiently. In this sense, the foregone welfare benefits of an efficiently managed fishery represent an upper bound on the long run cost of invasion.

In the next section, previous estimates of the economic costs of the invasion of the Black Sea by *Mnemiopsis* are critiqued, and it is suggested that these may be overestimated. A key shortcoming is recognized as the lack of a properly specified biological relationship between *Mnemiopsis* and anchovy. Subsequently, a bioeconomic model is developed to provide improved estimates of the costs of the invasion. As the biological component of the model is critically important, considerable detail is provided on the development of a behavioral model of the anchovy–*Mnemiopsis* relationship. After establishing this relationship, the influence of *Mnemiopsis* on anchovy population dynamics is incorporated as a structural change in anchovy recruitment. Further sections describe the economic component and solve the full bioeconomic model using optimization techniques. The final sections of the paper provide the resulting economic cost estimates associated with the invasion of the Black Sea and discuss their implications for planning and management. Welfare losses in the commercially dominant anchovy fishery are found to be an order of magnitude lower than the losses reported previously for this invasion event. Nonetheless, the commercial fishery losses are substantial and represent only a portion of the total damages from the invasion.

2. A review and critique of previous estimates of the cost of invasion in the Black Sea

As a result of its highly degraded state, the Black Sea has become a paradigm for the situation of many inland or semi-enclosed seas in the world (Mee, 1992). Environmental degradation has led to a gradual reduction in the value and importance of Black Sea fisheries, culminating in the collapse of the important anchovy fishery at the end of the 1980s. A significant factor was the introduction of the comb jelly *M. leidyi*, originating from the Chesapeake Bay area of the northeastern coast of the US (GESAMP, 1997). Initially, there was an explosion in its population in response to favorable ecosystem conditions (e.g. eutrophication and overfishing of competing pelagic species) and the absence of natural controls. Ultimately, the combination of elevated nutrient levels and high pelagic harvests may have conspired to create an opening for *Mnemiopsis* (J.F. Caddy, personal communication, 1997).

Previous efforts to estimate the commercial fishing losses from the degradation of the Black Sea, including its invasion by *Mnemiopsis*, suggest a major economic disaster. Estimates for the decline in the value of fish catches from the mid-1980s to early 1990s range from US$240 million to US$309 million, the latter referring to Turkey alone (Campbell, 1993; Caddy, 1992). Scraping of redundant fishing vessels and losses in the incomes and profits at processing plants forced to operate with excess capacity have been documented as well. Including these considerations, total losses from the decline of the Black Sea fishery are reported to be US$1 billion per year for the entire Black Sea fishery (Caddy, 1992). Most of these losses are attributable to a collapse in the Turkish-dominated anchovy fishery, the largest fishery by weight and value. Of course, not all the losses can be attributed to the invasion by *Mnemiopsis*. Travis (1993) reports losses associated with *Mnemiopsis* alone of about $250 million, although it is unclear whether these are intended as annual or cumulative losses.

A number of comments on these estimates are in order, most of which involve inconsistencies with proper welfare measurement and the use of economic impact measures instead. For example, replacement cost is used to value idled capital but more correctly such investments should be viewed as sunk. Consequently, only the true scrap value has relevance, and this represents a positive asset value, rather than a negative one. More importantly, idled fishing capital needs to be considered in light of the management regime governing the fishing industry. Since open
access leads to excess resources devoted to the industry, leading to overcapitalization, care must be taken when interpreting the idling of this capital as a social loss. If the optimal number of fishing vessels was about one-third the actual number engaged in the fishery (FAO, 1993 and this paper), then the remaining boats would have constituted overcapitalization and their loss to the industry would be of lesser concern.

Furthermore, simply comparing the value of catches after the fishery has declined to some earlier benchmark is liable to misrepresent economic losses in terms of sustainable catch levels. During the pre-invasion period, fishing effort likely exceeded sustainable levels and probably could not have been maintained in the long run. In addition, a comparison of pre- and post-invasion catch levels does not explicitly account for the impact on the fishery arising from *Mnemiopsis* in isolation. Given that the Black Sea ecosystem was under intense pressure from a variety of sources (e.g. pollution, water diversions, overharvesting), attributing all the decline to the invasion probably contributed to an overestimation of the cost of the invasion.

To improve on the estimates cited above requires proper specification of the underlying biological relationships, explicit consideration of the institutional regime governing the fishery and the application of correct welfare measurement criteria. For instance, accepting that open access characterized the Black Sea fisheries at the time of invasion requires the application of correct welfare measurement techniques for this situation (Freeman, 1993). Thus, the welfare loss would be composed of changes in consumers’ and producers’ surplus, where the average cost curve serves as the industry supply curve in determining the latter. The entry of *Mnemiopsis* into the Black Sea shifted the industry supply curve upwards, and assuming equilibrium conditions, this would result in a contraction in consumers’ surplus and temporary losses within the fishing fleet until the number of active vessels had adjusted to the new conditions. Ultimately, at the new long run equilibrium producers’ surplus would be reduced to zero once again. Taking the approach described here would result in estimates of loss quite different from those cited above, possibly much lower. For example, as anchovy is an internationally traded species, the price elasticity of demand would be relatively high so that the reduction in consumers’ surplus from deteriorating environmental conditions would be commensurately low.

As argued in the previous section, an alternative measurement would estimate the potential net economic returns in the long run under optimal management for the pre-invasion situation and contrast these with the net economic returns available once the marine system reached a new equilibrium with the invader present. Key features in such an approach would be explicit modeling of the influence of the invader (*Mnemiopsis*) on the harvested or valuable species (anchovy) and the use of proper welfare measurement. In the remainder of the paper, this approach is taken in developing a model of the economic cost of the invasion of the Black Sea by *M. leidyi* in terms of its impact on Turkey’s commercial anchovy fishery.

**3. A model of population dynamics of the Black Sea anchovy with biological invasion**

This section develops the biological component of the analysis. A behavioral model of the *Mnemiopsis*–anchovy relationship was used to capture changes in recruitment to the adult stock of anchovy once *Mnemiopsis* became established in the marine system. It is clear that *Mnemiopsis* had a substantial impact on anchovy recruitment success during its initial population explosion (Shiganova and Bulgakova, 2000; Kideys, 1994). This influence could be incorporated into the model in several ways. For example, the population dynamics could be based on a predator–prey relationship (Ragozin and Brown, 1985; Hannesson, 1983), but this approach was rejected for the reasons cited earlier. Instead, *Mnemiopsis* was modeled as a general influence on anchovy recruitment success during its initial population explosion (Shiganova and Bulgakova, 2000; Kideys, 1994). This influence could be incorporated into the model in several ways. For example, the population dynamics could be based on a predator–prey relationship (Ragozin and Brown, 1985; Hannesson, 1983), but this approach was rejected for the reasons cited earlier. Instead, *Mnemiopsis* was modeled as a general influence on anchovy recruitment with the biomass of *Mnemiopsis* treated as an independent argument in the recruitment relationship (see Vaughan et al., 1984).

Despite the advantages of this latter modeling approach, several concerns arose in applying it to the present case study. First, the biomass of anchovy and *Mnemiopsis* was likely to be determined simultaneously, requiring appropriate statistical measures such as specifying the biomass of *Mnemiopsis* as endogenous to the *Mnemiopsis*–anchovy
system. Second, adequate time series data for *Mnemiopsis* did not exist, despite some limited field surveying, making it difficult to incorporate *Mnemiopsis* as an independent variable in the recruitment function. Finally, the surprise nature of the invasion appears to have caused a discontinuous break in the anchovy stock-recruitment relationship (FAO, 1993), suggesting a structural change in the recruitment function rather than a smooth continuous change.

To address these concerns and to provide greater rigor, a formal behavioral model describing the influence of *Mnemiopsis* on anchovy was used to model structural change in the anchovy stock-recruitment relationship. Two structural alternatives for the anchovy stock-recruitment relationship were recognized, differing with respect to the presence or absence of *Mnemiopsis*. As a result, the anchovy recruitment function can be represented by $R_i(S)$, where recruitment depends on spawning stock escapement $S$ alone, with both variables measured in biomass terms ($\times 1000$ t). The notation $i$ in each structural variant of the recruitment function refers to the current ecological state, either pre- or post-invasion, with $i=1$ or 2, respectively.

Recruitment of anchovy was modeled as a Ricker function, which is used frequently to model recruitment in clupeid populations (Ricker, 1975). The standard Ricker model was modified to include an environmental variable, phosphates ($P$), since fluctuating nutrient inputs appear to have had a bearing on productivity in the Black Sea (Caddy, 1993). Beverton and Iles (1992) suggest several ways such a general environmental influence on recruitment can be included in the Ricker function. Initial testing supported a multiplicative approach. The modified Ricker function describing the initial or pre-*Mnemiopsis* situation, $R_1(S,P)$, was:

$$R_1(S_i, P) = S_\text{i}e^{\beta_0+\beta_1S_t P^\beta_2}$$  \hspace{1cm} (1)

where $\beta_0$ and $\beta_1$ are the standard Ricker parameters, here associated with recruitment in the pre-invasion situation, with $\beta_0$ unconstrained and $\beta_1<0$. It is assumed that $\beta_2>0$, since evidence suggests that, at least within certain limits, increasing phosphates have had a beneficial effect on anchovy spawning success by relaxing a nutrient constraint. It is assumed that the partial derivative $R_S$ has complex behavior, commensurate with a dome-shaped recruitment curve.

Establishment of the invader leads to a new anchovy stock-recruitment relationship, expressed initially as $G(S,P,M)$, where $M$ represents the biomass of *Mnemiopsis* and $G(\ldots)$ is the new anchovy stock-recruitment relationship. If the biomass of *Mnemiopsis* is determined endogenously as a function of $S$, then after invasion anchovy recruitment can be represented as $G(S,P,M)=G[S,P,M(S)]=G(S,P)$. Rewriting the function $G(S,P)$ as $R_2(S,P)$, we now have the second structural variant of the anchovy recruitment function. As expressed here, the function $R_2(S,P)$ incorporates *Mnemiopsis* as a modification in the parameters of the original recruitment function, $R_1(S,P)$.

To derive $R_2(S,P)$ from its antecedent $G(S,P,M)$, we begin with a description of the seasonal population dynamics of *Mnemiopsis*. Recognizing the influence of seasonal availability of food sources, the *Mnemiopsis* biomass normally expands from virtually nil in the spring to its annual maximum in the late summer/early fall, before contracting to just a few individuals over the winter period (Fig. 1). Its initial population level each year appears to be determined by random environmental conditions, rather than by the population level of the preceding year.\(^3\) It is also known that *Mnemiopsis* ingests prey in approximately linear proportion to prey abundance over a fairly wide range of population densities (Lebedeva and Shushkina, 1994). Distinguishing anchovy larvae from other prey, the growth in the *Mnemiopsis* biomass can be described by the following balance equation (Legovic, 1987):

$$\frac{1}{M} \frac{dM}{dz} = v_1 L(z, S_t) + v_2 w(z) - b$$  \hspace{1cm} (2)

where $M$ represents the *Mnemiopsis* biomass, $z$ measures time in continuous units (e.g. days) over the annual population cycle, $L(z, S_t)$ is the biomass of anchovy larvae expressed as a function of $z$ and the spawning stock $M$ in year $t$, $w(z)$ is the seasonally varying biomass of other prey, and $v_1$ and $v_2$ are parameters that reflect a linear predation rate and the conversion of ingested larvae and other prey into

\(^3\) Shiganova (1998) states that: “In February the abundance of *M. leidyi* in the Black Sea is dependent on temperature conditions over the winter.” (p. 306).
Mnemiopsis biomass. The term $b$ is the natural mortality rate of Mnemiopsis, measured in biomass terms, with $b > 0$.

Since we wish to concentrate on the relationship between anchovy and Mnemiopsis, $L(z, S_t)$ was modeled more precisely. Anchovy produce eggs in proportion to the anchovy spawning biomass $S$ but the spawning rate is liable to vary over the spawning season, rising initially and then declining. This effect is modeled using a coefficient on anchovy spawning biomass that varies over the annual population cycle, $a(z)$. As a result, the function $L(z, S_t)$ in Eq. (2) was specified as:

$$L(z, S_t) = a(z)S_t$$  

(3)

where $a(z) > 0$. Substituting Eq. (3) into Eq. (2) and solving the resulting differential equation, yields the instantaneous Mnemiopsis biomass at each moment $z$ over the Mnemiopsis population cycle during year $t$.

Since anchovy recruitment is measured in November of each year, we fix the biomass of Mnemiopsis as a single annual value at this point in time. Referring to this point in the annual population cycle as $Z$, then the expression for the instantaneous Mnemiopsis stock at $Z$ is:

$$M(Z) = M_t = M_{0(t)}e^{v_1S_t}t_0^a(z)dz + v_2 \int_0^a w(z)dz - bZ$$  

(4)

where $M_{0(t)}$ is the biomass of Mnemiopsis at the beginning of its annual population cycle. Based on Eq. (4), the seasonal population dynamics of Mnemiopsis would be expected to increase over the course of the season, culminating in a massive die-off with the advent of winter, as observed historically (Fig. 1).

It will be convenient to express the Mnemiopsis biomass terms in Eq. (4) as index values using the biomass of Mnemiopsis at the start of the annual population cycle, $M_{0(t)}$, at its mean as the numeraire. Defining the integral terms in Eq. (4) as $A(Z)$ and $W(Z)$, respectively, and distinguishing index values using a hat (‘$\hat{}$’), expression (4) can be restated as:

$$\dot{M}_t = \dot{M}_{0(t)}e^{v_1S_tA(Z)} + v_2W(Z) - bZ$$  

(4')

The anchovy recruitment function can be formulated now using Eq. (4’) to capture the direct influence of Mnemiopsis on anchovy as a predator of anchovy juveniles. However, this influence on anchovy may be augmented or diminished by various feedback effects arising from the invader’s presence in the marine system. To allow for these additional indirect effects on the anchovy stock resulting from Mnemiopsis, expression (4’) was incorporated as a general environmental influence on anchovy recruitment, similarly to phosphates in Eq. (1). Following Beverton and Iles, expression (4’) was inserted into the recruitment function and then the resulting expression was simplified as follows:

$$G(S_t, P_t, M_t)$$

$$= S_t e^{\beta_0 + \beta_1S_t}P_t^{\beta_2} \hat{M}_t^{\beta_3}$$

$$= S_t e^{\beta_0 + \beta_1S_t}P_t^{\beta_2} \left[ \hat{M}_{0(t)}e^{v_1S_tA(Z)} + v_2W(Z) - bZ \right]^{\beta_3}$$

$$= S_t e^{(\beta_0 + v_2W(Z)\beta_3 + v_2W(Z)) + \{v_1S_tA(Z)\beta_3\} + \{v_1S_tA(Z)\beta_3\}S_t P_t^{\beta_2} \hat{M}_{0(t)}^{\beta_3}$$  

(5)

where the parameter $\beta_3$ modifies the effect of Mnemiopsis on the anchovy stock so that it represents a general environmental influence, with $\beta_3 < 0$.

One concern with Eq. (5) was that the post-winter Mnemiopsis biomass $M_{0(t)}$, while very low, was unobservable. Since this variable is determined by random environmental factors, it is unlikely to be correlated with the anchovy spawning biomass (see footnote 3). Moreover, since this term is randomly determined and has a unitary mean, it serves as a multiplicative stochastic disturbance modifying the deterministic anchovy recruitment function. Reed (1979, p. 362) analyzes this type of stochastic
recruitment specification, demonstrating that optimal escapement is identical in this model to that of the underlying deterministic model, as long as several conditions are met. Knowler and Barbier (2002) verify that these conditions are met for this problem. Thus, we can ignore the stochastic disturbance term \( \bar{M}_{0(t)} \) and henceforth treat the problem as deterministic. Following Reed, the last term in Eq. (5) vanishes and we can ignore the stochastic disturbance term.

Following Reed, the last term in Eq. (5) vanishes and we can ignore the stochastic disturbance term. Consequently, the parent stock size at maximum recruitment is

\[
G(S_t, P_t, M_t) = S_t e^{(p_0 + v_2 W(Z) \beta_3 - bZ \beta_3) + (\beta_1 + v_1 A(Z) \beta_3) S_t P_t^{b_2}}
\]

Expression (6) shows the influence of \( Mnemiopsis \) as a structural change in the parameters of the pre-
\( Mnemiopsis \) recruitment function, \( R_1(S, P) \). Note that the shift term \( v_1 A(Z) \beta_3 \) increases the absolute value of the density dependent parameter in the Ricker function (second bracketed term), since \( v_1, A(Z) > 0 \) and \( \beta_1, \beta_3 < 0 \). Consequently, the parent stock size at maximum recruitment reaches its maximum value declines with \( Mnemiopsis \) present in the marine system. In contrast, the effect of \( Mnemiopsis \) on the density independent parameter (first bracketed term) is indeterminate, since the two new shift terms \( v_2 W(Z) \beta_3 \) and \( -bZ \beta_3 \), take opposite values. \( Mnemiopsis \) has a negative density independent effect if \( v_2 W(Z) > bZ \). This result implies that the conversion of food sources, other than anchovy, into \( Mnemiopsis \) biomass exceeds the loss of \( Mnemiopsis \) biomass to natural mortality, at time \( Z \). Determining whether this condition holds is an empirical matter; it depends on when anchovy recruit, which determines \( Z \), and the reliance of \( Mnemiopsis \) on species other than anchovy at this time of year.

Setting \( \beta_0 + v_2 W(Z) \beta_3 = z_0 \), \( \beta_1 + v_1 A(Z) \beta_3 = z_1 \) and \( \beta_2 = z_2 \) in Eq. (6), the second structural variant of the anchovy stock-recruitment relationship can be expressed more simply as:

\[
R_2(S_t, P_t) = S_t e^{20 + z_1 S_t P_t^{0.117}}
\]

Expression (1) was used together with Eq. (7) to describe anchovy recruitment in the pre- and post-invasion situations, respectively.

Details of the calibration of the anchovy recruitment functions shown in Eqs. (1) and (7) were provided in an earlier study (Knowler, 2001). While several formulations of the recruitment model were tested, the best fitting model was the following:

\[
R_t = S_t e^{-[0.000614 + 0.00101D]} S_t P_t^{0.117}
\]

Adjusted \( R^2 = 0.70 \quad F[3, 22] = 20.22 \)

where \( D \) is a dummy variable with \( D=0 \) prior to invasion and \( D=1 \) after invasion, yielding \( \beta_1 = -0.000614 \) and \( z_1 = -0.001624 \). Of interest in Eq. (8) is the absence of a density independent term in the recruitment model, implying that \( \beta_0 = z_0 = 0 \). The significance of this finding is that the two shift terms, \( v_2 W(Z) \) and \( bZ \), are approximately equal and, therefore, offsetting. Finally, the estimation procedure generated values for the coefficient on the phosphate term, with \( \beta_2 = z_2 = 0.117 \). The sign on this coefficient is consistent with the expectation that phosphates had a positive effect on recruitment success. For the empirical modeling, the exogenous level of phosphates (\( \tilde{P} \)) was set at 5.5 \( \mu \)M, about equal to the average ambient level during the period leading up to the invasion by \( Mnemiopsis \) (Cociasu et al., 1997).

4. Economic profits in the commercial anchovy fishery in the Black Sea

The economic component of the model describes the economic profits (rent) generated by the commercial anchovy fishery. Accordingly, the long run economic cost of the invasion was represented by the decline in these economic profits as a result of the influence of \( Mnemiopsis \). Since anchovy is an internationally traded commodity, its domestic demand curve
can be regarded as perfectly elastic, leading to the following statement for economic profits:

\[ \pi(X_t, h_t) = ph_t - C(X_t, h_t) = ph_t - cE(X_t, h_t) \]  

(9)

where \( \pi(X, h) \) are economic profits, \( X \) is the exploitable anchovy stock measured at the beginning of the fishing season (November), \( h \) is the annual catch of anchovy, \( p \) is the real ex-vessel net price for anchovy, and \( C(X, h) \) is the cost function of the anchovy fishery. The cost function is composed of two terms, a unit cost of effort \( c \) and a fishing effort function \( E(X, h) \). The latter function describes aggregate fishing inputs consisting of labor and capital tied up in Turkish purse seine vessels in the Black Sea.

The effort function was specified by inverting a standard catch function, \( h(X, E) \). Several catch functions were considered but since the VPA analysis used to estimate the anchovy stock was consistent with the discrete form of the Schaefer-Gordon harvest function \( \text{Prodanov et al., 1995} \), this functional form was selected. The discrete Schaefer-Gordon catch function is shown below, along with the associated effort function:

\[ h_t = X_t(1 - e^{-qE_t}) \]

\[ E_t = \frac{1}{q} \ln \left( \frac{X_t}{X_t - h_t} \right) \]  

(10)

Substituting the effort function from Eq. (10) into Eq. (9), and using the identity \( S = X - h \), the variable \( h \) was eliminated from the profit expression. Rearranging yielded the following statement for profits separable in the variables \( X \) and \( S \):

\[ \pi(X_t, S_t) = p(X_t - S_t) - \frac{c}{q} \ln X_t + \ln S_t \]

\[ = \theta_A(X_t) - \theta_B(S_t) \]

where

\[ \theta_A(X) = pX_t - \frac{c}{q} \ln X_t \]

\[ \theta_B(S) = pS_t - \frac{c}{q} \ln S_t \]  

(11)

In the following sections, we confine ourselves to the region where \( \theta^*_j, \theta_j^* > 0 \), for \( j = A, B \).

Economic parameters were obtained from a study of the Turkish Black Sea purse seine fishery \( \text{Dincer, 1992} \). The price for fresh anchovy \( (p) \), ex-vessel and net of the crew share, was US$90 per tonne and annual costs per vessel \( (c) \) were US$256,000. These values were expressed as real 1989 values and were representative of the range of values experienced during the period. Expressing the unit vessel cost in thousands of US dollars gives a cost-price ratio of 2.84. The catchability coefficient \( (q) \) was estimated at 0.005 (\text{Knowler et al., 2002}). Finally, the social discount rate \( d \) was set at 5%.

Combining Eq. (11) and the biological component of the model described earlier results in a bioeconomic model of a fishery subject to invasion. The next section formulates the bioeconomic model in optimal management terms and shows how this model can be used to assess the welfare losses from an invasion.

5. Optimal management of a fishery subject to invasion

Assessing the potential long run welfare losses in the commercial anchovy fishery in response to an invasion required estimates of steady state economic profits with and without this invasion event, on the assumption the fishery was managed efficiently. Assuming the level of phosphates is exogenous and fixed, i.e. \( P_i = \bar{P}_i \), we can ignore this term in our formulation. As a result, the planner’s problem can be expressed as:

\[ \text{max} \sum_{t=0}^{\infty} \rho^t \pi(X_t, S_t) = \sum_{t=0}^{\infty} \rho^t [\theta_A(X_t) - \theta_B(S_t)] \]

s.t. \( X_{t+1} = \sigma S_t + R_i(S_t) \)  

with \( 0 \leq S_t \leq X_t \), \( i = 1, 2 \) and \( S_0, X_0 \) given  

(12)

where \( \rho \) is the discount term, defined as \( 1/(1+\delta)^t \), with \( \delta \) denoting the appropriate social discount rate and \( \sigma \) is the adult survival rate from 1 year to the next. Note that this formulation distinguishes between biological situations, i.e. with and without invasion, and treats each case in isolation.

A similar discrete optimization problem is solved by Clark (1985, pp. 140–142) using change of summation index to eliminate the variable \( X \). As a result, the
planner's problem can be simplified to the maximization of a function $V(S)$ in the variable $S$ alone:

$$V(S_t) = qh(A_r S_t + R_i S_t) - \frac{R_i S_t}{(C_1 h B S_t) (1/h)}$$ (13)

The solution to Eq. (13) can be described as a constant optimal escapement rule where the resulting optimal escapement value depends upon the recruitment function in place, i.e. $R_i(S_t)$. For the pre-invasion situation ($i=1$), optimal escapement was designated as $S^*$. Substituting functional forms from earlier sections into the solution to Eq. (13) and dividing the resulting expression by $p/p$, gives an implicit statement for $S^*$:

$$\left[\sigma + (e^{\beta_0} - \beta_1 S^*) e^{-\beta_1 S^*}\right] \times \frac{1 - \frac{\xi}{s} [q S^* (\sigma + e^{\beta_0} - \beta_1 S^*)]^{-1}}{1 - \frac{\xi}{s} (q S^*)^{-1}} = \frac{1}{\rho} = 1 + \delta$$ (14)

Expression (14) also was used to find optimal anchovy escapement for the post-invasion situation ($i=2$), and the resulting solution value was denoted as $S^{**}$. To determine $S^{**}$ using Eq. (14), the parameters of the recruitment function, $\beta_0$ and $\beta_1$, were replaced with the new recruitment parameters from Eq. (7), $\sigma_0$ and $\sigma_2$. After solving for $S^*$ and $S^{**}$, the economic profits expression in Eq. (11) was used to determine the welfare loss from the invasion. Expression (14) was calibrated using parameters from the various sources cited earlier (see Table 1).

Assuming the function $V(S)$ is quasi-concave and the expression for economic profits is separable in $X$ and $S$, then adjustment to the optimal escapement is governed by a most rapid approach path under either recruitment regime. Taking pre-invasion conditions, the harvest decision rule is (see Fig. 2):

$$\begin{cases} X_t \geq S^* & \Rightarrow h_t = X_t - S^* \\ X_t < S^* & \Rightarrow S_t = X_t \text{ and } h_t = 0 \end{cases}$$ (15)

However, the initial adjustment to the new optimal escapement $S^{**}$ upon invasion is not a trivial matter, since it has both biological and management (harvest) dimensions. If the impact of the invader on the harvested species was very rapid then the empirical challenges can be reduced by treating this aspect as instantaneous (Clark, 1985; pp. 75–77). This approach focuses attention on the adjustment in harvest alone, and under optimal management the rules governing this adjustment are straightforward. Once the marine system is invaded, the decision rule in Eq. (15) changes, with $S^*$ replaced by $S^{**}$. Letting $X_n$ denote the fish stock at the time of invasion, then if $X_n \geq S^{**}$ holds in each time period. The optimal harvest strategy is given now by $h^{**} = X^{**}/C_0 S^{**}$. If the reverse situation holds, $X_n < S^{**}$, then the stock should be allowed to recover to its new optimal level $X^{**}$, before commencing harvesting down to $S^{**}$ in each subsequent time period.
A final theoretical consideration concerns the stability of the bioeconomic system once invaded. If the disturbance caused by invasion satisfies $X_n \geq S^{**}$, then stability per se is not an issue since excess stock is immediately harvested (Fig. 2). Where invasion causes the stock to fall below the new optimal level of escapement, $X_n < S^{**}$, the stability of the system is ruled by the population dynamics of anchovy in the absence of harvest. Whether the system will be stable after invasion depends upon the following condition (Clark, 1976):

$$-1 - \sigma < R_S^{**} < 1 - \sigma.$$  \hspace{1cm} (16)

where $\sigma$ is the anchovy adult survival rate. Note that the domain of stability will be different once the system is invaded because of the structural change in the underlying stock-recruitment relationship. Of course, condition (16) also applies in the pre-invasion situation, except that $R_S^{**}$ is replaced with $R_S$. Whether Eq. (16) is satisfied in either case is purely an empirical matter.

6. Results and discussion

The results from bioeconomic modeling demonstrate that *Mnemiopsis* had a dramatic impact on potential catches and economic profits in the Black Sea anchovy fishery. Using the base case parameters for the anchovy recruitment function (Table 1), the optimal catch during the pre-*Mnemiopsis* period was estimated at almost 400,000 t per year (Table 2). However, the optimal catch declined by 90% to a mere 40,000 t per year with *Mnemiopsis* present. As a result, economic profits in the fishery dropped from US$17 million to US$0.3 million per year, a potential dead-weight loss of US$16.7 million per year to the Black Sea fishing nations (primarily Turkey). In present value terms, the loss amounts to hundreds of millions of US dollars over several decades. When sensitivity analyses were undertaken, involving alternative recruitment models, there was no significant change in the estimated losses from invasion.

To ensure the optimal value of escapement and the associated economic losses reported here are a unique and global maximum, the function $V(S)$ must be quasi-concave. Empirical estimates of this function for the pre- and post-invasion situations indicated that this necessary and sufficient condition was met (Fig. 3).

![Fig. 3. The function $V(S)$ for the pre- and post-invasion situations in the Black Sea anchovy fishery under optimal management.](image)

Table 2
Long run equilibrium values for the Black Sea anchovy fishery under optimal management and pre- and post-invasion conditions (US$, 1989–1990)

<table>
<thead>
<tr>
<th>Ecological regime</th>
<th>Escapement $S^*$, $S^{**}$ ($\times 1000$ Mt)</th>
<th>Recruitment $R^*$, $R^{**}$ ($\times 1000$ Mt)</th>
<th>Stock $X^*$, $X^{**}$ ($\times 1000$ Mt)</th>
<th>Harvest $h^*$, $h^{**}$ ($\times 1000$ Mt)</th>
<th>Effort $E^*$, $E^{**}$ (vessels)</th>
<th>Economic profits $\pi^*$, $\pi^{**}$ ($\times 1000$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) Pre-<em>Mnemiopsis</em></td>
<td>1518</td>
<td>730</td>
<td>1914</td>
<td>396</td>
<td>72</td>
<td>17080</td>
</tr>
<tr>
<td>(1971–1986)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(B) Post-<em>Mnemiopsis</em></td>
<td>946</td>
<td>249</td>
<td>986</td>
<td>40</td>
<td>13</td>
<td>290</td>
</tr>
<tr>
<td>Difference due to invasion</td>
<td>$-572$</td>
<td>$-481$</td>
<td>$-928$</td>
<td>$-356$</td>
<td>$-59$</td>
<td>$-16790$</td>
</tr>
</tbody>
</table>
the opening discussion. In light of this discrepancy, the calculations presented here are argued to provide a more suitable measure of the losses in the commercial anchovy fishery due to *Mnemiopsis*. However, fish species perform valuable functions aside from providing commercial catches, and these functions should be considered too (Holmlund and Hammer, 1999). Unfortunately, little is known of the ecosystem role played by the Black Sea anchovy, but this presumably had a positive value and was diminished by the invasion. Moreover, *Mnemiopsis* likely disturbed the productivity of other fish species, and even if the resulting commercial losses were small, these losses would increase the total damages due to the invasion. As a result, the welfare losses presented here represent a lower bound for fishery-related damages. Even so, it is unlikely that the upper bound would approach the prior estimates of loss cited earlier.

Obviously, welfare losses are not the only consideration in assessing damages from an invasion. The economic impact of the comb jelly undoubtedly was devastating for local fishing communities dependent on the industrial anchovy fishery. Hundreds of purse seine vessels in Turkey alone were idled by the collapse in stocks, due in part to the invasion by *Mnemiopsis*, but also to overcapitalization. However, it has already been argued that many of these vessels represented a waste of national resources because their numbers exceeded what was needed to make an optimal catch in an efficient manner. Instead, the bioeconomic model can be used to determine an optimal fleet size in the pre-*Mnemiopsis* period and then this figure can be compared to the optimal fleet size after the invasion. The results show that 72 vessels would have been adequate for the task in the former case, but this figure is reduced to only 13 with *Mnemiopsis* present. Although this adjustment does not present a picture as alarming as the idling of hundreds of vessels, described by some commentators, these losses are still significant. Given that each vessel accommodates 20 to 30 crews, the direct impact would be the loss of several thousand jobs and millions of dollars in annual incomes from coastal communities, even if the fishery were managed efficiently.

7. Conclusion

This paper developed a framework for assessing the economic costs of an invasion by an exotic species and applied this to a case study involving the commercial anchovy fishery in the Black Sea. It was suggested that previous estimates of the losses in the anchovy fishery from *Mnemiopsis* may have been overestimated, perhaps by as much as 10-fold. It is worth noting again that the estimates presented here were contingent upon the optimal management of the fishery and, therefore, provide a measure of potential loss as efficient management has not been the case historically with this particular fishery. Ironically, if a pure open access situation had been modeled it is likely the estimate of losses from invasion would have been much lower than under optimal management, since open access leads to the dissipation of economic rent both with and without the invasion. Contributing to such a result is the presence of a perfectly elastic demand curve characterizing the fishery, so that changes in benefits to consumers (consumers surplus) were not a factor. Nonetheless, the invasion clearly had a profound economic impact (e.g. job losses, idling of fishing vessels), but this is a different measure of economic loss and should not be confused with losses in economic welfare.

Additionally, the approach taken compared economic profits from the fishery at the steady state under pre- and post-invasion conditions. While the economic aspects of the anchovy fishery allowed modeling of a rapid adjustment in harvest upon invasion, and the underlying population dynamics met stability conditions, reality may be more complex. With many invasive species, ecological-economic adjustment will be intertwined and may require a lengthy period, although modeling this process empirically is likely to be challenging. In the case of *Mnemiopsis*, there was an initial population explosion followed by periods of reduced and then increasing biomass (GESAMP,
1997), which may or may not herald on-going fluctuations in the comb jelly’s influence on the commercial anchovy fishery in the future. If fluctuating conditions prevail, then the estimation of long term losses in the fishery would need to reflect this situation.

Better estimates of the losses from biological invasions will help in preventing invasions and establishing recovery programs for damaged ecosystems. The Black Sea case study demonstrates that bioeconomic analysis can be used to derive theoretically defensible estimates of the impacts of biological invasions and that these impacts can be modeled using a structural change approach.

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