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Effects of environmental variables on recruitment of anchovy in the Adriatic Sea

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ABSTRACT: The anchovy *Engraulis encrasicolus* is an important fishery resource in the Adriatic Sea. Fluctuating recruitment of young fish to the stock over time can be related to changes in the environment. The trend of anchovy recruitment in the northern and central Adriatic from 1975 to 2001 was analysed with the aim of identifying possible effects related to 5 environmental factors: surface air temperature, surface atmospheric pressure, quadrant specific wind stresses, Po River runoff and North Atlantic Oscillation (NAO) index. Particular emphasis was placed on 1987, a year of anchovy collapse and fishery crisis. Different types of regression models were applied, both linear and non-linear (simple and multiple), with predictor variables being environmental factors and parental stock abundance. Positive relationships of number of recruits with autumnal SSE and ESE wind stress and both annual and autumnal Po River runoff were found, with a strength comparable to the relationship between recruits and parental stock. Low levels of these environmental factors were observed just before the 1987 collapse, together with a high frequency of occurrence of NE winds and an extreme positive value of the NAO index in the previous autumn (which may have been unfavourable to recruitment in 1987). All 5 environmental factors could be related to increased or reduced food availability for young stages of anchovy in autumn.

KEY WORDS: Anchovy · Adriatic Sea · Recruitment · Population dynamics · Wind · Po River runoff · NAO index

1. INTRODUCTION

Recruitment of young fish is highly variable, even on the scale of a small number of years, and underlies fluctuations in abundance of small pelagic fish (Blaxter & Hunter 1982). Recruitment levels in different years can be influenced by parental stock biomass levels, i.e. it can be linked to the number of eggs laid (Beverton & Holt 1957, Jacobson & MacCall 1995). Moreover, recruitment could be the result of different mortality rates in early life-history stages (i.e. eggs, larvae, juveniles), related to disease or predation (Bailey & Houde 1989, Mann 1993, Cushing 1996). Changes in mortality of larvae and juveniles are caused by changes in the environment that affect recruitment directly or indirectly via food availability and/or prey encounter rate (Shepherd et al. 1984, Smith 1985, Heath 1992, Mann 1993, Leggett & Deblois 1994, Dower et al. 1997, Cole & McGlade 1998).

The anchovy *Engraulis encrasicolus* (Linnaeus, 1758) is an important fishery resource in the Adriatic Sea. The mean annual catch of anchovy was 24 000 tonnes between 1975 and 2001, with a peak of >50 000 tonnes in 1978–1980. Catch primarily comprises 1 to 2 yr old fish, thus relying heavily on recruitment strength. The small pelagic fishery is particularly widespread in the northern and central Adriatic Sea. Anchovy is mainly fished by the Italian fleet, with catches from Slovenia, Croatia and the former Yugoslavian fleets accounting for <1000 tonnes per year (Cingolani et al. 1996, 2002, Grbec et al. 2002, Santojanni et al. 2003). The Italian fleet comprises about 140 (70 couples) pelagic trawlers (volante) mainly operating from Trieste to Ancona (Fig. 1) and about 40 purse seiners (lampara) which

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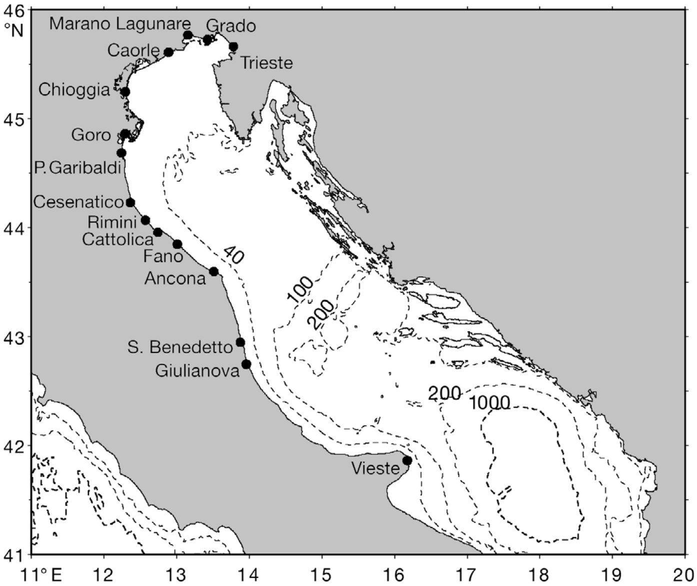

Fig. 1. Geographic extent of small pelagic fish data collection: Vieste harbour represents the southern limit. Dashed lines: bathymetry contours (m)

operate mainly in the central Adriatic, i.e. south of Ancona (Cingolani et al. 1996, 2002).

Since 1975, the Istituto di Scienze Marine (ISMAR) has been conducting research on the biology and stock assessment of anchovy (together with sardine) in the northern and central Adriatic by means of population dynamics methods. The southern limit of data collection is represented by Vieste (Fig. 1). Anchovy stock assessments have revealed strong fluctuations in biomass and, in particular, a collapse that occurred in 1986–88 coupled with a fall in catches and a strong fishery crisis from the end of 1986 and throughout 1987. One or 2 yr of very poor recruitment almost certainly contributed to this crash (Cingolani et al. 1996, 2002, Santojanni et al. 2003).

The aim of the present study was to investigate how some environmental factors could have influenced recruitment fluctuations in the Adriatic anchovy stock, with particular attention on the 1987 collapse. Six main variables were available with a sufficient degree of spatial and/or temporal coverage for the 1975–2001 period (the time series for anchovy): parental stock size (i.e. biomass of anchovies spawning at sea), surface (2 m) air temperature, sea surface atmospheric pressure, wind stress, river runoff and the North Atlantic Oscillation (NAO) index, and they were investigated for possible correlations with recruitment strength.

Parental stock size is at least partially linked to fishing mortality. Although heavy commercial exploitation was not the only factor deemed responsible for variation in recruitment, and the link between parental stock size and recruitment is not usually expected to be strong in fish populations (Hilborn & Walters 1992), a partial effect could be expected and was investigated.

Sea surface air temperature and pressure are indicative of climatic conditions over the study area, so these variables were investigated to find eventual anomalous conditions that could have affected recruitment.

In the Adriatic Sea, winds can cause water column mixing, advection and deepening of the strong spring-summer stratification in the outflow region of the Po River (Russo & Artegiani 1996). Dominant winds are the Bora and the Sirocco. The Bora is a cold dry wind blowing from the Balkans and channelling along the valleys of the Dinaric Alps. It is very strong in specific areas where it reaches the Adriatic Sea due to a katabatic effect, and it causes very intense heat loss from the sea surface. Its direction varies locally (NNE to NE) according to orography, and its duration typically spans a few (2 to 3) days, with a higher occurrence in winter. The Sirocco is a moderate, warm and wet wind blowing from the SE along the major axis of the basin. It is more frequent in spring and autumn and its duration is generally similar to that of the Bora. Wind causes turbulence and mixing in the water column making nutrients available for phytoplankton. Moreover, wind mixing can enhance the encounters between predator and prey at larval stages, but when too strong could reduce such encounters and cause the advection of planktonic stages of fish from nursery areas and, hence, influence their survival (Sinclair 1988). For these reasons, variations in recruitment as a function of wind speed/stress or water turbulence are thought to be non-monotonic, and a dome-shaped curve is usually suggested (Wroblewski & Richman 1987, Kiørboe et al. 1988, Cury & Roy 1989, Dower et al. 1997, Cole & McGlade 1998, Visser & Stips 2002).

River runoff transports nutrients thereby enhancing plankton production, and in the resulting estuarine circulation surface layers move offshore allowing deeper water to inflow upwards. Furthermore, when temperate waters are changing from winter mixed conditions to summer stratified ones, river runoff can cause an earlier stratification of lighter freshwater at the surface. This can lead to an earlier start of the plankton spring bloom and higher levels of its total production (Mann 1993, Grimes & Kingsford 1996). In the northern Adriatic system, the Po River provides >50% of the freshwater as well as ca. 50% of the total input of nutrients (Malanotte-Rizzoli & Bergamasco 1983, Russo & Artegiani 1996, Pettine et al. 1998). The seasonal peaks of phytoplankton production in the northern Adriatic tend to coincide with maximum Po River flow rates (Revelante & Gilmartin 1976). In a Mediterranean context, Palomera (1992), García & Palomera (1996) and Lloret et al. (2004) pointed out the positive effects of the runoff of the Rhône and

Ebro rivers in the Catalan Sea and the Gulf of Lion on anchovy abundance.

Possible effects on Adriatic anchovy recruitment due to climatic fluctuations over a wider area were also examined using the NAO index. This is defined as the difference in sea level pressure anomalies between Gibraltar and Reykjavik, and is representative of weather conditions over Europe. In particular, the NAO index could have a link with salinity variation in the intermediate layer of the Adriatic, with positive values being associated with higher salinity (Grbec et al. 2002, 2003).

Initially, data were visually inspected by means of raw plots of recruitment levels versus each environmental variable. In the most promising cases, simple and multiple linear regressions were then fitted. Finally, when fitting nonlinear models, an attempt was made to test the predictive capability of the relevant variables.

2. MATERIALS AND METHODS

2.1. Recruitment and biomass estimates

Estimates of the annual number of recruits and spawners were derived from 2 different population dynamics assessment methods applied to the Adriatic anchovy fishery: Virtual Population Analysis (VPA) and the DeLury model with recruitment index.

VPA is based on analysis of the age frequency distributions of annual total catches (Hilborn & Walters 1992) and produces an estimate of the number of fish at sea for each age class and year. The annual age classes obtained ranged from 0 to 4+, with the latter class including individuals older than 4 yr. VPA estimates of age class 0, i.e. individuals in their first year of life, were considered as recruits, while individuals from age 1 onwards were considered as spawners (Santojanni et al. 2003). Since the reproduction of Adriatic anchovy is particularly intense in spring-summer (Regner 1996), and a conventional birth date on 1 June is more coherent with the biology of this species, VPA assessment was carried out using 1 June as the birth date of anchovy. Split-year data were thus used, where Year *x* was referred to as the time interval ranging between 1 June of (calendar) Year *x* – 1 and 31 May of Year *x* (Santojanni et al. 2003).

The DeLury model with recruitment index is a stock depletion model that uses total catch and catch per unit of effort (CPUE) data, which also takes into account interannual variability in recruitment (Hilborn & Walters 1992, Santojanni et al. 2003). It provides an overall annual estimate of abundance at sea, regardless of age classes. The annual recruitment index employed in this model and used in the present study was calculated as the CPUE-weighted sum of proportions of 9 to 10.9 cm anchovies in the monthly catches of Porto Garibaldi, the most important fishing harbour for anchovy in the Adriatic (Santojanni et al. 2003). The model allows us to distinguish the estimated number of 'non recruits', N_t, from the corresponding recruits in the same year *t*; the former group was used as the spawning stock.

The values of total and spawning biomass estimated by VPA and DeLury models are shown in Fig. 2. The 2 assessment methods produce a similar trend; however, a higher contrast is observed in DeLury data (Fig. 2b), along with higher values in the 1970s and most recent years. The lowest values always correspond to the 1986–1988 period and match to the crisis of fishery. Current biomass estimates indicate partial recovery, but biomass has not yet risen to the higher levels of the second half of 1970s.

2.2. Environmental data

Six hour reanalyses (1979–2000 period) from the European Centre for Medium-Range Weather Forecasts (ECMWF) were used. They include 2 m air and

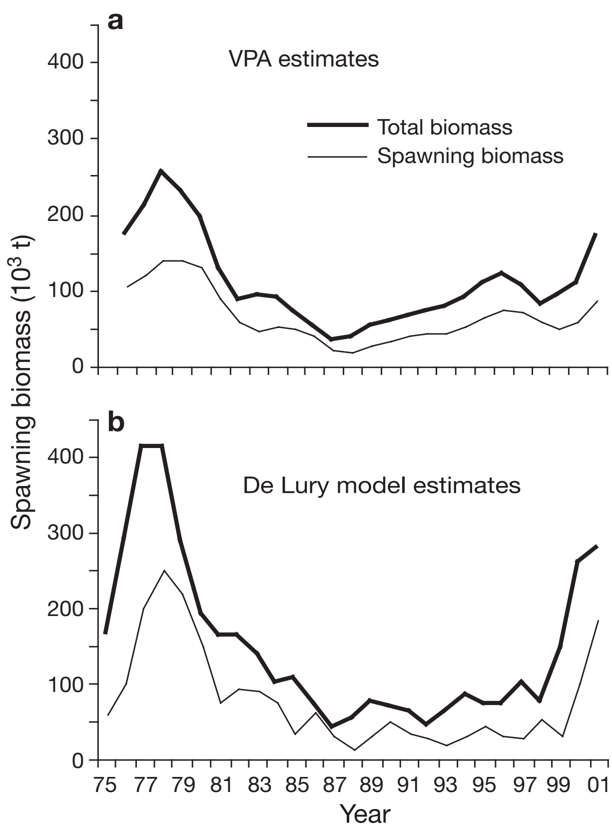

Fig. 2. *Engraulis encrasicolus.* Total and mid-year spawning biomass values over time, estimated by (a) split-year Virtual Population Analysis (VPA) and (b) calendar year DeLury model

dew point temperature, sea surface atmospheric pressure and 10 m wind components. Since atmospheric forcing datasets are divided into different time windows at different horizontal resolutions, 2 datasets were considered separately. One dataset covers 1979–1993 on a T106 Gaussian grid, corresponding to about 200 km spectral truncation; the other dataset covers 1994–2000 on a T213 grid, corresponding to ca. 90 km spectral truncation (during this latter period the spatial resolutions had some further slight variations). This change in horizontal resolution caused a discontinuity in the behaviour of variables, particularly evident for wind. Thus, whole data series was never considered. In comparisons with anchovy recruits, emphasis was placed on the 1979–1993 dataset, because it covers a longer time interval including the years of stock collapse. Two time series were used from ECMWF reanalysis: one single gridpoint in the North Adriatic (the only one in open sea), and a wide area (42 to 46°N, 12 to 16°E) average. Analysis of correlations with fishery data showed that the former was most promising, so only the single gridpoint is considered hereafter.

The 2 m air temperature (°C) was used here as a raw proxy for sea surface temperature, while sea surface atmospheric pressure can provide indications of anomalous meteorological conditions that may affect anchovy recruitment.

Starting from the zonal and meridional components, wind directions were calculated and then grouped into 8 quadrants according to their origins: NNE, ENE, ESE, SSE, SSW, WSW, WNW, NNW. Quadrant specific winds were calculated, squaring their intensity to get physical dimensions of wind stresses ($m^2\ s^{-2}$). As westerly winds showed a rare occurrence, only NNE, ENE, ESE, SSE were considered in the analyses.

The NAO index for the period 1975–2000 was obtained from the Climate Research Unit (www.cru.uea.ac.uk) and was computed as the difference in sea level pressure anomalies between Gibraltar and Reykjavik.

Monthly values of the Po River flow rate ($m^3\ s^{-1}$) between January 1975 and June 2001 were obtained from Magistrato del Po (Parma, Italy). Both annual (always calendar) and seasonal averages were calculated for Po River flow rate, 2 m air temperature, surface atmospheric pressure, quadrant specific squared wind intensity and NAO index. Seasonal averages were calculated for 3 mo periods: January-February-March (JFM; winter), April-May-June (AMJ; spring), July-August-September (JAS; summer), October-November-December (OND; autumn).

The annual values of the Po River flow rate are shown in Fig. 3a, while the mean for each month of the year computed over the considered period is shown in Fig. 3b. The AMJ and OND intervals capture the 2 peaks over the year (Russo & Artegiani 1996).

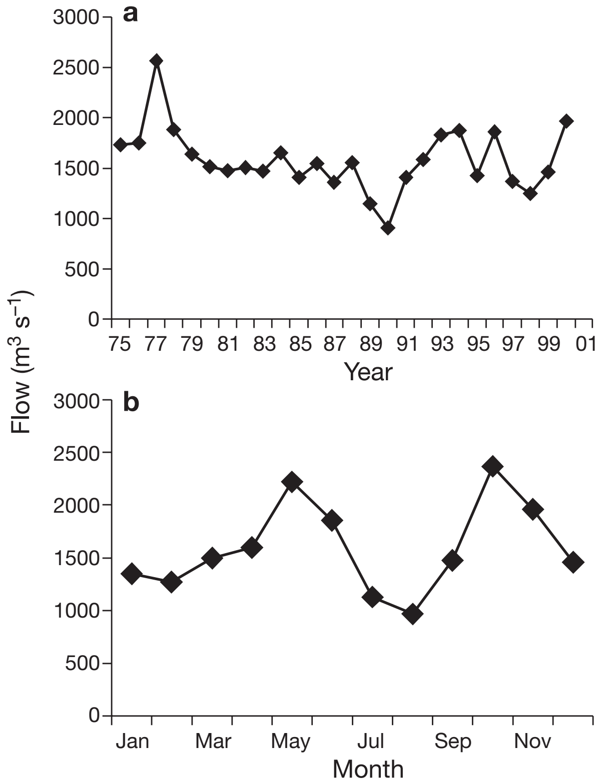

Fig. 3. (a) Annual and (b) monthly average 1975–2000 Po River flow rate

2.3. Data analysis

After a preliminary extensive exploratory analysis, regression analysis was used in order to evaluate the possibility of correlating recruitment with environmental variables. Recruit values for Year x were always related to the annual/seasonal environmental variables of Calendar Years $x - 1$ or $x - 2$. This time lag is justified by the fact that anchovy recruits to the fishery at the end of its first year of life (Cingolani et al. 1996), but environmental variables are likely to have an effect on recruitment during the spawning period, or on the larval and early juvenile stages, i.e. 1 yr before recruitment. Spawning biomass was always considered for Year $x - 1$. Analyses with time lag $x - 2$ were tried with VPA data only, because the actual time interval from Split-Year x to Calendar Year $x - 1$ is only 6 mo. Lognormal distribution of statistical errors was always assumed: such an assumption is a common procedure in stock-recruitment relationship studies (Stocker et al. 1985, Hilborn & Walters 1992, Prager & MacCall 1993, Jacobson & MacCall 1995, Daskalov 1999).

The regression models employed were of 3 kinds: (1) simple and linear, relating recruitment to spawners or 1 environmental variable; (2) multiple and linear, relating recruitment to spawners and 1 or 2 environmental variables, or to >1 environmental variable; (3) nonlinear, represented by the classic stock-recruitment model proposed by Beverton & Holt (1957) and an alternative version modified ad hoc to take into account at least 1 environmental variable (Hilborn & Walters 1992).

The Beverton-Holt model is the most commonly used model in the analysis of stock-recruitment relationships and it relies on the reasonable assumption that there is competition for food and space among juveniles, and that the mortality rate of juveniles (i.e. recruitment) is thus density dependent. The basic equation is as follows:

$$R = [aS \times (b + S)^{-1}]e^{\varepsilon} \quad (1)$$

where R is the number of recruits in Year x; S is the spawning biomass in the Year $x - 1$; the parameter a is the maximum number of recruits produced; the parameter b is the spawning stock needed to produce a recruitment level equal to half the maximum (i.e. $a \times 0.5$) and is strongly related with the shape—in particular the initial steepness—of the curve; the term e^{ε} accounts for the lognormal distribution of statistical errors.

The same model, when taking into account an additional environmental variable, can be built according to the following equation:

$$R = [aS \times (b + S)^{-1}]e^{zE}e^{\varepsilon} \quad (2)$$

where E (e.g. the annual Po River flow rate in Year $x - 1$) is the deviation from the mean calculated on the entire time series and z a parameter accounting for the effect of E, estimated by fitting, as are a and b. Log transformation of Eq. (2) allows the conversion of ε from multiplicative into additive, as follows:

$$\ln(R \times S^{-1}) = \ln a - \ln(b + S) + zE + \varepsilon \quad (3)$$

Normal distribution was thus assumed for the statistical error, now represented by the term ε.

Initially, Eq. (3) was fitted without including the term zE. The fitting was then repeated including zE in order to evaluate possible improvements in predictability of recruitment. The Levenberg-Marquardt algorithm in the SPSS software package was used for nonlinear regression.

3. RESULTS

The number of recruits at the beginning of Year x was plotted as a function of spawning biomass in the middle of Year x – 1, for both VPA and DeLury data (Fig. 4). Dispersion of data points is quite pronounced. DeLury model estimates are more scattered, and the plot in Fig. 4b could be suggestive of a dome-shaped curve in the stock-recruitment relationship as predicted by the model proposed by Ricker (Hilborn & Walters 1992).

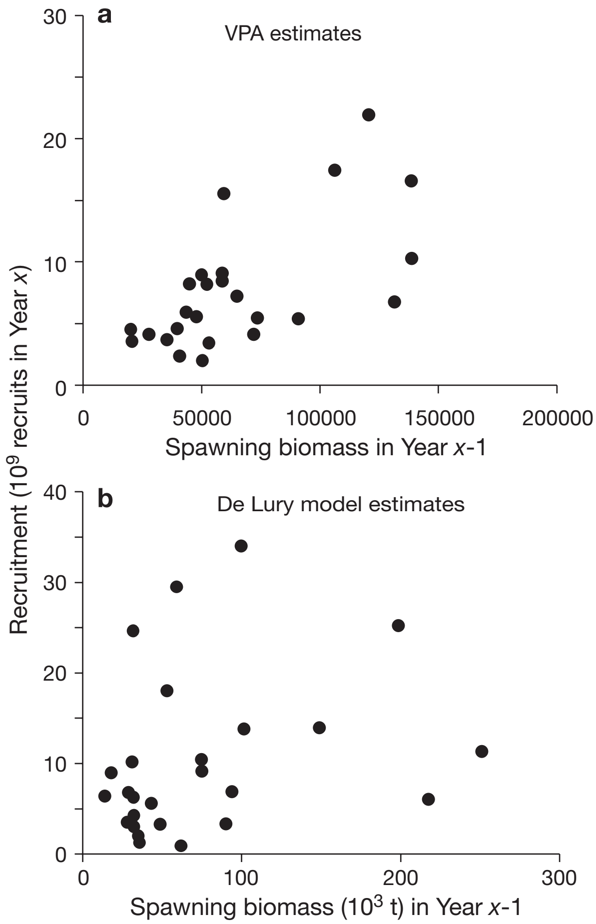

Fig. 4. *Engraulis encrasicolus.* Stock-recruitment relationship: no. of recruits at the beginning of Year x plotted as a function of spawning biomass in the middle of Year $x - 1$. Estimates of both recruits and spawners are derived from (a) split-year VPA and (b) calendar year DeLury model

Recruitment was plotted against annual (Fig. 5) and seasonal 2 m air temperature averages obtained using data for this variable up to 1993; no relationship emerged from the simple regression analysis, as at no time was the slope significant ($p > 0.05$). Similar results emerged for sea surface pressure (not shown).

Plots relative to the seasonal squared wind intensity by quadrant revealed a certain degree of positive influence on recruitment for SSE and ESE in autumn. The best result was obtained through the application of a linear regression model on recruits fitted using autumn SSE squared wind intensity as the predictor variable. Using DeLury recruits, R^2 was equal to 0.41 and the slope was positive and significant ($p < 0.05$) (Fig. 6). The results obtained using autumn squared wind intensity from ESE as a predictor variable were

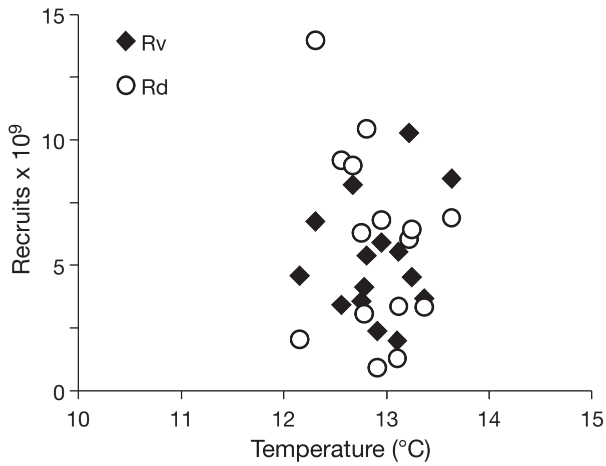

Fig. 5. *Engraulis encrasicolus.* Recruit numbers in Year *x*, estimated by split-year VPA (Rv) and calendar year DeLury model (Rd), plotted as a function of annual 2 m air temperature in Calendar Year *x* – 1. Temperature dataset 1979–1993

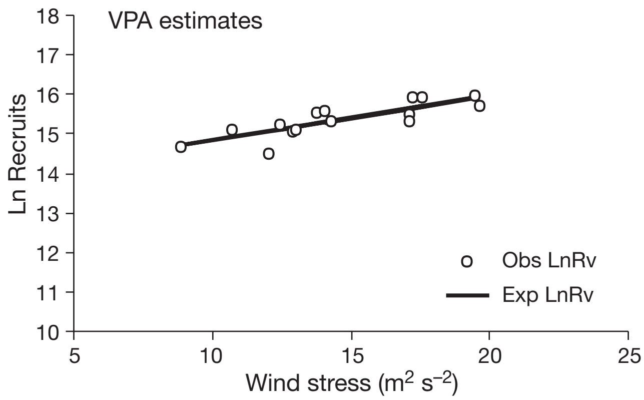

Fig. 7. *Engraulis encrasicolus.* Observed (Obs) log recruit numbers (Rv) in Year *x* estimated by split-year VPA and corresponding expected (Exp) number from the regression model fitted using autumn (OND) SSE squared wind intensity in Calendar Year *x* – 2 ($p < 0.01$, $R^2 = 0.69$) as the predictor variable. Wind dataset 1979–1993

very similar ($R^2 = 0.38$). When VPA recruits were fitted, R^2 values were equal to 0.53 and 0.69 for autumn SSE squared wind intensity in Years *x* – 1 and *x* – 2, respectively. The slope was positive and highly significant ($p < 0.01$) in both cases, as shown for Year *x* – 2 in Fig. 7. When the Autumn squared wind intensity was taken from ESE in Year *x* – 1, fitting gave $R^2 = 0.51$ and a significant positive slope ($p < 0.01$), while in Year *x* – 2 an R^2 value equal to 0.23 and a non-significant positive slope ($p = 0.069$) was obtained. The Durbin-Watson test was performed to check for first order autocorrelation of residuals over time: non-correlation hypothesis was never rejected or, as in 1 case that suggested positive autocorrelation, the test was inconclusive (Table 1).

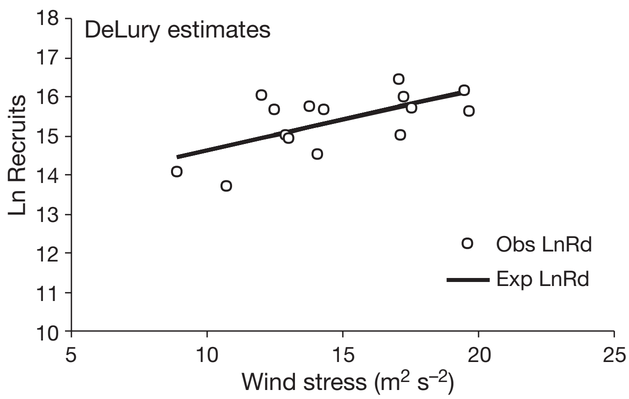

Fig. 6. *Engraulis encrasicolus.* Observed (Obs) log recruit numbers (Rd) in Year *x* estimated by calendar year DeLury model and corresponding expected (Exp) numbers from the regression model fitted using autumn (OND) SSE squared wind intensity in Calendar Year *x* – 1 ($p < 0.05$, $R^2 = 0.41$) as the predictor variable. Wind dataset 1979–1993

Plots of recruitment versus NAO index were rather inconclusive overall (the slope of regression line was always not significant). Despite this, upon comparison of VPA and DeLury recruit values with the autumn NAO index over the years (Fig. 8), a high, positive autumn NAO index value is evident for 1986, just at the beginning of the anchovy fishery crisis.

A link between recruitment and Po River flow rate in Year *x* – 1 seems to exist when the flow rate was calculated both as an annual average and as a seasonal average for autumn (and to a lesser extent for summer). Regression analysis was carried out using (1) the annual value of Po River flow rate in Year *x* – 1 (or *x* – 2) and (2) the corresponding autumn value as predictor variables.

When DeLury recruits were fitted using the annual flow rate (in Year *x* – 1), the slope was positive and significant ($p < 0.05$), but R^2 value was low at 0.21. The high dispersion of data points around the straight line is shown in Fig. 9. The point in the top right-hand corner represents recruitment in 1978: thus, the highest flow rate (1977) corresponded to one of the highest levels of recruitment. The results were slightly improved using the autumn flow rate: R^2 was equal to 0.26 and the positive slope was highly significant ($p < 0.01$).

When the model with annual flow rate in Year *x* – 1 was fitted to VPA recruits, R^2 was equal to 0.41 and the slope was positive and highly significant ($p < 0.01$) (Fig. 10). Again, the point in the top right-hand corner represents the highest level of recruitment, which occurred in 1978 and is associated with the highest flow rate (1977). When the same flow rate was taken in Year *x* – 2 instead of *x* – 1, fitting yielded a significant positive slope ($p < 0.05$) but a low R^2 value (0.17). With autumn flow rates, the results were similar (R^2 = 0.30

Table 1. *Engraulis encrasicolus.* Results of Durbin-Watson test for simple linear regression models fitted to log recruit numbers in Year *x* derived from calendar year DeLury and split-year Virtual Population Analysis (VPA). Predictors and no. of data points fitted (N) are given along with estimated values of Durbin-Watson statistics (DW). This is compared with tabulated lower and upper boundaries of DW at the 1% level of significance. H_0 (non-correlation of residuals) was accepted when DW was higher than the DW upper value and rejected when the DW was less than DW lower value (positive autocorrelation); the test was inconclusive when DW was between the 2 values

Data	Predictor variable	N	DW estimated	DW lower	DW upper	H_0
DeLury	Annual flow rate in Year *x* – 1	26	1.250	1.072	1.222	Accepted
VPA	Annual flow rate in Year *x* – 1	26	0.875	1.072	1.222	Rejected
VPA	Annual flow rate in Year *x* – 2	25	0.655	1.055	1.211	Rejected
DeLury	Autumn flow rate in Year *x* – 1	26	1.132	1.072	1.222	Inconclusive
VPA	Autumn flow rate in Year *x* – 1	26	0.709	1.072	1.222	Rejected
VPA	Autumn flow rate in Year *x* – 2	25	0.840	1.055	1.211	Rejected
DeLury	Autumn SSE wind in Year *x* – 1	15	1.922	0.811	1.070	Accepted
VPA	Autumn SSE wind in Year *x* – 1	15	1.896	0.811	1.070	Accepted
VPA	Autumn SSE wind in Year *x* – 2	15	1.549	0.811	1.070	Accepted
DeLury	Autumn ESE wind in Year *x* – 1	15	1.912	0.811	1.070	Accepted
VPA	Autumn ESE wind in Year *x* – 1	15	1.304	0.811	1.070	Accepted
VPA	Autumn ESE wind in Year *x* – 2	15	0.881	0.811	1.070	Inconclusive

and 0.23 for the rates from Years *x* – 1 and *x* – 2, respectively). On the basis of the Durbin-Watson test, positive autocorrelation emerged in some cases, and these were all relative to models computed using VPA data (Table 1).

Two predictors were used in multiple linear regression models: the spawning biomass in Year *x* – 1 (VPA or DeLury), and Po River flow rates (annual [*x* – 1 or *x* – 2] or seasonal [from autumn of Year *x* – 1 back to winter of Year *x* – 2]). When recruitment from DeLury data were used the fitting was not good, while better results were obtained when VPA data were used (Table 2). The best model was obtained when using spawning biomass in Year *x* – 1 and autumn Po River flow rate in Year *x* – 1 (Table 2, Model 4): the R^2 was equal to 0.62 and the partial regression coefficients were both positive and highly significant ($p < 0.01$). The values of the partial R^2 for autumn Po River flow rate and spawning biomass were 0.38 and 0.48, respectively, thus suggesting comparable importance of the 2 predictors in explaining the variability of recruitment data. The observed numbers of recruits and those expected from this model are compared over the years in Fig. 11. The highest recruitment levels, which occurred in the split-year 1978–1979, are not well portrayed, but based on the agreement between trends of empirical and theoretical data the fitting seems to be reasonably good from 1980 onwards. The possibility of including 2 flow rates was also tested (Table 2, models 3 and 6), but no significant improvement of the explanatory power of the model was obtained.

Of all 6 multiple linear models summarised in Table 2, positive autocorrelation occurred in 2 cases (models 1 and 2), with values of the Durbin-Watson test statistic

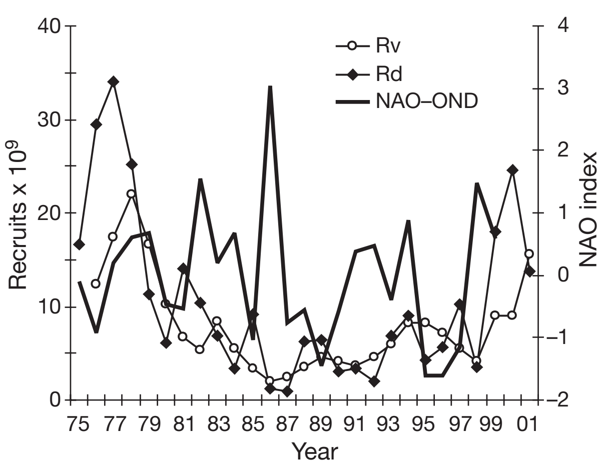

Fig. 8. *Engraulis encrasicolus.* Recruit numbers (thousands) in Year *x*, estimated by split-year VPA (Rv) and calendar year DeLury model (Rd), compared with autumn NAO index (NAO–OND) in Calendar Year *x*

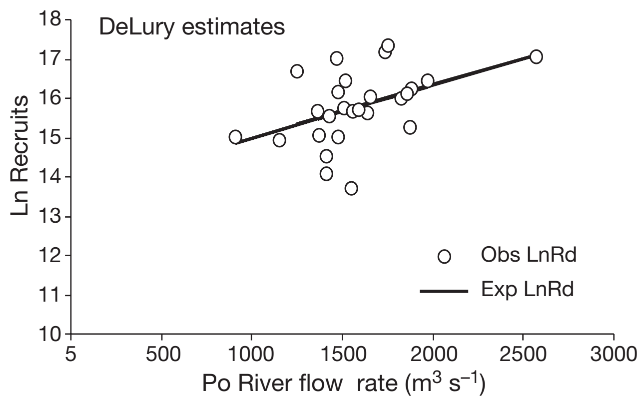

Fig. 9. *Engraulis encrasicolus.* Observed (Obs) log recruit numbers (Rd) in Year *x* estimated by calendar year DeLury model and corresponding expected (Exp) numbers from the regression model fitted using annual Po River flow rate in Calendar Year *x* – 1 ($p < 0.05$, $R^2 = 0.21$) as the predictor variable

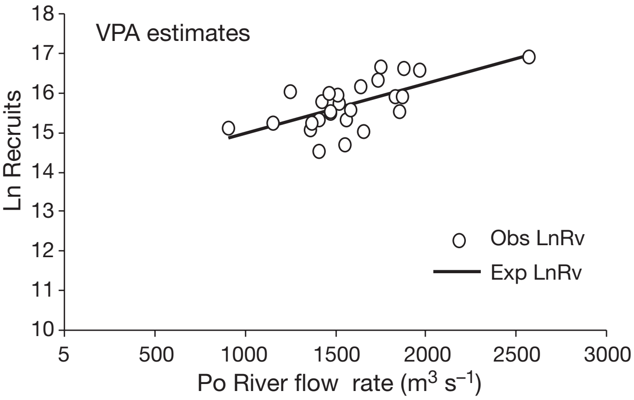

Fig. 10. *Engraulis encrasicolus.* Observed (Obs) log recruit numbers (Rv) in Year *x* estimated by split-year VPA and corresponding expected (Exp) numbers from the regression model fitted using annual Po River flow rate in Calendar Year $x-1$ ($p < 0.01$, $R^2 = 0.41$) as the predictor variable

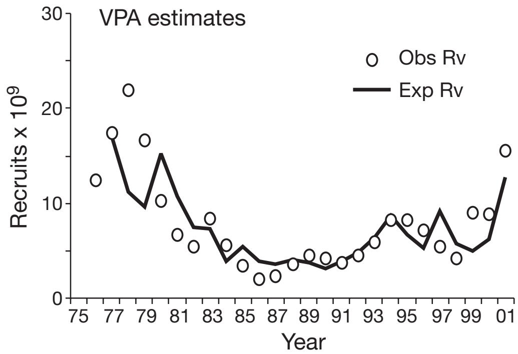

Fig. 11. *Engraulis encrasicolus.* Observed (Obs) and expected (Exp) values of recruits (Rv) over time. Expected values obtained from a multiple regression model fitted to log recruits estimated by split-year VPA ($R^2 = 0.62$) (see Model 4 Table 2), with 2 predictor variables: spawners in Split-Year $x-1$ ($p < 0.01$), and autumn (OND) Po River flow rate in Calendar Year $x-1$ ($p < 0.01$)

being estimated as equal to 0.91 and 0.73, respectively. These values are not particularly low (as they are not close to 0)—not much lower than the tabulated lower boundary of 0.981 that corresponds to a 1% level of significance (N = 25, 2 independent variables). In the other cases the test was inconclusive: the best model, which corresponded to Model 4 (and Fig. 11), showed a Durbin-Watson value equal to 1.299, which is slightly lower than the tabulated upper boundary of 1.305, thus suggesting acceptance of a non-correlation hypothesis.

It is likely that the wind dataset was too short (1979–1993) to safely estimate regression parameters. The multiple regression models with spawners and autumn squared wind intensity from SSE or ESE in Year $x-1$ (or $x-2$) always yielded very poor fitting, with at least one of the partial regression coefficients being non-significant.

Poor results were also obtained with multiple regression models when considering 2 environmental variables but without spawners; however, compared to simple regressions with only one predictor, some slight improvements of the fitting were found. For example, when DeLury recruits were fitted, the 'addition' of summer Po River flow rate to the simple model with autumn flow rate increased the value of R^2 from 0.26 (see above) to 0.41.

Table 2. *Engraulis encrasicolus.* Results of 6 multiple linear regression models fitted to log recruit numbers in Year *x* derived from split-year VPA. Predictor variables were the corresponding spawning biomass in Split-Year $x-1$ and the annual and autumn (OND) Po River flow rate in Calendar Years $x-1$ or $x-2$. All partial regression coefficients were positive, except 1 case (*) that was not statistically significant

Model	Predictor variables	α error	R^2
1	Spawning biomass in Year $x-1$	$p < 0.05$	0.54
	Po River flow rate in Year $x-1$	$p < 0.05$	
2	Spawning biomass in Year $x-1$	$p < 0.05$	0.38
	Po River flow rate in Year $x-2$	$p > 0.05$	
3	Spawning biomass in Year $x-1$	$p = 0.05$	0.54
	Po River flow rate in Year $x-1$	$p < 0.05$	
	Po River flow rate in Year $x-2$	$p > 0.05$*	
4	Spawning biomass in Year $x-1$	$p < 0.01$	0.62
	Autumn Po River flow rate in Year $x-1$	$p < 0.01$	
5	Spawning biomass in Year $x-1$	$p < 0.01$	0.48
	Autumn Po River flow rate in Year $x-2$	$p = 0.05$	
6	Spawning biomass in Year $x-1$	$p < 0.01$	0.68
	Autumn Po River flow rate in Year $x-1$	$p < 0.01$	
	Autumn Po River flow rate in Year $x-2$	$p = 0.06$	

Finally, the common version of the Beverton-Holt stock-recruitment model and the ad hoc modified model (including annual or autumn Po River flow rate in Year $x-1$) were fitted: results are shown in Table 3 and Figs. 12 & 13. The fitting of the Beverton-Holt model alone was always poor, but it was improved by the inclusion of the flow rate variable in the ad hoc version. The highest value of R^2 was obtained when including the autumn Po River flow rate in Year $x-1$ and DeLury recruitment data. The agreement between the observed and expected trends of recruits over time can be evaluated in Figs. 12 & 13. The high level of recruitment in the 1970s was well portrayed by the model when the Po River flow in Year $x-1$ was employed with VPA recruitment data (Fig. 13). On the other hand, the best model predicting low recruitment in the 1986–1988 period (the fishery collapse years) was obtained using Po River flow rate in the autumn of

Table 3. *Engraulis encrasicolus.* Common and ad hoc modified versions of the Beverton-Holt (BH) model, fitted to log recruit numbers derived from calendar year DeLury model and split-year VPA. The modified BH model (with *z*) takes into account annual (*F*1) or autumn (*F*OND1) Po River flow rate in Calendar Year *x* – 1

Parameter	DeLury			VPA		
	Value	SE	R^2	Value	SE	R^2
a	12 554 300	6 114 610	0.20	25 252 800	18 499 200	0.08
b	35 960	40 135		161 776	161 550	
a	9 141 090	3 387 570	0.34	11 806 100	4 424 480	0.30
b	12 547	20 033		43 924	36 599	
z(*F*1)	0.00124	0.00056		0.00088	0.00033	
a	12 220 400	5 038 450	0.43	18 213 800	8 669 440	0.35
b	33 611	32 833		100 006	74 566	
z(*F*OND1)	0.00052	0.00017		0.00029	0.00010	

Year *x* – 1 and DeLury recruitment data (Fig. 12), even though none of the models were able to predict the actual magnitude of this event.

4. DISCUSSION

There is no perfect method of measuring recruitment and biomass trends in a fish population and the 2 data series here presented both positive features and drawbacks. VPA data rely on the assumption that fish ageing procedures are free of error: mistakes and inconsistencies in the ageing process can bias the subdivision into age classes, thus affecting recruitment estimates. DeLury data series are based on length frequency distributions of catches and are, therefore, coarser. The corresponding recruitment index, which is calculated as the proportion of small fish landed, could be very sensitive to changes in fishing behaviour of the fleet: for example, targeting of larger individuals or discarding at sea of smaller individuals for market reasons could affect recruitment estimates. Plots of stock-recruitment relationships are very seldom conclusive in fishery science and the Adriatic anchovy is no exception. Many models could equally fit the dispersed data presented in Fig. 4. In particular, the dome-shaped Ricker model could equally describe the DeLury data in Fig. 4b. The Ricker model takes into account a decrease in recruitment at higher values of parental stock size. Such a pattern is thought to be particularly realistic when cannibalism of adults on younger stages occurs, but Tudela & Palomera (1997) did not find any evidence of cannibalism in anchovy in the northwestern Mediterranean, owing to the spatial and temporal segregation of feeding and spawning activity, and this is likely to be true for the Adriatic as well.

The fact that no clear effects of surface air temperature on recruitment were found is not surprising. Although in recruitment studies sea surface temperature is often taken as a proxy for wind-induced upwelling, this seems to be unlikely to happen in the case of Adriatic anchovy. Wind-induced upwelling is not particularly strong in the Adriatic (Russo & Artegiani 1996), particularly along the western coast where anchovy spawning areas are mainly located (Piccinetti 2001). It is also known that sea-water temperature can influence the recruitment of small pelagic species by directly affecting the metabolism of both spawners and young stages (Stocker et al. 1985, Prager & McCall 1993, Jacobson & MacCall 1995, Daskalov 1999). Despite this, no evidence of any effect was found. As mentioned previously, air temperature was considered

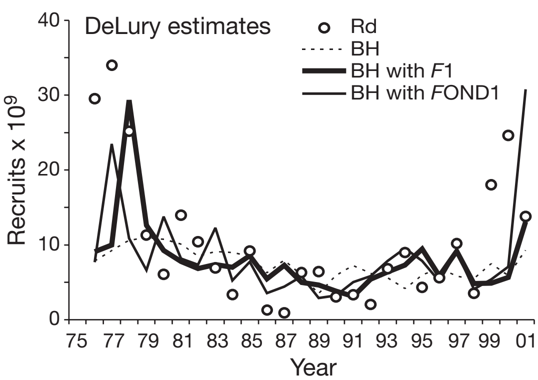

Fig. 12. *Engraulis encrasicolus.* Observed and expected values of recruits (Rd, in thousands) over time. Expected values obtained by fitting the Beverton-Holt (BH) model to log recruits estimated by calendar year DeLury model. The BH model was simple or ad hoc modified with predictor variable *F*1 or *F*OND1 (annual and autumn Po River flow rate in Calendar Year *x* – 1, respectively; see Table 3)

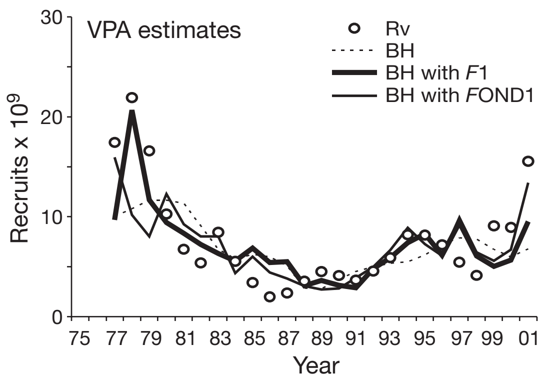

Fig. 13. *Engraulis encrasicolus.* Observed and expected values of recruits (Rv) over time. Expected values obtained by fitting the Beverton-Holt (BH) model to log recruits estimated by split-year VPA. The BH model was simple or ad hoc modified with predictor variable *F*1 or *F*OND1 (annual and autumn Po River flow rate in Calendar Year *x* – 1, respectively; see Table 3)

here as a raw proxy for sea surface temperature and this could have further confounded any possible effect.

The analogous absence of a correlation between recruitment and surface atmospheric pressure indicates that there was no influence on recruitment of particular local meteorological conditions (such as anomalously persistent high pressure, or increased transit of depressions, over the northern Adriatic).

Negative effects, due to advection of eggs and larvae from favourable nursery areas or due to disrupted stratification (hindering larval feeding, Lasker 1978) during the spawning period, were expected upon examination of quadrant specific squared wind intensity. In contrast to this, positive effects due to vertical mixing and increased plankton production could be expected before and after the spawning period that takes place in spring and summer in the Adriatic (Regner 1996). Wind stress from the quadrants SSE and ESE (1979–1993 dataset) seemed to exert a positive influence on recruitment when their averages were calculated for autumn. In particular, the lowest values from SSE and ESE quadrants were recorded in 1985–1986 and 1986, respectively, just prior to the 2 yr of low recruitment (1986 and 1987). The autumn SSE and ESE wind stress could cause moderate mixing of the water column and, as a consequence, enhance plankton productivity. Increased prey encounter rate in favour of young anchovies could be suggested as well. Young anchovies recruit mainly from October to February (Cingolani et al. 1996): the hypothetical increase of zooplankton production/predation associated with wind action seems to fit this time period. A positive influence due to autumnal storms was suggested to occur for herring *Clupea harengus* larvae in the North Sea: storms would make new nutrients available to larval herring prey, i.e. immature copepods (Kiørboe et al. 1988). Similar observations were also made by Wroblewski & Richman (1987) for the phytoplankton eaten by northern anchovy larvae *Engraulis mordax*.

However, such an explanation for the Adriatic anchovy does not agree with the fact that the same positive relationship was not observed for ENE and NNE winds, which are potentially more likely to cause mixing of the water column in this system. An alternative explanation could be sought. Both SSE and ESE wind stress are able to modify the Western Adriatic Coastal Current (WACC) (Zavatarelli & Pinardi 2003), which conveys nutrient-rich freshwaters coming from Po River as well as other western rivers towards the southeast. In particular, through Ekman transport, they displace the surface freshwaters present along the Italian coast further offshore, thus increasing the extension of the area favourable to recruiting of post-larval anchovies (which in autumnal months start to depart from the coastal zone). In contrast, in the area south of the Po River delta, northerly wind stresses tend to concentrate nutrient-rich freshwaters very close to the shore, and induce a narrow, intense southeastward current along the western Adriatic coast.

The NAO index did not prove to be very helpful, except for the single fact that, in Autumn 1986, the NAO index showed a very high positive value and recruitment in the subsequent 1987 was at its lowest. As a very tentative explanation, this could be related to higher salinity, in accordance with some data reported by Grbec et al. (2002, 2003). This possible increase in saltier water in the northern Adriatic could have caused the freshwater and, hence, the nutrient load from the Po and other western rivers to be closer than usual to the coast, reducing favourable conditions for zooplankton production.

The Po River flow rate, which was based on a time series of data longer than that for SSE and ESE wind stress, also showed some degree of correlation with recruitment. This holds true not only for the annual average, but also for the seasonal average calculated for autumn (less so for summer). The effect of river flow was evident in simple linear regressions as well as in multiple linear and nonlinear models, which included spawning biomass as well. As for wind stress, low values of flow rate were observed in 1985 and 1986, prior to the 2 yr of low recruitment (1986 and 1987). Moreover, high values were observed for both annual and seasonal flow rates (autumn in particular) in the mid-1970s, when the highest recruitment of anchovy (together with the highest stock biomass) was estimated. Hopkins (2002) proposed that excessively high Po River flow rates could be detrimental for recruitment, because eggs and larvae could be transported offshore to less favourable environments. A non-monotonic function could thus be expected for recruitment as a function of the flow rate. Our data do not support this hypothesis, at least within the range of flow rate values observed in our study.

Although the link between river runoff and small pelagic fish production is well established for a number of species and in different estuarine areas of the world, e.g. the Mississippi (Grimes 2001), Black Sea (Daskalov 1999), and northwestern Mediterranean (Lloret et al. 2004), the actual mechanism is still a matter of speculation. In particular, for Mediterranean anchovy Lloret et al. (2004) found a rather strong correlation between Ebro river runoff in spring and anchovy landings 1 yr later. They suggest that river runoff influences spawning and the survival rate of anchovy early stages (mainly in spring-summer), which depend on food availability at the surface; food availability should be related to nutrient content of surface water, which in late spring and summer depends on river runoff (Salat 1996). Our results suggest a slightly different picture, where river runoff in autumnal months seems to play a major role. Northern and central Adriatic Sea anchovy spawn from April to October (Regner 1985, 1996). Anchovy spawning areas are on the western side of Adriatic and, in particular, off the Po River mouth. Here, stratification of the water column is very strong in late spring, summer and early autumn and is enhanced by river runoff. Egg development lasts a few days, while development of larvae, post-larvae (individuals not metamorphosized) and early juveniles lasts several months (Palomera et al. 1988, E. Arneri pers. comm.). Post-larval and juvenile anchovies remain close to the western Adriatic until January and, as mentioned previously, recruit to the fishery mainly from October to February (Piccinetti 1970, Cingolani et al. 1996). A possible, purely speculative explanation of the impact of autumnal Po River runoff lies in the importance of the WACC in this period. This current has a strong eastern boundary separating coastal nutrient-rich freshwaters from open sea oligotrophic Adriatic waters. Post-larval and juvenile anchovies concentrate in the former area. Here, phytoplankton and zooplankton productivity are high in autumn (Revelante & Gilmartin 1976, 1983, Zavatarelli et al. 2000), thus providing anchovy with optimal survival and growth conditions. In years with higher flow rates the WACC expands further offshore, and might consequently increase food availability for post-larval and juvenile anchovy.

A combination of the previously observed events may furnish an explanation for unsuccessful recruitment in 1986 and 1987. In autumn 1986, the low values of SSE and ESE wind stress and of the Po River runoff, combined with a possible major inflow of saltier water from southeast, could have caused freshwater to remain close to the western coast, thus reducing the area favourable for juvenile feeding and growth. This effect could have been enhanced by the fact that, in 1986, the autumn NNE wind showed the maximum occurrence of the whole period. In turn, this could also have increased the WACC intensity and thereby freshwater exports from the northern Adriatic, and larvae could have been advected from their optimal nursery grounds. Moreover, it may have reduced the predator-prey encounter to the detriment of anchovy. In winter 1987, the ENE winds reached the maximum intensity within the considered period, thus protracting the anomalous situation.

Evidence of negative effects on food availability caused by a disruption of the stratification in the outflow region of Po consequent of winds in spring and summer was not observed. The possibility of increased larval mortality in response to such reduction in the same area and period has been investigated by several authors (Conway et al. 1998, Giovanardi 1998, Coombs et al. 2003), but despite an effective decrease in the abundance of potential food no significant change in mortality was observed. This was explained, at least partially, by the fact that the superficial layer of freshwater somehow locally maintains stratification in the immediate river plume area. Furthermore, plasticity in the diet of the anchovy larvae with changing composition of plankton due to wind mixing has also been observed. Such findings confirm the difficulties in searching for links between this factor and the recruitment of Adriatic anchovy.

In conclusion, although the correlations obtained from the regression models fitted to log recruits are not strong, we believe that the main mechanism of recruitment strength determination is driven by the behaviour of the WACC in the previous autumn. This current has a strong eastern boundary separating coastal nutrient-rich freshwaters from open sea oligotrophic Adriatic waters. The presence of high Po River flow rates together with moderate SSE and ESE wind stress will expand a nutrient rich WACC offshore, sustaining an increased phytoplankton and zooplankton biomass and thus increasing the extension of the area favourable to recruitment of post-larval anchovies.

When evaluating possible short-term scenarios for the recruitment of Adriatic anchovy, it may be wise to take into account the potential input of nutrients from the Po River, wind stress in autumnal months and, perhaps, extreme values of NAO index, even though the effects of this and of other atmospheric indices deserve further investigation. Integration of the information obtained from all these environmental variables with that regarding the abundance of spawners, as estimated by routine stock assessment procedures, would thus provide stock management with more reliable forecasting tools.

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