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Fisheries Research 84 (2007) 275–281

FISHERIES RESEARCH

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Estimation of a stock–recruitment relationship for Black Sea anchovy (*Engraulis encrasicolus*) under the influence of nutrient enrichment and the invasive comb-jelly, *Mnemiopsis leidyi*

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Received 6 May 2004; received in revised form 31 October 2006; accepted 6 November 2006

Abstract

The Black Sea is typical of a highly degraded marine ecosystem. Nutrient loads increased dramatically in the 1970s, which appeared to benefit the Black Sea anchovy (*Engraulis encrasicolus*). However, the accidental introduction of the comb-jelly *Mnemiopsis leidyi*, which preys on young anchovy and competes with adults, contributed to a collapse in the anchovy fishery in the late 1980s. Recent efforts to model Black Sea anchovy population dynamics emphasize general environmental influences and do not take these ecosystem shocks explicitly into account. In this paper, I estimate anchovy recruitment using the traditional Ricker model and under rapid nutrient enrichment. *Mnemiopsis*' influence on anchovy is captured as a shift in the parameters of the recruitment function. By incorporating these environmental disturbances, the seemingly monotonic relationship between parent stock and recruitment for anchovy disappears and is replaced by a dome-shaped stock–recruitment relationship subject to regime shifts.

Keywords: Biological invasion; Environment; Eutrophication; Regime shift; Ricker model

1. Introduction

Although it is severely polluted, the Black Sea is fairly typical of a number of degraded semi-enclosed seas (Mee, 1992). One of the most serious signs of its environmental degradation was the collapse of the economically important anchovy (*Engraulis encrasicolus*) fishery in the late 1980s. Overfishing and accidental introduction of the ctenophore (comb-jelly) *Mnemiopsis leidyi*, which preys on anchovy larvae and competes with anchovy adults, were instrumental in the collapse (Kideys, 1994). While both of these influences had a negative impact on the anchovy stock, an earlier boost in primary productivity from increased nutrient loadings likely benefited anchovy during the 1970s (Caddy et al., 1995). Early efforts to estimate a stock–recruitment curve for the Black Sea anchovy were unsuccessful, leading Ivanov and Beverton (1985, p. 43) to state that "there is as yet no indication of the relationship between stock and recruitment for Black Sea anchovy". However, their analysis made use of limited time series data and did not incorporate environmental influences such as nutrient enrichment. Presumably the subsequent establishment of *Mnemiopsis* in the Black Sea in the late 1980s only further complicated the system's dynamics, with obvious consequences for modelling anchovy recruitment.

More recently, progress has been made in understanding the dynamics of fish stocks in the Black Sea. For example, trophodynamic modelling of the Black Sea has been carried out (Berdnikov et al., 1999). Of critical importance to this paper is the significant study by Daskalov (1999) that attempted to relate fish recruitment (e.g. Black Sea anchovy) to environmental conditions in the Black Sea using general additive models (GAMs). Using time series of fish biomass from virtual population analysis (VPA), he identified a monotonic relationship between historical time series of recruitment (log) and spawning biomass for anchovy. While the use of traditional recruitment models (e.g. Ricker, Beverton and Holt) is possible with the GAMs approach, these were not incorporated in the study. Among environmental variables, river discharge in the northwest part of the Black Sea and wind speed were found to be significant (together with spawning biomass) in explaining recruitment. In the latter case (wind speed), the relationship was somewhat weak and

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doi:10.1016/j.fishres.2006.11.003

did not appear at all in bivariate regressions with log recruitment. River discharge's significance is explained in relation to its influence on marine physics (positive), as well as the transport of nutrients and pollution into the sea (generally negative). No mention is made in the study of specific environmental events, such as the rapid increase in nutrient discharge in the early 1970s or the invasion of the Black Sea by *Mnemiopsis* in the 1980s.

In this paper, I derive an anchovy recruitment function for the pre- and post-*Mnemiopsis* situations under rapid nutrient enrichment, recognizing these environmental events describe several distinct environmental regimes that have governed the anchovy's population dynamics. As part of a larger bioeconomic modelling exercise, my purpose was to develop a predictive model that accounts for the variability in anchovy recruitment by incorporating the effects of both rapid nutrient enrichment and sudden predation by ctenophores. This approach recognizes that these influences have inter-annual effects on anchovy recruitment and more persistent effects via changes in the parameters of the anchovy recruitment function. Some researchers have expressed doubts about the merits of including environmental influences in fisheries models (Walters and Collie, 1988). Despite these concerns, the empirical results in this paper support calls for inclusion of environmental disturbances in the estimation of stock–recruitment relationships, particularly for species such as anchovy (Csirke, 1980).

2. Data and model specification

2.1. Data

I used data from the same VPA estimates for recruitment and spawning stock as Daskalov (1999). These data were obtained from Prodanov et al. (1997), who used VPA to analyse the main commercial fish stocks of the Black Sea, including the Black Sea anchovy. I used their time series for the biomass of the 0+ age class in November as a measure of anchovy recruitment, because this represents the offspring spawned earlier the same year. The VPA estimates are based upon full recruitment in November (Table 1). The anchovy spawning stock was estimated as biomass in May, just prior to the commencement of spawning (Prodanov et al., 1997). A scatterplot of historical values for 1968–1993 indicated a positive relationship between spawning stock and recruitment (Fig. 1). Not surprisingly, this mimics the finding by Daskalov (1999), but it is also consistent with analyses of other anchovy stocks, such as the Peruvian and Northern anchovy populations in the Pacific Ocean (Csirke, 1980; Opsomer and Conrad, 1994), although at odds with the earlier analysis of the Black Sea anchovy by Ivanov and Beverton (1985).

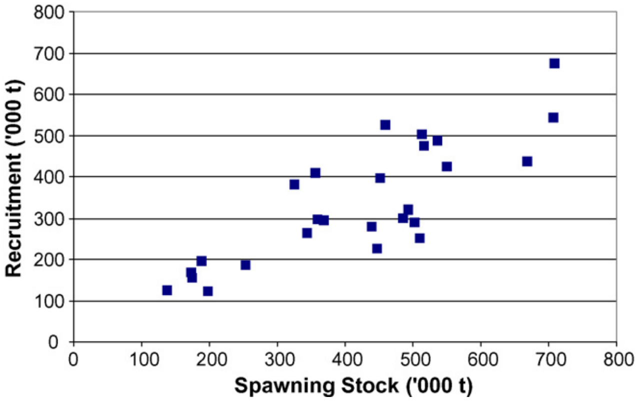

Fig. 1. Plot of Black Sea anchovy spawning stock, measured as total biomass in May in thousands of tonnes, and anchovy recruitment, measured as biomass of age 0+ in November in thousands of tonnes, 1968–1993 (*source*: Prodanov et al., 1997).

The environmental data series used in the estimation of parameters of the model consisted of nutrient data associated with the Black Sea and the Danube River (which drains into the Black Sea). Conveniently, a long-running data set for phosphorus was available (Table 1), but not for nitrogen. The implications

Table 1
Data used in the estimation a Ricker stock–recruitment relationship for the Black Sea anchovy, 1967–1993, with spawning stock measured as biomass of all age classes in May, recruitment measured as biomass of 0+ age class in November and phosphates measured as concentration off the Romanian Black Sea coast

Year	Spawning stock[a] (×1000 tonnes)	Recruit.[b] (×1000 tonnes)	Phosphate conc.[c] (μM)	Year	Spawning stock[a] (×1000 tonnes)	Recruit.[b] (×1000 tonnes)	Phosphate conc.[c] (μM)
1967	294.8	353	0.1	1981	667.2	439	1.6
1968	438.6	282	0.25	1982	549.3	426.3	5
1969	484.2	300.8	0.3	1983	515.3	474.7	4.2
1970	492	322.4	0.4	1984	451.3	398.1	6.2
1971	509.2	253.8	3.5	1985	512.1	502.9	5
1972	446.1	228.9	5.15	1986	534.9	488.8	6.1
1973	367.4	297	4.6	1987	501.6	291.4	12.2
1974	342.4	265.6	5.6	1988	252.3	187.5	6.3
1975	325.2	381.6	9.65	1989	188.1	196.5	4.25
1976	358.9	298	7.05	1990	137.5	125.5	6.2
1977	355.9	410.3	5	1991	173.2	157.9	4.25
1978	458.7	526.4	6.05	1992	197.6	123.1	1.7
1979	708.1	676.8	7.5	1993	172.1	170.1	3
1980	705.9	545.2	5.6				

[a] Post-harvest and pre-spawning season stock including all age groups and measured in May, from Table 37 in Prodanov et al. (1997).
[b] Recruitment measured as 0+ age group of the exploited biomass from Table 38 in Prodanov et al. (1997).
[c] Interpolated from Cociasu et al. (1997) and measuring phosphate concentration off the Romanian Black Sea coast.

of this choice are discussed later. I used annual time series data for phosphates for the period 1968–1993, measured in micromoles (μM), from Cociasu et al. (1997). Only a limited time series of data measuring the presence of the invading comb-jelly *M. leidyi* in the Black Sea was available (Mutlu et al., 1994) so that alternative methods were needed, as described below, to incorporate its influence on anchovy recruitment.

One concern with using an environmental variable, such as the level of nutrients, as an explanatory variable in the recruitment function is a possible correlation with the spawning stock variable. In such cases, a perceived relationship between the environmental variable and recruitment could be spurious, reflecting the spawning stock's influence instead (Iles, 1994). However, an analysis of these data showed little correlation between the spawning stock of anchovy and phosphate concentrations in the Black Sea for the period 1968–1993 ($r = 0.031$).

2.2. Model

Unlike Daskalov (1999), I estimate anchovy recruitment using a traditional recruitment model. The Ricker (1975) stock–recruitment model is frequently used to model clupeid populations (Csirke, 1980) and can be expressed as:

$$R_t = S_t \exp\{\alpha + \beta S_t\} \tag{1}$$

where recruitment in year t is R_t, spawning biomass is S_t, and α and β are the density-independent and density-dependent parameters of the Ricker model, respectively. Eq. (1) can be estimated using linear regression by transforming it to:

$$\ln\left(\frac{R_t}{S_t}\right) = \alpha + \beta S_t + \varepsilon_t \tag{2}$$

where ε_t is a normally distributed regression error term with a mean of zero and constant variance. Hilborn (1985) has shown that the parameters derived from a regression based on (2) are unbiased. In addition, Iles (1994) has demonstrated that an F-test applied to this regression model is actually a test of the Ricker model against a null hypothesis of a proportional model describing the stock–recruitment relationship. Eq. (2) was defined as Model 1 and served as a reference model because it omits environmental variables for the Black Sea.

As noted above, several sudden environmental and biological changes have affected the Black Sea in recent years. First, the Black Sea experienced a sharp increase in nutrients beginning in the early 1970s (Fig. 2). Cociasu et al. (1996) documented a statistically significant break in the mean nutrient loads for the Black Sea during this period. While 1971 shows a rapid increase in the level of phosphates, the response was not evident in anchovy recruitment per unit of spawning stock biomass until after 1972 (Fig. 2). Nutrient measurement problems may be at fault since monitoring was occurring near a large fertilizer plant on the Romanian coast that began operations in 1971 (Cociasu et al., 1996). Thus, the sudden increase in nutrients at this time is argued to have been largely localized with dissipation over the larger area used by anchovy for spawning having occurred over several years.

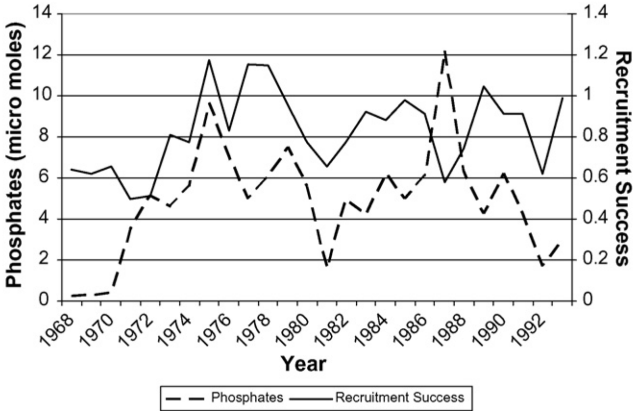

Fig. 2. Plot of Black Sea anchovy recruitment success, with recruitment measured as biomass (tonnes) of 0+ age class in November and spawning stock as biomass (tonnes), and phosphate concentration, measured off the Romanian Black Sea coast in micromoles (μM), 1968–1993 (*source*: Cociasu et al., 1997; Prodanov et al., 1997).

Mnemiopsis' invasion of the Black Sea during the latter half of the 1980s constituted a second major ecosystem shock. The population explosion of *Mnemiopsis* was first recorded in the fall of 1987 (Mutlu et al., 1994), although some accounts date this from 1988 (Shiganova, 1998). Possibly influencing the success of this invasion were high zooplankton stocks that resulted from large catches of anchovy and elevated nutrient levels (Shiganova, 1998). While there is competition between anchovy adults and *Mnemiopsis*, one of the primary influences of *Mnemiopsis* on the anchovy stock occurs via predation on larvae and juveniles (Kideys, 1994), leading to reduced annual recruitment.

To examine the effects of these biological and environmental changes on the recruitment of anchovy, several hypotheses were formulated as research questions:

(a) Is the traditional Ricker model an appropriate model for the stock–recruitment relationship governing the Black Sea anchovy?
(b) Is there any significant influence of the enrichment level (represented by the level of phosphates) on anchovy recruitment?
(c) Does correcting for possible measurement error affecting the phosphate variable in the early 1970s (when rapid enrichment was occurring) lead to a better predictive model?
(d) Is there any significant impact of the comb-jelly invasion on anchovy recruitment?

An alternative to the standard Ricker model in Model 1 was formulated to capture the main sources of environmental change in the Black Sea during the period 1968–1993. The inter-annual influence of nutrient enrichment was captured by including phosphate concentrations as an explanatory variable in the Ricker function. To meet admissibility criteria, which require that recruitment at a zero spawning stock is zero (Iles, 1994), nutrients were introduced multiplicatively with the spawning stock variable. This new variable could take several forms, such as $\gamma \ln P$ or in exponential form as γP, where P refers to the phosphate load and γ is a parameter (Iles and Beverton, 1998). In

Table 2
Two-stage least squares estimation (2SLS) of the Black Sea anchovy stock–recruitment function using the Ricker model and data for 1968–1993

Variables	No *Mnemiopsis* or phosphates	With *Mnemiopsis* and phosphates			
	Model 1	Model 2	Model 3	Model 4	Model 5
Constant	−0.075	−0.215	−0.181*	−0.066	−0.061
Spawning stock (S_t)	−0.00034	−0.0003	−0.00024	−0.00047	−0.00053**
Intercept dummy, 1971–1972 (D_1)	–	−0.501***	−0.451**	−0.510**	−0.541***
Intercept dummy, 1987–1993 (D_2)	–	0.327	–	−0.121	–
Slope dummy, 1987–1993 (D_2S_t)	–	−0.0022**	–	–	−0.00093**
Phosphates ($\ln P_t$)	–	0.160***	0.077**	0.090**	0.128***
Adjusted R^2	0.02	0.64	0.45	0.54	0.69
F-statistic	1.47	9.96	7.94	8.42	15.00
Autocorrelation	0.46	−0.08	0.12	0.04	−0.09
AIC$_c$	−71.29	−93.85	−85.18	−88.77	−98.98

The dependent variable is $\ln(R_t/S_t)$ and for all regressions, $N = 26$. AICc is the small sample Akaikie Information Criterion.
[*] $P < 0.1$.
[**] $P < 0.05$.
[***] $P < 0.01$.

testing both forms the non-exponential multiplicative approach had a lower standard error, so only these estimates are reported below. Second, a dummy intercept term was included for the years 1971–1972 to account for the apparent measurement error in the nutrient variable during this period. The use of these specific years was determined through trial and error since *a priori* information about the exact nature of the measurement error was lacking.

Since reliable time series data for the *Mnemiopsis* biomass were not available, it was not possible to model this environmental influence explicitly as a predator–prey relationship. Instead, the influence of the invader was treated as a structural change in the parameters of the anchovy recruitment function arising from predation on the anchovy stock by *Mnemiopsis*. Several approaches can be used to test for changes in the parameters of a stock–recruitment function, including the Chow test or the dummy variable technique (Maddala, 1992; Chow, 1960). As the Chow test was not practical, because of the limited times series, I used the dummy variable technique to test for a change in the parameters of the Ricker function beginning in 1987 (Maddala, 1992). Analysis of variance (ANOVA) can be used to determine whether the coefficients on these dummy variables are individually or jointly significant.

Incorporating the environmental influences described above into the standard Ricker stock–recruitment relationship (Model 1) provided the following new general model (Model 2):[1]

$$\ln\left(\frac{R_t}{S_t}\right) = \alpha + \beta S_t + \delta D_1 + \zeta D_2 + \eta D_2 S_t + \gamma \ln P_t + \varepsilon_t \tag{3}$$

where $D_1 = 1$ for the years 1971–1972 and zero otherwise, to capture possible measurement problems with the nutrient variable, and $D_2 = 1$ for the period 1987–1993 and zero otherwise, to allow for a shift in both the density-independent (α) and density-dependent (β) mortality factors, as a result of the invasion by *Mnemiopsis*. Expectations of the signs on the additional regression coefficients were $\gamma > 0$ and δ, ζ, $\eta < 0$.

To examine the influence of *Mnemiopsis* in more detail, I conducted further statistical testing. A series of null hypotheses was formulated to describe the precise nature of the change in the density dependent and independent recruitment parameters due to the presence of the comb-jelly; then these hypotheses were tested separately against an alternative hypothesis comprising Model 2. Three additional models served as the basis for this procedure:

(a) Model 3 (no dummy variable on the intercept and slope terms).
(b) Model 4 (dummy variable on the intercept term only).
(c) Model 5 (dummy variable on the slope term only).

Each model was estimated following the same procedure described above (Table 2). Subsequently, *F*-tests were carried out treating Model 2 as the unrestricted model and Models 3, 4 and 5 as restricted (Greene, 1993, p. 213).

Several statistical concerns were anticipated in estimating Models 2–5. First, the anchovy–*Mnemiopsis* system may have been jointly or simultaneously determined; that is, the influence of *Mnemiopsis* on anchovy recruitment may not have been truly independent, since the comb-jelly depends on anchovy as a food supply. If so, the use of ordinary least squares (OLS) regression could lead to biased estimates of the regression coefficients (Bence, 1995). To avoid bias, the estimation was undertaken using two-stage least squares (2SLS), an instrumental variables technique (Maddala, 1992). Second, residuals may be heteroscedastic, which could arise from a change in the parameters of the anchovy recruitment function once *Mnemiopsis* became established, possibly leading to a change in

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[1] An alternative general model could be formulated that includes a dummy variable on phosphates for the period 1987–1993, to capture a change in the influence of phosphates on anchovy recruitment once *Mnemiopsis* had become established. This formulation was examined but dismissed because of the impact on the residual sum of squares, which increased by a factor of 10 compared to the model used. Clearly, this effect was not present and its inclusion only served to invalidate the entire model. Results for this alternative model are available from the author.

Table 3
Analysis of Variance (ANOVA) tests for changes in the parameters of the Ricker stock–recruitment relationship for Black Sea anchovy with establishment of *Mnemiopsis leidyi* in the Black Sea in 1987 ($N = 26$)

Hypothesis	Variables deleted	RSS	No. of restrictions	d.f.	F-statistic
Unrestricted regression (Model 2)					
1. Change in both parameters	–	0.323	0	–	–
Restricted regressions					
2. No change in parameters (Model 3)	D_2, D_2S_t	0.596	2	20	8.43
3. No change in slope parameter (Model 4)	D_2S_t	0.455	1	20	8.15
4. No change in intercept (Model 5)	D_2	0.307	1	20	−1.00*

Note: (*) indicates null hypothesis cannot be rejected at the 5% level of significance ($P > 0.05$).

the variance of the error term. To check for this problem, I estimated the fully restricted and unrestricted recruitment models (see below) using ordinary least squares and then used the Breusch–Pagan Lagrange Multiplier test to check for the presence of heteroscedasticity (Greene, 1993). In both cases the test statistic was not significant ($P > 0.05$), leading to the conclusion that the models were not heteroscedastic.

3. Results

The initial regression estimates based on Eq. (2) tested the standard Ricker stock–recruitment model (Model 1) against a null hypothesis that the relationship was a simple proportional one. The possibility of a proportional relationship between spawning stock and recruitment seemed obvious from visual inspection of the data (Fig. 1). Not surprisingly, the coefficients estimated in Model 1 were individually and jointly insignificant and the model appeared to be a very poor fit to the data (Table 2). This model also indicated large autocorrelation in the residuals ($\rho = 0.455$), which is often noted in time series obtained from VPA. However, autocorrelation can also result from the omission of important variables or from model mis-specification (Maddala, 1992). For example, the anchovy stock–recruitment relationship may be more complex and involve important environmental influences and its parameters may be changing over time, so that the impression it is proportional may be mistaken. Model 2, the new general regression model, showed a substantial improvement over Model 1 (Table 2). Whereas Model 1 provided virtually no explanatory power, the adjusted R^2 in Model 2 rose to 0.64 (F-test: $P < 0.01$). While the R^2 statistic must be interpreted with caution in the Ricker model and when using two-stage least squares (Iles, 1994), these results are suggestive of improved explanatory power with Model 2. Moreover, autocorrelation was no longer a concern with Model 2 ($\rho = -0.083$). The coefficient on phosphates was highly significant and positive ($\gamma = 0.16$; $P < 0.01$), indicating the importance of this environmental influence. In addition, the dummy variable accounting for possible measurement problems during 1971–1972 was significant and substantially improved the predictive power of the estimated equation. However, the intercept and coefficient on anchovy spawning stock were not significant ($P > 0.1$). Furthermore, the dummy variables on the intercept term and on spawning biomass (D_2), which were intended to capture the presence of *Mnemiopsis*, showed mixed results: the former was not significant ($P > 0.10$), while the latter was ($P < 0.05$).

This latter finding suggested that the introduction of *Mnemiopsis* into the Black Sea may have induced a change in the parameters of the anchovy stock–recruitment relationship. Results from the F-tests conducted on Models 3–5 confirmed that the parameters of the anchovy recruitment function changed once *Mnemiopsis* was present (Table 3), since the null hypothesis that this did not occur was rejected ($P < 0.05$ for Model 3). Further testing made it possible to confirm the source of this change. A null hypothesis of no shift in the slope term (density-dependent parameter) was rejected ($P < 0.05$ for Model 4). Instead, the shift in parameters evidently occurred with the slope coefficient, since a test of the null hypothesis of no change in the intercept term (density-independent parameter) could not be rejected ($P > 0.05$ for Model 5). Interestingly, the coefficient on spawning stock becomes significant in Model 5 ($P < 0.05$), but not the intercept. Amongst Models 2–5, the ANOVA tests for changes in the parameters of the stock–recruitment relationship and the AIC$_\mathrm{c}$ for each model provide a basis for preferring Model 5 (with only the slope dummy included), over the alternative specifications.

Based on Model 5, the resulting stock–recruitment relationship can be written as:

$$R_t = P_t^{0.128} S_t \exp\{-0.061 - 0.541 D_1 - (0.00053 + 0.00093 D_2) S_t\} \tag{4}$$

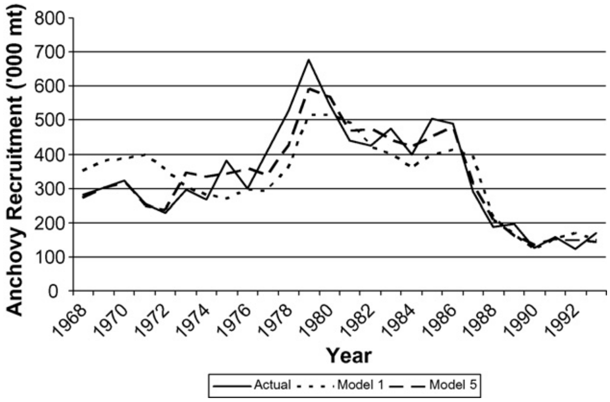

Fig. 3. Plot of Black Sea anchovy recruitment, measured as actual biomass (tonnes) of 0+ age class in November and predicted biomass (tonnes) using Models 1 and 5 (*source*: this study and Prodanov et al., 1997).

To test its predictive power, recruitment estimates from Eq. (4) were plotted against actual recruitment of Black Sea anchovy from the input data set (Table 1) and recruitment estimates from Model 1, the traditional Ricker model (Fig. 3). Visual inspection of the plots suggests a close match for Model 5 with actual recruitment and a substantial improvement over Model 1.

4. Discussion

While Ivanov and Beverton (1985) suggested there was no evidence of a stock–recruitment relationship for the Black sea anchovy, more recent data and VPA modelling suggest otherwise (Fig. 1). However, this paper has attempted to dispel the notion that the anchovy stock–recruitment relationship is a single monotonic function, once specific environmental events are incorporated. Casual observation suggests that a sudden rise in nutrient inputs may have improved recruitment, but it also may have created conditions favourable for *Mnemiopsis*, whose establishment further modified the recruitment relationship. As a result, a more defensible view is that the dome-shaped Ricker model should be applied to Black Sea anchovy recruitment with these environmental changes leading to regime shifts. Ignoring this finding could lead to inappropriate assessments of recruitment associated with a given spawning stock size when there are changes in environmental conditions.

By explicitly incorporating specific environmental events, the anchovy recruitment modelling produced useful insights for environmental management in the Black Sea, although these differ somewhat from the results in Daskalov (1999). Evidence of recurring *Mnemiopsis* outbreaks in the Black Sea coincides with the description of this exotic species as a Type B invader (Shiganova, 1998; GESAMP, 1997). Under these conditions, recruitment of anchovy in the Black Sea may alternate between higher and lower recruitment curves, rather than obeying a single recruitment curve. When *Mnemiopsis* is dormant, a higher curve would be relevant ($D_2 = 0$), while during outbreaks of *Mnemiopsis*, managers would be wise to base management planning on a lower recruitment curve ($D_2 = 1$). The recent entry into the Black Sea of the Mediterranean ctenophore *Beroe ovata* may necessitate further refinement, as this species is known to prey on *Mnemiopsis* (Shiganova et al., 2001).

In addition to the presence or absence of *Mnemiopsis* outbreaks, fisheries managers also need to take into account the level of nutrients. While continued enrichment is always a threat, several factors suggest that this may not occur in the future. First, the demise of the Soviet Union in the early 1990s lead to reduced use of phosphate inputs in agriculture and the ambient phosphate concentration in the Black Sea declined (Fig. 3). More recently, a basin-wide effort has been initiated to address the problem of nutrient enrichment, indicating that nutrient loads may decline further in future. However, caution is advised since several key Black Sea Basin countries acceded to the EU in 2004 and two more will join in January, 2007 (Bulgaria and Romania). The impact of these events on local economic growth may result in offsetting increases in phosphate loads, despite commitments to meet European environmental standards as part of the accession process. These developments suggest that the nutrient influence on anchovy recruitment be re-evaluated regularly as a component of fisheries management in the Black Sea.

The case for vigilance in monitoring nutrient loads is strengthened by the finding here that phosphates positively influence anchovy recruitment, which is consistent with results found elsewhere (Boddeke and Hagel, 1991). As a result, nutrient abatement policies could have a negative impact on the anchovy fishery, although the special case where higher nutrient levels may trigger outbreaks of *Mnemiopsis* leads to more complex outcomes (Knowler, 2005). Existing environmental strategy documents pertaining to the Black Sea do not appear to consider these potential outcomes, creating further challenges for fisheries management (BSEP, 1996). Additional research into the link between recruitment in small pelagic stocks, outbreaks of *Mnemiopsis* and nutrient loads should be a high priority.

Several aspects of the modelling of anchovy recruitment warrant further discussion. The selection of phosphates as the measure of nutrient loads, in part, reflected data availability. Phosphate and silicate concentrations off the Romanian Black Sea coast were available for the period commencing in the early 1960s, while data for nitrate concentration and various nutrient ratios were available only for the period since 1980 (Cociasu et al., 1997). The nitrate content of the Danube River has been measured since at least 1970 (Mee, 1992), but this time series was not found to have a relationship with anchovy recruitment in preliminary modelling. Nevertheless, some authors have argued that marine coastal systems may be limited more by nitrogen than by other nutrients such as phosphorous (Ryther and Dunstan, 1971), but arguably this is less likely to be true where the N:P ratio is very high, as has been documented for the Black Sea (Cociasu et al., 1997). Mee (1992) points out that different nutrients may have limited productivity in the Black Sea at various times and that there is no consensus on the topic. In the end, the finding of a statistically significant influence of phosphates on recruitment of anchovy in the Black Sea suggests that this nutrient has played a substantial role, even if other nutrients may be important to the marine ecosystem as well.[2]

In addition, several other analyses have dated the first outbreak of *Mnemiopsis* from 1988 (Shiganova, 1998). The modelling presented here found a statistically significant change in the parameters of the recruitment function beginning in 1987, after testing alternative switching points from 1985 to 1990. Modelling a change in the parameters in a stock–recruitment relationship can only indicate that a change took place and cannot verify its cause; however, it is highly circumstantial that a major ecosystem event (*Mnemiopsis*) occurred at about the same time the modelling discerned a shift in parameters. Although some observers of the *Mnemiopsis* invasion also cite 1987 as the first year of its impact (Mutlu et al., 1994), differences in dat-

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[2] In addition, I carried out experimental estimations incorporating the two environmental variables found by Daskalov (1999) to significantly influence anchovy recruitment (river discharge and wind speed), using the data provided in that paper. Including both together and separately in log form the estimated coefficients were not statistically significant. Interestingly, the concentration of phosphates did not correlate significantly with river discharge ($P = -0.203$), so that the two influences are not likely to be conflated.

ing the invasion may result from variations in location-specific measurements, rather than any fundamental disagreement on timing.

Despite the limitations of the analysis, its findings have a wider relevance for the management of fisheries in semi-enclosed seas similar to the Black Sea throughout the world. Eutrophication is present in many of these marine systems, and results here suggest that the influence of nutrients on recruitment must be modelled carefully. Moreover, periodic outbreaks of invading species and blooming algae may require managers to rely on more than one recruitment curve for a given fish stock.

Acknowledgements

The author thanks Ed. Barbier, Ivar Strand and John Caddy for important discussions and inputs, as well as Franz Mueter and Randall Peterman for helpful comments on the draft manuscript. Laurence Mee and Christopher Cosslett at the Black Sea Environment Programme (BSEP) provided funding. Furthermore, this work was a component in a larger bioeconomic modeling exercise that could not have been undertaken without support from the Social Sciences and Humanities Research Council (SSHRC) of Canada, the Committee of Vice-Chancellors and Principles of the Universities of the United Kingdom, and the University of York (U.K.). I also wish to acknowledge very helpful comments from two reviewers of this paper.

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