The influence of the Atlantic and regional climate variability on the long-term changes in gelatinous carnivore populations in the northwestern Mediterranean

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Abstract

We investigated potential connections between climate and the population size of gelatinous carnivores in the northwestern Mediterranean. The interannual variability of large- and meso-scale climate factors was related to gelatinous carnivore dynamics by means of a multivariate regression model. Gelatinous carnivore population dynamics integrate the climate-related changes in the northwestern Mediterranean with close correlations between climate and the population size of the Calycophoran siphonophores *Chelophyes appendiculata* and *Abylopsis tetragona* and the Hydromedusae *Rhopalonema velatum* and *Solmundella bitentaculata*. We show that the sensitivity of particular gelatinous carnivore species to environmental forcing relates to their seasonal appearance and peak of abundance. Our results advocate the occurrence of short time windows, during which gelatinous carnivores appear more sensitive to environmental conditions, and favorable conditions may therefore substantially enhance their annual peaks. Furthermore, there were threshold values from which climate effects on gelatinous carnivores become noticeable, indicating that the climate–gelatinous carnivore relationship intensifies according to the strength of climate forcing. The possibility of using the North Atlantic climate variability for assessing and predicting interannual abundance changes of these organisms in the northwestern Mediterranean is considered.

Pelagic gelatinous carnivores are of particular ecological importance in marine ecosystems because of their potential effect on the population size of mesozooplankton, including fish eggs and larvae (Purcell and Arai 2001). High abundances of these organisms may channel the energy flow away from fish and affect the fish : primary production ratio (Sommer and Stibor 2002). Several investigations have also emphasized the effects of gelatinous carnivores on fisheries. In British Columbia, the hydromedusa *Aequorea victoria* exerts a top-down control on the Pacific herring larvae (*Clupea pallasi*) (Purcell and Grover 1990); in the Bering Sea, high abundances of the scyphomedusa *Chrysaora melanaster* affect recruitment and population size of pollock (*Theragra chalcogramma*) (Brodeur et al. 2002); in the Baltic and North Seas, the scyphomedusa *Aurelia aurita* appears as a main predator of herring larvae (*Clupea harengus*) (Möller 1984; Lynam et al. 2005*b*). Also

in the North Sea, other scyphomedusae, such as *Cyanea capillata* and *Cyanea lamarckii,* exert a top-down control on plaice (*Pleuronectes platessa*) and salmon (*Salmo salar*) larvae (Lynam et al. 2004, 2005); in the Black Sea, the collapse of stocks of anchovy (*Engraulis encrasicolus*), Mediterranean horse mackerel (*Trachurus mediterraneus*), and sprat (*Clupeonella cultriventris*) in the late 1980s has been linked to the introduction of the ctenophore *Mnemiopsis leidyi* (FAO 1997). Massive proliferations of gelatinous carnivores (e.g., medusae, ctenophores, and siphonophores) reported in some coastal areas and temperate seas in the last few decades may therefore be indicative of considerable changes in the functioning of marine ecosystems (Mills 2001; Purcell 2005; Hay 2006). Under climate warming scenarios, the recurrence of triggering factors for gelatinous outbreaks (e.g., warm waters and the subsequent enhancement of the water column stratification) makes ecologically plausible a higher predation or competition pressure upon fish stocks. A current challenge is, then, to identify how climate interacts with the population size of these organisms and to identify the potential for the consequent effects such interaction may have on the pelagic realm (Brodeur et al. 2002; Lynam et al. 2004).

Retrospective investigations have proved very useful in exploring impending relationships between climate, hydrographic environment, and marine populations (Chiba et al. 2006). Particularly sensitive and observable indicators of

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these interrelations involve the space–time patterns of plant and animal biological events (Edwards and Richardson 2004; Chiba et al. 2006). This is especially evident in environments characterized by a marked seasonality (e.g., the Ligurian Sea, northwestern Mediterranean, in which seasonal biological patterns [i.e., growth and reproduction] of marine species are usually restricted to a short time window). Modifications in the external forcing during such periods may thus affect the seasonal life-cycle timing and population growth of pelagic organisms, perhaps subsequently affecting trophic interactions (e.g., match–mismatch in interspecies dependencies). If they are sustained, such changes could lead to modifications in food-web structure and potentially to ecosystem-wide changes (Edwards and Richardson 2004). In the present study, we aim at identifying the underlying mechanisms through which variations in climate interact with the population size of gelatinous carnivores in the Ligurian Sea. Further, we explore the possibility of assessing long-term changes in these species based on climate variability and discuss the potential of these organisms as indicators of ecosystem-level changes.

Methods

Study area—The Ligurian Sea, northwestern Mediterranean, is characterized by a permanent cyclonic circulation that governs the coastal zone. The study site is influenced by open sea conditions, since the narrow continental shelf and local geological structures, such as the Villefranche canyon, indicate that in close proximity to the sampling station the water depth reaches 2,000 m.

Biological data—Plankton samples for analysis were collected weekly from November 1966 to December 1993 from a depth of 80 m (Point B: 43°41′N, 7°19′E). Zooplankton sampling used a zooplankton net (Juday-Bogorov, 330-μm mesh size) hauled vertically from the bottom to the surface. The gelatinous carnivores investigated belong to superclass hydrozoa (*Liriope tetraphylla, Solmundella bitentaculata,* and *Rhopalonema velatum*), including the siphonophores *Abylopsis tetragona* and *Chelophyes appendiculata*, and in the phylum Ctenophora, *Pleurobrachia rhodopis*. Although standard nets used (e.g., Juday-Bogorov net) may damage gelatinous zooplankton (CIESM 2001) and therefore affect the estimation of its densities, the high number of observations (>1,000 samples) and consistent sampling and quantification protocols during the whole study period allow these data to be compared through time.

Physical data—Environmental variables (i.e., hydrographic, meteorological) corresponding to different spatial scales were used to identify interrelationships linking local processes (e.g., water column stratification) and large-scale phenomena.

As indicators of local forcing we used water temperature variability, recorded weekly at 1-, 20-, 50-, and 75-m depths, and those atmospheric factors acknowledged to affect the survival of gelatinous carnivores (i.e., precipita-

tion, wind strength, and irradiance) (CIESM 2001). These data were derived from daily time-series measurements at the Cap Ferrat Semaphore (~1.5 km from the studied site). The regional scale investigated extends from 6°E to 10°E and from 44°N to 42°N. We assessed atmospheric variability by means of monthly anomaly fields of sea surface temperature, surface atmospheric pressure, 500-hPa geopotential height, and precipitation records for the period ranging from 1966 to 1993 from the Climate Diagnostics Center reanalysis fields (Kalney et al. 1996). The large-scale atmospheric forcing was assessed by means of key modes of atmospheric circulation over the Northern Hemisphere (i.e., Northern Annular Mode [AO/NAO], East Atlantic pattern [EA], Gulf Stream/Northern Current Index, East Atlantic Western Russian pattern, and the Northern Hemisphere Temperature [NHT]). All of these indices have effects on the western Mediterranean ocean climate (Dünkeloh and Jacobeit 2003). The main signal of the North Atlantic climate forcing on the northwestern Mediterranean was obtained by means of Principal Component Analysis (PCA). The first principal component (PC1, 47% of the total variance) was used as a proxy of the North Atlantic climate variability (Molinero et al. 2005*a*). Including all these climate indices reduces the possibility of omitting signals that could be weak but biologically important (Taylor et al. 2002; Voigt et al. 2003).

Data analysis—Biological time series were first log-transformed. All time series were then analyzed in their standardized and nondimensional form as standard deviations (SDs) from the mean of the time series. Statistical analysis was performed using Matlab Software.

The analysis was divided in two main steps. In the first step, we analyzed local hydro-climate factors that may have an effect on the survival of gelatinous carnivores and their larvae (Goy et al. 1989; Buecher 1999). These factors were precipitation, irradiance, thermal stratification of the water column, and the mean Ekman layer depth. Thermal stratification of the water column was calculated as the average temperature difference m^{-1} of the 0–75-m depth layer. The Ekman layer depth h_E was estimated at 10 m from the wind velocity: $h_E = 0.4(u^*/f_{Cor})^{1/2}$, where u^* is the value of the surface friction velocity (m s^{-1}): $u^* = (\tau/\rho_a)^{1/2}$; f_{Cor} is the Coriolis parameter (10^{-4} s^{-1}); τ is the surface wind stress (kg m^{-1} s^{-2}); and ρ_a is the air density (1.22 kg m^{-3}).

Cumulative *z*-score plots were used to identify the main periods of hydro-climate parameters (i.e., North Atlantic climate, irradiance, precipitation, Ekman transport, and thermal stratification of the water column). *z* scores are standardized anomalies, calculated as deviations from the mean of the time series divided by the SD. Plots of these cumulative *z* scores indicate periods with predominantly positive or negative anomalies and can be used to determine the dates of trend initiation. The periods identified were compared (by bootstrapped *t*-test) using the original time series to assess whether significant differences exist between them.

In the second step of the analysis we identified the main abundance periods of gelatinous carnivores. We investigat-
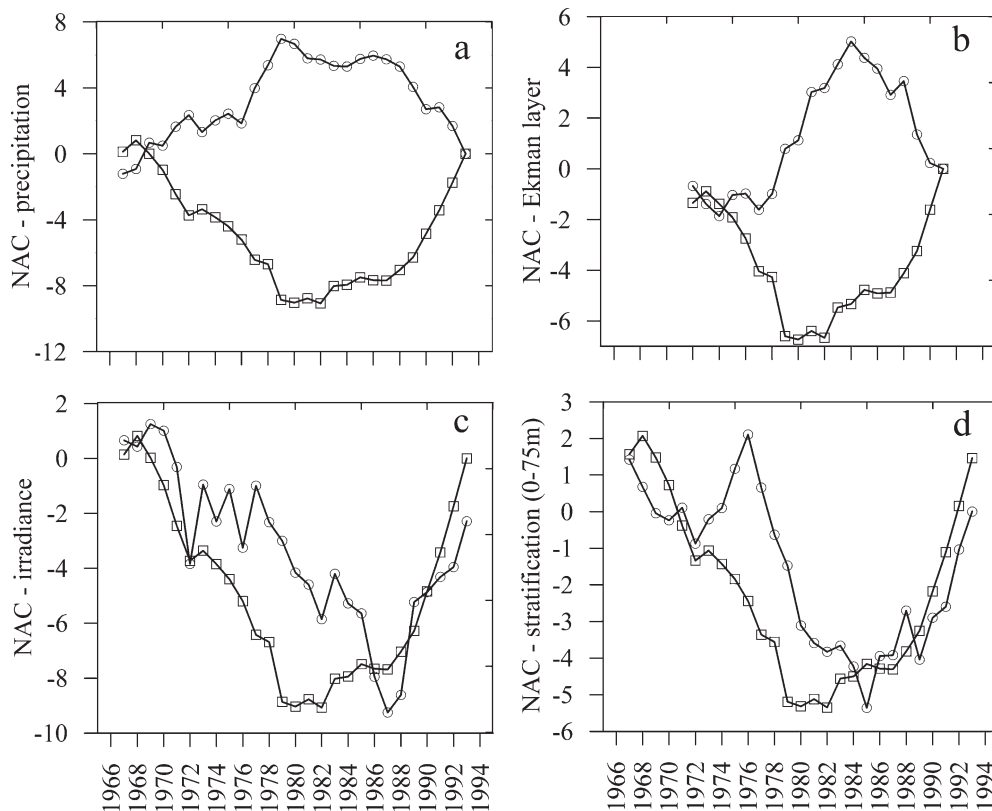
Fig. 1.   Cumulative *z* scores of atmospheric and hydrological variables and the North Atlantic climate. Cumulative *z* scores allow for the identification of predominantly positive or negative anomalies and the date of trend initiation: (a) North Atlantic climate (NAC) and precipitation; (b) NAC and Ekman layer; (c) NAC and irradiance; (d) NAC and thermal stratification of the water column (0–75 m).

ed the variability in the timing of their annual maxima and we tested a potential link between seasonal water mass transport, as indexed by the Ekman transport, and the abundance changes in gelatinous carnivores. Also, we explored the possibility of assessing the species abundance by means of a multivariate model based in hydrographic and climate variability.

The main periods of abundance changes of gelatinous carnivores were identified by means of cumulative *z* scores. The mean annual cycle of the gelatinous carnivores in each one of these periods was computed, and changes in the timing of the seasonal peak were assessed after decomposition of the original time series. Among the time-series decomposition techniques, we used the Census method, which assumes that original observations, Xt, are the product of a general trend (Ct) and seasonal (St) and stochastic (It) components. A detailed description of this technique is described in Fromentin and Ibanez (1994). For the purpose of our study, we retained the seasonal component, which is expressed in a nondimensional form. Changes in the timing of gelatinous carnivores are indicated by the occurrence of the main peak during the year.

The possible link between water mass transport and the abundance of gelatinous carnivores was assessed by correlation test between time series of seasonal water mass transport (i.e., spring, summer, autumn, winter) from the

computed monthly Ekman transport and the abundances of gelatinous populations recorded in the same seasons.

Model fitting—To explore the potential climatic control on the thermal stratification of the water column, as well as on the timing and population size of gelatinous carnivores, we used an approach based on the statistical down-scaling model of von Storch et al. (1993) and Dippner et al. (2001). This is a multivariate approach that explores correlations between the regional and local observations of interest (i.e., thermal stratification of the water column) and potentially important climate variables operating at larger scales (i.e., North Atlantic climate). The first step involved in building the model consists of an evaluation of the interrelations between the Atlantic climate and the regional atmospheric variability at the Ligurian region. The variables showing the highest explanatory power were selected to build the down-scaling model. Afterwards, PCA was used to extract the main signals of predictor (climate) and to reduce the number of climatic parameters of the model. PCA was applied on a matrix, Z, comprising the ensemble of variables (i.e., years × climatic variables: North Atlantic climatic modes, regional atmospheric variables). Next, Canonical Correlation Analysis (CCA) was performed between the leading PCs of climate (as predictors) and thermal stratification of the water column. To build up the

Table 1. Cross-correlation coefficients for large-scale climatic modes, regional atmospheric factors, and thermal stratification of the water column. Significant correlations are indicated in bold type.†

	EA	EA/WRUS	NHT	AO/NAO	GSI	SST	Prcp.	500 hPa	SAP	TSWC
EA	1									
EA/WRUS	−0.15	1								
NHT	**0.60***	−0.28	1							
AO/NAO	−0.03	0.04	**0.33***	1						
GSI	0.12	0.06	**0.40***	**0.42***	1					
SST	0.19	**0.29***	0.22	0.25	0.20	1				
Prcp.	0.20	0.11	−0.10	**−0.40***	**−0.42***	**0.54****	1			
500 hPa	**0.57****	0.07	**0.71****	**0.57****	0.42	**0.48****	−0.08	1		
SAP	**0.54****	0.04	**0.71****	**0.63****	0.37	0.29	**−0.25***	**0.92****	1	
TSWC	0.02	0.12	**0.35***	**0.57****	0.23	**0.39***	0.03	**0.55****	**0.48****	1

† EA, East Atlantic Pattern; EA/WRUS, East Atlantic Western Russian pattern; NHT, Northern Hemisphere Temperature; AO/NAO, Northern Annular Mode; GSI, Gulf Stream Index; SST, sea surface temperature; Prcp, precipitation; 500 hPa, geopotential height; SAP, surface atmospheric pressure; TSWC, thermal stratification of the water column.

* $p < 0.01$; ** $p < 0.001$; effective probability after correction for temporal autocorrelation.

model, several combinations with different lags and seasons between climate and thermal stratification of the water column were evaluated. A conservative alpha level of 0.01 was used to minimize the likelihood of committing a type I error. The same procedure was used to build up the model for the timing and population size of gelatinous carnivores.

In addition, we used down-scaling models to consider data from years in which North Atlantic climate anomalies were higher than 0.5 SD. High values of North Atlantic climate have been suggested as discrimination thresholds for the Atlantic atmospheric circulation forcing on the northwestern Mediterranean region (Vignudelli et al. 1999). This supposes that hydrographic changes are greater during high-value periods of the North Atlantic climate anomalies (e.g., higher positive values may give higher stratification). Therefore, by taking into account only such values when building up the models, we expect higher model explanatory power.

Validation of the model and skill factor—To validate the model we used a cross-validation technique in combination with Monte-Carlo simulations (*see* Dippner et al. [2001] for a detailed description of this technique). For the cross validation, all of the data were used. From all combinations tested, the results with the highest skills were selected. As skill factors, correlation coefficient r (between the regional observations and the cross-validated estimations) and Brier-based score β were used. The Brier-based score is defined as $\beta = 1 - \sigma_e^2 / \sigma_o^2$, where σ_e^2 and σ_o^2 are the variances of the errors (i.e., observation minus model) and observations, respectively. $\beta = 1$ means that model and observation are identical, whereas $\beta = 0$ means that the error of the model has the same size as the variance of the observations (Livezey 1995).

Results

During the studied period the variability of local meteorological parameters underwent marked changes. Precipitation was higher before the 1980s and decreased noticeably during the mid-1980s, particularly during the

late 1980s (Fig. 1a). Also, the Ekman layer was deeper before the 1980s and shallower afterwards, in the late 1980s (Fig. 1b). Opposite patterns were found in irradiance and thermal stratification of the water column. Before the 1980s, low irradiance, related to higher precipitation and cloudiness, characterized the atmospheric conditions in the Ligurian Sea and led to weaker stratification. In contrast,
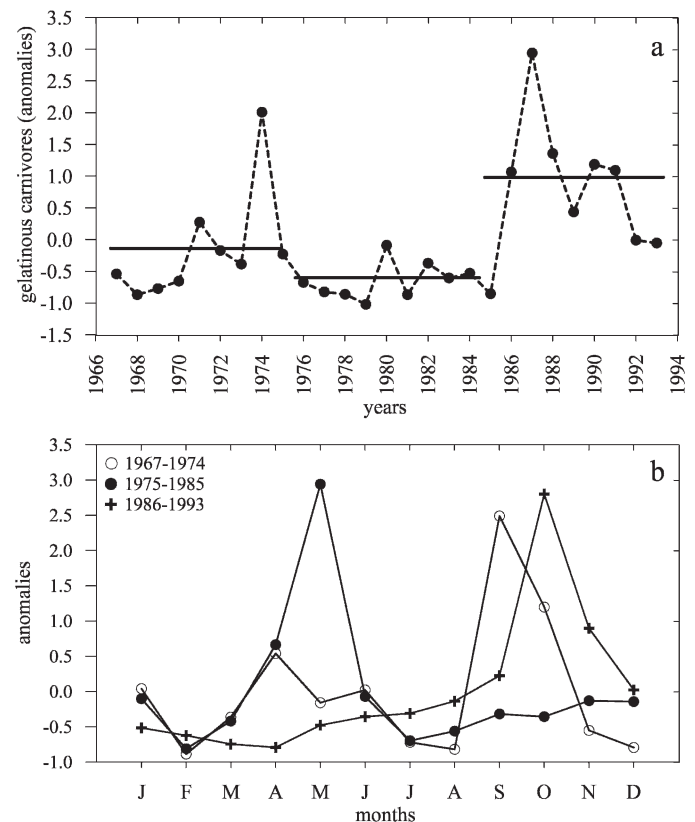

Fig. 2. (a) Interannual variability of the total abundance of gelatinous carnivores and mean abundances (solid horizontal lines) during the main periods identified by the cumulative z scores; (b) Mean annual cycle of the total abundance of gelatinous carnivores associated with each period.

Table 2. Mean densities of gelatinous carnivore populations during the main periods identified by the cumulative z scores: 1966–1974, 1975–1985, and 1987–1993. Abundances are given as individuals by $10\ m^{-3}$.

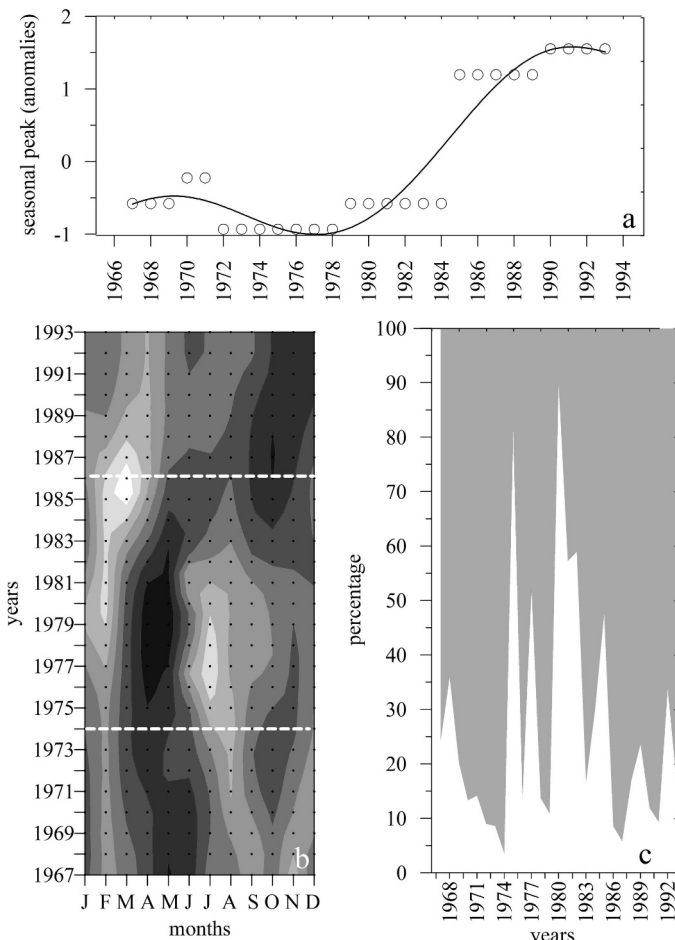|	1966–1974	1975–1985	1986–1993
Chelophyes			
Mean	8	13	38
Max	21	37	56
Abylopsis			
Mean	5	5	12
Max	8	11	20
Pleurobrachia			
Mean	8	31	3
Max	29	168	5
Rhopalonema			
Mean	35	15	73
Max	52	29	228
Liriope			
Mean	143	11	252
Max	641	44	654
Solmundella			
Mean	4	13	27
Max	13	54	58

Fig. 3. (a) Variability of the seasonal peak of gelatinous carnivores over the period ranging from 1967 to 1993. (b) Month–year map of the seasonal peak. It was bimodal during the period ranging from 1967 to the mid-1970s and became unimodal during the late 1970s through early 1980s and was characterized by a spring peak. Afterwards the seasonal peak shifted to a summer–autumn annual peak. (c) Interannual variability of the occurrence (%) of spring (white) and summer–autumn (gray) gelatinous carnivore species. The variability of seasonal groups shows a general dominance of spring species in the period between 1975 and the early 1980s, whereas the summer–autumn species dominated the early 1970s and particularly after the middle 1980s.

during the 1980s drier conditions and higher irradiance governed the atmospheric situation, which together with higher temperatures allowed enhancement of the thermal stratification of the water column (Fig. 1c,d). Table 1 displays the correlation coefficients among the climate modes and the hydro-climate factors in the Ligurian Sea during the period investigated. Most of the significant correlations, with the exception of that for precipitation, indicated a positive response of hydro-climate variability in the Ligurian region to climate patterns in the North Atlantic.

Interannual variability of the total abundance of gelatinous carnivores showed three peaks of abundance in 1974, 1980, and 1987 (Fig. 2a). The peaks appeared to be related to the main periods identified by the cumulative z

scores, 1967–1974, 1975–1985, and 1986–1993, during which the annual patterns were significantly different ($p < 0.05$, t-test). The period ranging from 1967 to 1974 showed a bimodal annual pattern, with a lower peak in spring and a higher one during late summer–autumn. In contrast, the years ranging from 1975 to 1985 showed a single and strong peak during late spring (May), and the period ranging from 1986 to 1993 was characterized by higher abundances of gelatinous carnivores and a unimodal annual peak, with a maximum of abundance in summer–autumn (Fig. 2b).

A noticeable change occurred in the timing of gelatinous carnivores around 1985, which was characterized by a shift of the annual peak from spring to summer–autumn (Fig. 3a,b). Examination of the year-to-year variation in the percentage of spring and summer–autumn species also showed marked changes during the study period. The main pattern was characterized by a spring recurrence of the ctenophore *P. rhodopis* and calycophoran siphonophores *A. tetragona* and *C. appendiculata*, whereas the hydromedusae *L. tetraphylla*, *R. velatum*, and *S. bitentaculata* mainly peaked during the summer–autumn period. While the seasonal signal revealed a dominance of spring species between the mid-1970s and the early 1980s, summer–autumn species were more abundant in the early 1970s and the late 1980s (Fig. 3c). It was also noticed that mean annual abundance of all species except the ctenophore *P. rhodopis* increased in the late 1980s. These changes were also reflected in the species-specific abundances of gelatinous carnivores (*see* Table 2). Calycophorans siphonophores *C. appendiculata* and *A. tetragona* doubled their mean abundances between the years 1967–1974 and 1986–1993. A higher increase was generally noticed in hydromedusae. *R. velatum* and *S. bitentaculata* reached abundances that measured fourfold higher in the years 1986–1993, and
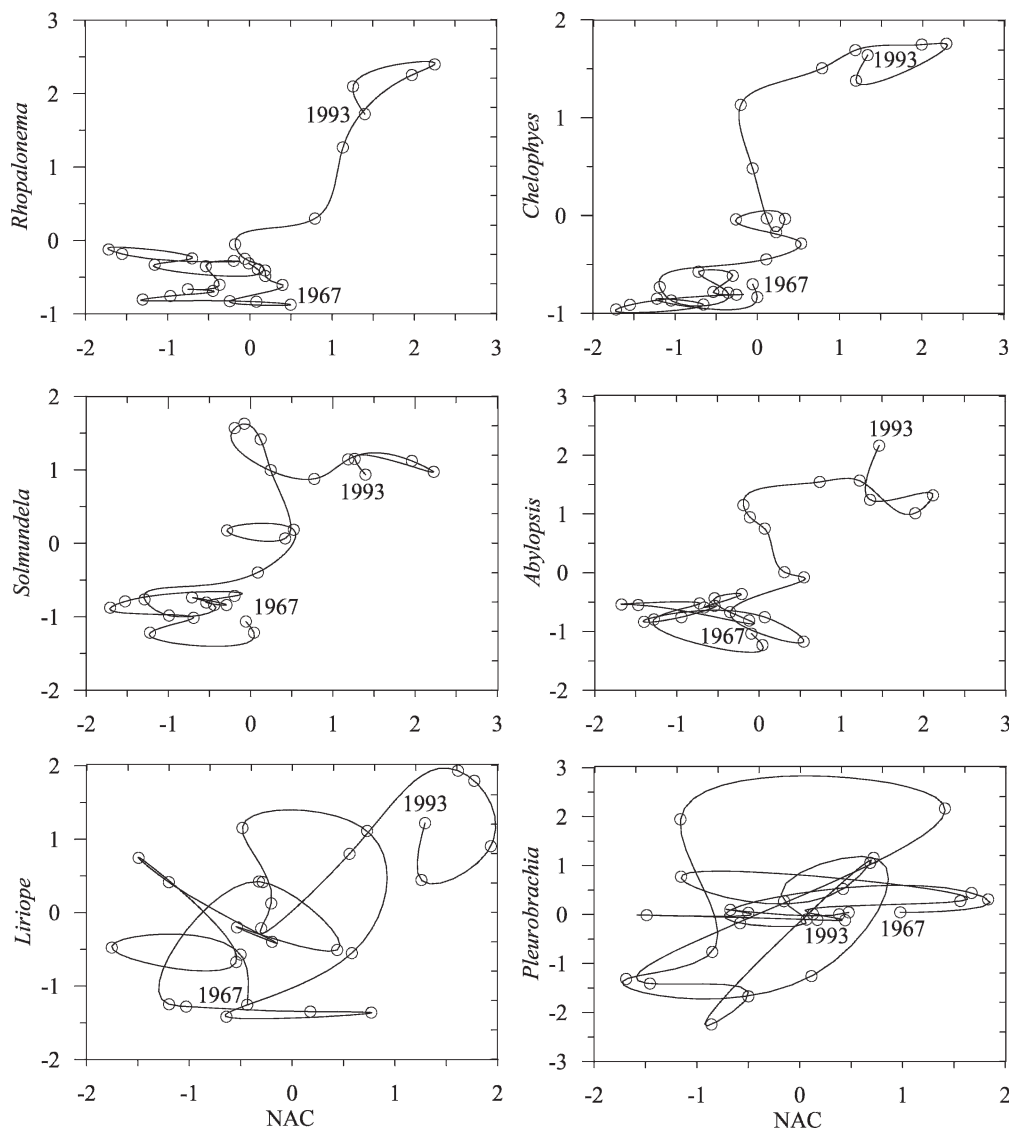
Fig. 4.　Variability of the relationship between gelatinous carnivore species and the North Atlantic climate (NAC). Most of the diagrams show a stable behavior associated with low or negative NAC values, whereas high values of NAC showed a marked change in the variability of such relationships. The pattern shown by the hydromedusae *Liriope tetraphylla* is less clear, although the species abundance also rose in the late 1980s. The ctenophore *Pleurobrachia rodophis* showed a totally different pattern.

L. tetraphylla doubled its mean abundance compared to that measure during the years 1967–1974. The ctenophore *P. rhodopis,* however, showed major mean abundances (fourfold higher) during the years 1975–1985.

Although a potential link between water mass transport and the abundance of these organisms is plausible, we did not detect any significant correlation (not shown) between the abundance of gelatinous carnivores and inshore or offshore transport, as indicated by the seasonal water mass transport within the Ekman layer. The species-specific link to climate variability is illustrated in Fig. 4. Dispersion diagrams reveal that in most of the species investigated, the relationship with climate shifted from one regime of variability to another in the early–middle 1980s, depending on the species. The shift occurred in 1986 for *R. velatum*

and *C. appendiculata*, in 1985 for *A. tetragona,* and in 1982 for *S. bitentaculata*. A less clear pattern was observed in *L. tetraphylla* and the ctenophore *P. rhodopis*. Although *L. tetraphylla* substantially increased during the late 1980s, it also showed a remarkable peak in 1974, when North Atlantic climate anomalies remained low, whereas *P. rhodopis* showed major peaks in 1975 and 1980.

CCA revealed highly significant links between the climate and the interannual variability of thermal stratification of the water column over the period ranging from 1967 to 1993 (Fig. 5a). The same model revealed a significant relationship between climate and the timing in the annual peak of gelatinous carnivores (Fig. 5b). As climate predictors of thermal stratification we used the Atlantic climate modes AO/NAO, EA, and NHT as well as
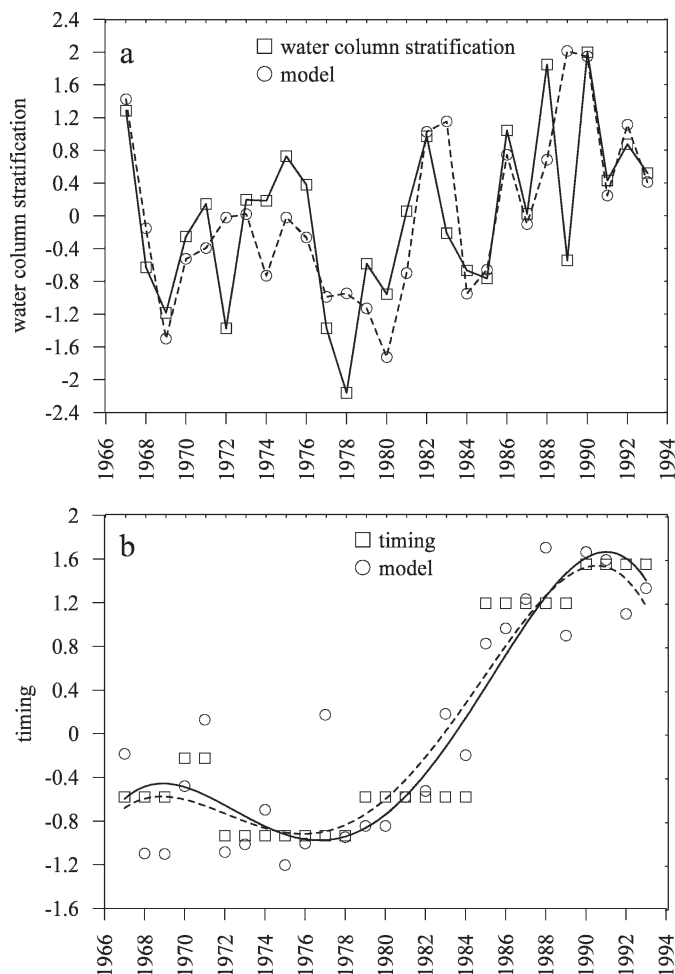
Fig. 5. (a) Observed interannual variability of the thermal stratification of the water column (anomalies: open squares) and that predicted from the three leading PCs of large-scale and regional climate signals (open circles) during the period ranging from 1967 to 1993. Correlation of cross-validation is 0.64, and the model skill (β) is 0.57. (b) Observed interannual variability of the timing of maximal abundance of gelatinous carnivores (anomalies: open squares) and that predicted from the three leading PCs of large-scale and regional climate signals and thermal stratification of the water column (open circles) during the period ranging from 1967 to 1993. Correlation of cross validation is 0.70, and the model skill (β) is 0.42. Trends of observed (solid line) and predicted (dashed line) anomalies are estimated by a fourth-order polynomial function.

regional atmospheric variability (precipitation, surface atmospheric pressure, 500-hPa geopotential height, and sea surface temperature during the winter–spring period). Table 3 displays the results of the down-scaling model for thermal stratification of the water column. CCA further showed that siphonophores (*A. tetragona* and *C. appendiculata*) as well as hydromedusae (*R. velatum* and *S. bitentaculata*) are highly significantly correlated to climate signals governing at large and regional scales (Table 3; Fig. 6). Species-specific sensitivity was also found. While siphonophores (*A. tetragona* and *C. appendiculata*) were driven by conditions in winter and spring, hydromedusae

(*R. velatum* and *S. bitentaculata*) were more sensitive to spring environmental conditions. However, over the whole period, the CCA did not reveal any significant relationships between climate and the abundances of *L. tetraphylla* and *P. rhodophis*. As climate predictors of the abundances of these species we used the North Atlantic climate modes (AO/NAO, EA, and NHT), atmospheric variability in the Ligurian region (precipitation, atmospheric pressure, 500-hPa geopotential height, and sea surface temperature), and thermal stratification of the water column. The correlations displayed are significant with respect to the 99% confidence level. It is worth noting, however, that all models, including those for *L. tetraphylla* and *P. rhodophis*, were substantially improved when considering only the years in which the North Atlantic climate anomalies were higher than 0.5 SD (Table 3). *L. tetraphylla* was more sensitive to spring forcing, as were the other hydromedusae, and *P. rhodophis* was sensitive to winter environmental conditions. These results indicate threshold values from which climate effects become noticeable and that the relationship between climate forcing and gelatinous carnivore abundance increases with the strength of climate forcing.

Discussion

Our results provide evidence of the influence of North Atlantic climate variability on factors regulating long-term changes of abundances of gelatinous carnivores in the Ligurian Sea. The down-scaling of the connection emerges from the evident sensitivity of regional fields of atmospheric parameters and temperature to the North Atlantic climate.

Local hydroclimate response to large-scale climatic forcing—Underlying processes linking wide field climate variation with variations in the local environment are expressed through changes in the mesoscale circulation and hydrographic features in the northwestern Mediterranean. This is particularly evident for wintertime (Demirov and Pinardi 2002), when air–sea interactions exert the greatest degree of control on the seasonal variability in water mass transport through the Corsica channel (Astraldi and Gasparini 1992). This flux is linked to the NAO state (Vignudelli et al. 1999), the negative phase of which enhances differences in the sea level between the Ligurian and the Thyrrhenian Seas, differences that may reach 16 cm (Vignudelli et al. 2002). Such variation contributes to a higher seasonal flux from the Tyrrhenian Sea to the Ligurian Sea. The higher the heat loss induced by air–sea interaction processes and deep water formation during the negative phase of the NAO, the stronger is the input from Thyrrhenian waters (Astraldi and Gasparini 1992). The apparent total volume transport varies strongly on the seasonal scale, being 1.5 Sverdrup (Sv; 1 Sv = 1×10^6 m³ s⁻¹) in winter and dropping by a factor of 10 during summer, when the sea level difference falls to 2 cm (Vignudelli et al. 2002). Significant links between sea-level changes in the Northwestern Mediterranean and the NAO variability have been also shown (Tsimplis and Josey 2001). Given that the West Corsica current is a large component

Table 3. Results of down-scaling models. Predictors and predictands are given, as are 99% confidence intervals (CIs) of Canonical Correlation Analysis coefficients (CCA), the correlation coefficients after cross validation (CC), and the skill model (the Brier-based score, β). The predictor climate encompasses the leading three first principal components (PCs) of large-scale climatic modes (East Atlantic pattern [EA], Northern Hemisphere temperature [NHT], Northern Annular Mode [AO/NAO]) and regional atmospheric variables (precipitation, sea surface temperature, and 500-hPa geopotential height). The predictor hydro-climate encompasses the leading three first PCs of large-scale climatic modes, regional atmospheric variables, and thermal stratification of the water temperature.

Predictor	Predictand	CCA	CC	β
Climate	Stratification	0.68	0.64	0.57
*Climate	Stratification	0.75	0.72	0.55
Hydro-climate	Timing	0.77	0.70	0.42
*Hydro-climate	Timing	0.81	0.75	0.66
Hydro-climate	*Chelophyes*	0.72	0.63	0.40
*Hydro-climate	*Chelophyes*	0.80	0.72	0.64
Hydro-climate	*Abylopsis*	0.60	0.54	0.65
*Hydro-climate	*Abylopsis*	0.92	0.85	0.84
Hydro-climate	*Rhopalonema*	0.65	0.61	0.57
*Hydro-climate	*Rhopalonema*	0.84	0.75	0.71
Hydro-climate	*Liriope*	—	—	—
*Hydro-climate	*Liriope*	0.66	0.58	0.90
Hydro-climate	*Solmundela*	0.59	0.55	0.66
*Hydro-climate	*Solmundela*	0.71	0.65	0.50
Hydro-climate	*Pleurobrachia*	—	—	—
*Hydro-climate	*Pleurobrachia*	0.73	0.55	0.53

*Models built up when considering only those years in which North Atlantic climate anomalies were higher than 0.5 standard deviations (SDs).

of the Northern Current (Bethoux 1980), it is suggested that over the long-term scale the interannual variability of the seasonal transport through the Corsica channel may act in a seesaw mechanism, varying the warmer water inputs into the Ligurian Sea. The changes reported here produced a warmer and hyperhaline regime during the 1980s, one that favored the rising abundance in most of the gelatinous carnivores, excluding the ctenophore *P. rhodopis,* which appears to be associated with low temperatures and high salinities.

Gelatinous carnivores and climate—A comprehensive review showed that the abundance of temperate species of gelatinous carnivores increases in warmer conditions (Purcell 2005). A nonexhaustive list reported by Purcell (2005) included the ctenophore *Mnemiopsis leidyi* in the Narragansett (Mills 2001; Purcell and Decker 2005), the scyphomedusae *Pelagia noctiluca* in the western Mediterranean (Goy et al. 1989), *Chrysaora quinquecirrha* in the Chesapeake Bay (Cargo and King 1990), *Chrysaora melanaster* in the Bering Sea and Gulf of Alaska (Anderson and Piatt 1999; Brodeur et al. 2002), and *Aurelia* spp. in the Inland Sea (Uye and Ueta 2004). Climate control on the abundance of gelatinous carnivores has also been reported for the Bering Sea (Brodeur et al. 1999), the North Sea (Lynam et al. 2004; Attrill et al. 2007), Chesapeake Bay (Purcell and Decker 2005), and the Black Sea (Oguz et al. 2006). The life-history traits of gelatinous carnivores make this group highly sensitive to environmental changes. In particular, with favorable conditions their population doubling rate is short compared with those of most other zooplankton predator types, such as euphausiids or

chaetognaths. We showed that when environmental modifications persist for long periods, as occurred in the Ligurian Sea, with the generally warmer waters during the 1980s becoming more extensive until the early 1990s, the recurrence and strength of gelatinous carnivore outbreaks become more frequent and the population size increases considerably. This indicates substantial modifications in the productivity of the pelagic food webs, fueling increased predator production and predation pressure on zooplankton and fish larvae.

We have shown that a significant part of the long-term variations in population abundances of gelatinous carnivores reflects their integration of the effects of North Atlantic climate on plankton food-web productivity in the Ligurian Sea during the years 1966 to 1993. This is fully consistent with previous efforts to forecast medusa occurrence in the Northwestern Mediterranean (Goy et al. 1989). In fact, Goy et al. (1989) revealed that a lack of rainfall, associated with high temperatures and atmospheric pressure from May to August, appears to be the best predictor of high abundances of the holoplanktonic scyphozoan *P. noctiluca,* occurring with a cyclicity of around 12 yr. As shown here, regional fields of temperature, precipitation, and atmospheric pressure are modulated by the North Atlantic climate variability. This indicates a potential link between the cyclical occurrences of *P. noctiluca* and the low frequency variability of the North Atlantic climate. This hypothesis, however, should be verified. During the period investigated, *P. noctiluca* showed recurrent high abundances approximately every 12 yr (i.e., 1969–1970, 1982–1984, and 1993), and, when present, this species out-competed other gelatinous carni-
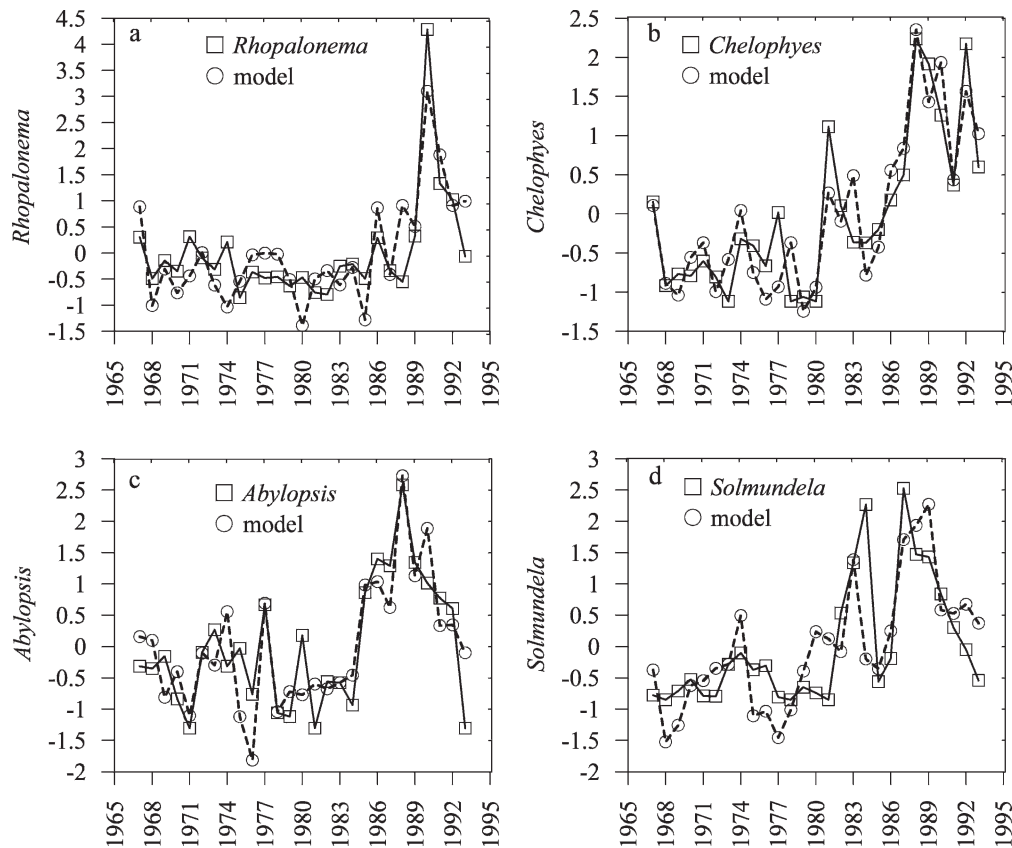
Fig. 6. Observed interannual variability of gelatinous carnivore species (anomalies: open squares) and that predicted from the three leading PCs of large-scale and regional climate signals and thermal stratification of the water column (open circles) during the period ranging from 1967 to 1993. Correlation of cross validation (CC) and the model skill (β) are as follows: (a) *Rhopalonema* (CC = 0.61, β = 0.57); (b) *Chelophyes* (CC = 0.69, β = 0.48); (c) *Abylopsis* (CC = 0.54, β = 0.65); and (d) *Solmundela* (CC = 0.55, β = 0.66).

vores whose seasonal peak matched that of *P. noctiluca* (Buecher 1999) (i.e., *L. tetraphylla, R. velatum*).

The sensitivity of particular gelatinous carnivore species to environmental forcing relates to their seasonal appearance and peak of abundance. Thus, the spring peak species (i.e., *A. tetragona, C. appendiculata,* and *P. rhodophis*) were found to be more sensitive to winter and spring environmental conditions, whereas the summer peak species (i.e., *R. velatum, S. bitentaculata,* and *L. tetraphylla*) were more sensitive to spring and summer environmental conditions. Our results advocate the occurrence of short time windows, during which gelatinous carnivores appear to be more sensitive to environmental conditions, and favorable conditions may therefore substantially enhance their annual peaks. We suggest the possibility of assessing and perhaps predicting the main patterns of the interannual variations in gelatinous carnivore abundances according to the patterns of variability of the North Atlantic climate, particularly if threshold values are considered (e.g., anomalies of climate >0.5 SD).

Impending interactions between exogenous (advection, transport) and endogenous (population growth) factors may hinder the identification of the main drivers of abundance changes of pelagic populations. For the gelatinous carnivores, their structure, with the lack of complex physiognomy and weak swimming abilities, means that they passively drift with the water current (Graham et al. 2001). The species investigated are characterized by holoplanktonic life cycles for which any pronounced change in water column feature (i.e., warm temperatures, strength of the stratification) may substantially affect their fitness and the availability of their prey resources. The Calycophoran siphonophores *A. tetragona* and *C. appendiculata* have two alternating pelagic generations: the asexual (polygastric) and the reproductive (eudoxid) stages. The ctenophore *P. rhodopis* produces its larvae via the fusion of gametes and sperm directly in the water column, whereas the hydromedusae *L. tetraphylla, S. bitentaculata,* and *R. velatum* have a direct development to medusa and a holoplanktonic life cycle. Our results did not show any significant correlation between the abundance of gelatinous carnivores and seasonal inshore or offshore water mass transport. However, it cannot be excluded that over shorter time scales the effect of water transport can be noticeable, as has been shown in sudden seasonal massive increases of gelatinous carnivores in nearshore areas of Japanese waters (Kaneda et al. 2007). In contrast, the recurrent higher abundances of these organisms observed in the 1980s were

instead closely linked to modifications in the hydrographic regime (e.g., warm temperature, enhancement of the stratification).

We suggest, therefore, that climate-related changes in the hydrological features during the 1980s enhanced environmental factors that triggered better recruitment and population growth of gelatinous carnivores. Through the control on regional atmospheric circulation, moisture transport, and local wind stress, the North Atlantic climate variability acts as a main forcing factor on the hydrological regime in the northwestern Mediterranean, leading to high temperatures and low water column mixing during its positive phases (Molinero et al. 2005*b*). This may explain why the 1980s were characterized by a large number of outbreaks of gelatinous carnivores. The climate-related environmental changes also improved the strength of the carnivores' seasonal peaks by a factor of three and led to a shift from spring to late summer–autumn peaks that was driven by the higher increase in the abundances of summer–autumn species. However, it is also noticeable that these environmental conditions impaired the population size of *P. rhodopis*. This species displayed a general affinity for low temperatures, and its maximum captures occurred during the years with the lowest temperature and the highest salinities (1975 and 1980) (Buecher unpubl.).

Ecological implications—Climate impacts may affect bottom-up processes via changes in the hydrographic environment and the subsequent modifications in the structure of primary producers (e.g., diatoms/nondiatoms). Gelatinous carnivores have likely benefited from pelagic ecosystem changes associated with the dominant hydrological regime in the 1980s. For instance, the lower abundances of chaetognaths may have favored a decrease of competitors (Molinero et al. 2008), and changes in phytoplankton structure may also benefit gelatinous populations, since they are able to exploit microplankton communities. In fact, empirical and field researchers have shown the important effects of gelatinous carnivores on the microbial food web preying on ciliates, which subsequently leads to a cascading impact on bacterial populations (Stoecker et al. 1987; Malej et al. 2007). Support for this has been also provided by Pitt et al. (2007), who showed the ability of jellyfish to exploit a wide range of size classes. Moreover, based on empirical work, the same authors showed that the impact of gelatinous carnivores on the structure of microzooplankton assemblages may in some cases favor the formation of red tides.

Significant changes in the abundances and seasonal peaks of gelatinous carnivores in marine food webs may produce structural changes in the pelagic ecosystems through enhanced or reduced predation on zooplankton, including consumption of fish eggs and larvae, and through competition for food with fish. Ultimately these changes may lead to ecosystem-wide disruptions (Mills 2001; Hay 2006). Long-term variations in gelatinous carnivores thus emerge as valuable ecosystem-state indicators. In accordance with this, the long-term variations of hydromedusae in the North Adriatic have been suggested as biological proxies of ecosystem changes in shallow marine ecosystems

(Benovic et al. 1987). Moreover, these organisms are now recognized as critical indicators and drivers of ecosystem performance and change (Hay 2006; Lynam et al. 2006). As these voracious predators may channel flows of energy and matter away from the economically important algae–copepods–fish food chain (Sommer and Stibor 2002; Stibor and Tokle 2003), their potential effect on the interannual variations in fish recruitment makes increasingly critical the integration of this understanding and data into an ecosystem approach to fishery management (Lynam et al. 2005*a,b*). In the case of the northwestern Mediterranean, the higher frequency of gelatinous carnivore outbreaks may enhance the predation pressure on, and feeding competition with, small pelagic fish, such as the European anchovy (*Engraulis encrasicolus*), whose spawning seasonality extends from May to September and matches with the peak of the voracious gelatinous predators. A potential effect on anchovy is therefore plausible, especially because anchovy is heavily dependent on the success of a few year-classes. Thus, an increase in the probability of stock collapse occurs when conditions for recruitment in a particular year are not favorable (e.g., combinations of high gelatinous predator density and strong fishing pressure). The analysis of gelatinous carnivores outbreaks and their potential links with fish population dynamics should therefore be a high priority for future research in the Mediterranean basin (CIESM 2000). Support for this position has been recently emphasized by the results of Knowler (2007), who has shown that in the Black Sea anchovy recruitment may alternate between higher and lower levels, corresponding, respectively, to low or high periods of abundances of gelatinous carnivores (e.g., *Mnemiopsis leidyi*).

A matter for current concern is, therefore, whether the reported hydrographic changes that have favored gelatinous carnivores have extended into recent years. Goffart et al. (2002) and Marty and Chiaverini (2002) showed that generally warmer temperatures and low wind stress have characterized the 1990s and have allowed for modifications in the structure of the Ligurian Sea phytoplankton communities (e.g., dominance of nonsiliceous cells). These conditions (i.e., low direct supply of inorganic nutrients, high stratification, and a predominance of animal excretion as the recycled nutrient source) favor food webs dominated by gelatinous zooplankton, including salps and appendicularians (Sommer and Stibor 2002). We then suggest that the evident modifications in the hydrographic regime of the Ligurian Sea that occurred during the last decade point to a pelagic ecosystem characterized by recurrent outbreaks of gelatinous carnivores, with consequent alterations in food-web structure and biogeochemical fluxes.

Our results alert us to the likelihood that the large population size of gelatinous carnivores may become more frequent in the northwestern Mediterranean if projections of NAO scenarios and higher temperatures in the Northern Hemisphere are confirmed. In fact, in global climate projections none of the analyzed models indicates a decrease in the dominance of the positive phases of the NAO (IPCC 2007). As shown here, the positive phases of the NAO are related to high atmospheric pressure, low precipitation, high temperatures, and low wind stress in the

northwestern Mediterranean. This points toward enhanced water column stratification and possible favorable environments for gelatinous carnivore growth. Since the ecosystem shifts from fish dominance to dominance of gelatinous carnivores may be irreversible, as these voracious predators may control fish eggs and larvae and compete with fish for food (Lynam et al. 2006), biological oceanographers, marine ecosystem modellers, and resource managers cannot afford to ignore these indicators. Within this framework, our results constitute ecological warning indications of substantial changes in the pelagic ecosystem of the northwestern Mediterranean. The extent to which the identified mediator factors capture the signal of climate relates directly to the validity of using these factors for forecasting the abundance of gelatinous carnivores in the Mediterranean Sea.

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