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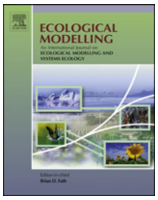

A model for temperature control of jellyfish (*Cotylorhiza tuberculata*) outbreaks: A causal analysis in a Mediterranean coastal lagoon

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ABSTRACT

Large outbreaks of jellyfish populations sporadically appear at the Mediterranean coasts without any self-evident cause creating public distress because of their impact on local ecosystems and economies. The exacerbated sensitivity of coastal societies has not been paralleled with comparable scientific understanding of the causal mechanisms controlling jellyfish population dynamics. Life-cycle and ecosystem complexities obscure the processes underlying medusa outbursts. Here we present evidence that helps explain population outbursts in a common Mediterranean species (*Cotylorhiza tuberculata*). Using a population-dynamics model and thermal forcing of its life cycle observed abundances of *C. tuberculata* could be reliably simulated within a coastal lagoon. Medusa populations fluctuate under the simple rule of "the warmer the better", with collapses after polyp mortality in severe winters and peaks in years with mild winters and long summers. Cause and effect are here resolved to seize the mechanics of climate forcing on jellyfish dynamics, an understanding that can help to explain past and future fluctuations of abundance in a thermally changing ocean.

1. Introduction

The Mar Menor is a large (135 km^2) and shallow (~4 m average depth) lagoon almost isolated from the western Mediterranean by a 22 km long sand bar (Fig. 1). A progressive increase in both human pressure on the shoreline and agriculture modification of the water catchments area modified the original benthic communities during the 1980s (Pérez-Ruzafa et al., 2002). Coherently with a habitat-degradation triggering of jellyfish populations (Pagès, 2001; Richardson et al., 2009), *Cotylorhiza tuberculata*, first began to manifest within the lagoon as massive outbreaks in early 1990s. *C. tuberculata* is a scyphomedusa frequently present on the Mediterranean coast with pelagic and polyp phases present during warm and cold months respectively (Avian, 1986; Kikinger, 1986). The dynamics of *C. tuberculata* abundance in Mar Menor has been observed since its first appearance without scientific understanding of the origin of fluctuation in the population. Because of the summer occurrence of the medusa phase, public alarm during blooming years triggered a local management program to reduce their impact on bathing activities. This program started in year 2000 and involved extracting medusa with fishing vessels. It generated a data set of landing and effort records similar to those used for modelling exploited fish populations (Punt and Hilborn, 1997). Economic information exists for other jellyfish fisheries (*e.g.* Omori and Nakano, 2001) but reports of medusa catch and effort data able to evaluate dynamics in a medusa population as commonly done for fish stock assessment are very scarce (Brodeur et al., 2008).

Although the available information on *C. tuberculata* life cycle is not as extensive as other scyphozoa (*e.g. Aurelia aurita*; Lucas, 2001), this shows strong components of environmental forcing. All life cycle phases are insensitive to the range of salinities found within the lagoon and polyp survival is not significantly affected by a wide range of light, macronutrients and food conditions (Prieto et al., 2010). Conversely, polyp mortality is strongly linked to low temperatures (Prieto et al., 2010). Like other scyphozoa species, *e.g. A. aurita* (Lucas, 2001) or *Chrysaora quinquecirrha* (Purcell et al., 1999), cold waters prevent strobilation (Kikinger, 1992). However, in contrast to other scyphozoa, *C. tuberculata* polyps only produce one ephyra (Kikinger, 1986) and strobilation is triggered at a narrow temperature range (Prieto et al., 2010). This response of their life cycle to environmental forcing, particularly to temperature, makes it plausible that the thermal-regime of the lagoon controls population dynamics. Although the link between environment and scyphozoa populations has been explored (Anderson and Piatt, 1999; Raskoff, 2001; Lynam et al., 2004; Attrill et al., 2007; Purcell et al., 2007; Gibbons and Richardson, 2008), most studies investigate statistical correlations between environmental indices and abundance, rather than identifying the mechanisms forcing the population dynamics of jellyfish through their impact on the life-cycle.

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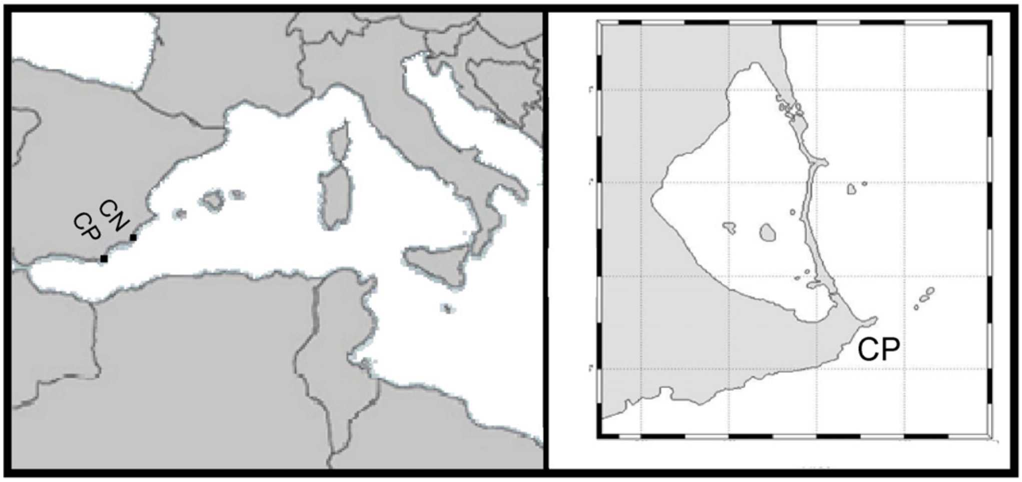

Fig. 1. Mar Menor location within the western Mediterranean. CP and CN stand respectively for capes Palos and La Nao.

The isolated nature of the Mar Menor presents an outstanding situation for examining *C. tuberculata* dynamics, as migration or advection of the population can be essentially neglected. Bayesian models can perform this analysis because they consistently combine fishery data, environmental records and the knowledge of the exploited-species life-cycle to account for the origin of population fluctuations (Ruiz et al., 2009). This is possible even when available data and knowledge are highly divergent in their characteristics; ranging from meteorological records or laboratory experiments to *in situ* observations or landing reports. In this manuscript we implement a Bayesian model to evaluate the hypothesis that the population dynamics of the jellyfish *C. tuberculata* in the Mar Menor is controlled by the sensitivity of its life cycle to the thermal regime within the lagoon. Our modelling analysis documents the significant role that temperature has in unravelling the underlying causal mechanisms leading to years of high or low *C. tuberculata* abundance in Mar Menor. This provides strong insights into the factors driving past changes in scyphozoan populations and a foresight into the future of warming oceans.

2. Life-cycle control of population dynamics

Methods to simulate population dynamics by state-space models under the Bayesian framework are described elsewhere (Meyer and Millar, 1999; Millar and Meyer, 2000; Rivot et al., 2004; Ibaibarriaga et al., 2008; Ruiz et al., 2009). Succinctly, a process model is defined for the population dynamics and its control by the environmental forcing of the life-cycle. An observational model is additionally defined to connect unobserved (latent) variables (*e.g.* stock size) with available records (*e.g.* landing and effort). Numerical techniques implement Bayes' theorem to update the prior probability of model parameters with the likelihood of the observations, *i.e.* to obtain the posteriors. A directed acyclic graph is frequently produced as the conceptual scheme for the joint process and observational models. This section describes the process and observational models for *C. tuberculata* as its life-cycle evolve between pelagic and benthic phases as well as the data included in the approach and the numerical procedures implemented.

2.1. Process model for the benthic phase

When planulae become polyps they fix and live in the benthos from fall to spring (Kikinger, 1992). Polyps have the ability to increase population through asexual reproduction (budding) but their numbers are mainly driven by their mortality in cold waters; when temperature drops below ∼16 °C mortality increases (Prieto et al., 2010). Survival in cold waters can be modelled through a decay equation with a coefficient (m, d^{-1}) for the mortality rate of the polyp population (P, number of individuals) that is dependent on water temperature (T_w, °C):

$$\frac{dP}{dt} = m(T_w)P \tag{1}$$

Polyp mortality by cold temperature is negligible for waters above 16 °C (Prieto et al., 2010). On the contrary, the values for $m(T_w)$ derived from the mortality curves in Prieto et al. (2010) abruptly change for temperatures below 4 °C (Fig. 2). These low temperatures are never reached in the proxy used for lagoon temperature. Therefore, there are only three useful points to explore the dependency of m on temperature. Fig. 2 suggests a linear response in the range between 4 and 16 °C, as evident after baseline fitting Eq. (2) to the three points.

$$m = \begin{cases} 0.016T_w - 0.256 & \text{if} \quad 4 \le T_w < 16\,^\circ\mathrm{C} \\ 0 & \text{if} \quad T_w \ge 16\,^\circ\mathrm{C} \end{cases} \tag{2}$$

The connection between m and T_w in Eq. (2) is used to create a *prior* for the fraction of the polyp population remaining after a

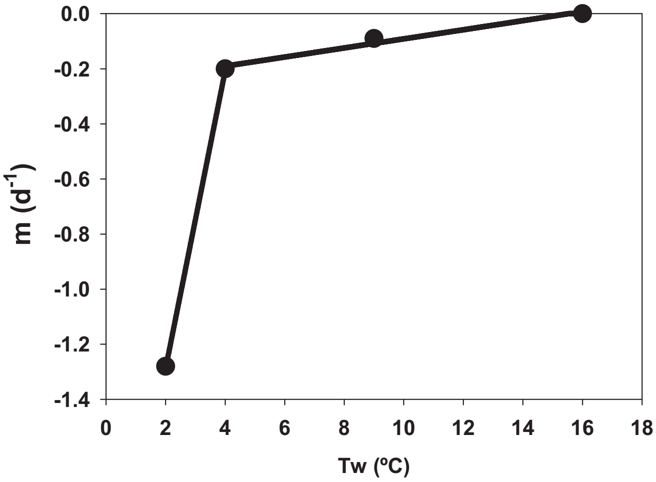

Fig. 2. Mortality rate of polyps. Dots are the coefficient for polyp decay as a function of temperature as derived after data from Prieto et al. (2010). Line above 4 °C was derived from Eq. (2).

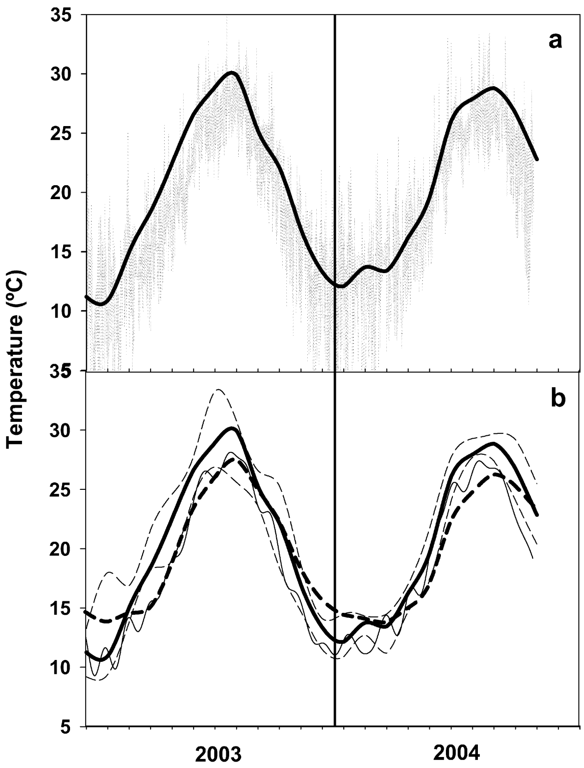

Fig. 3. Thermal inertia of lagoon water. (a) Thin and thick lines are the temperature of air at San Javier meteorological station and mean sea water temperature in the lagoon from Eurogel project, respectively. (b) Thin broken lines are the maximum and minimum monthly water temperatures recorded in the lagoon during Eurogel project, thin solid line is $T_{\mathrm{air}}^{\mathrm{Fourier}}$, thick solid line as in (a), thick broken line is the monthly mean of the sea surface temperature (AVHRR) at Mediterranean waters outside the lagoon.

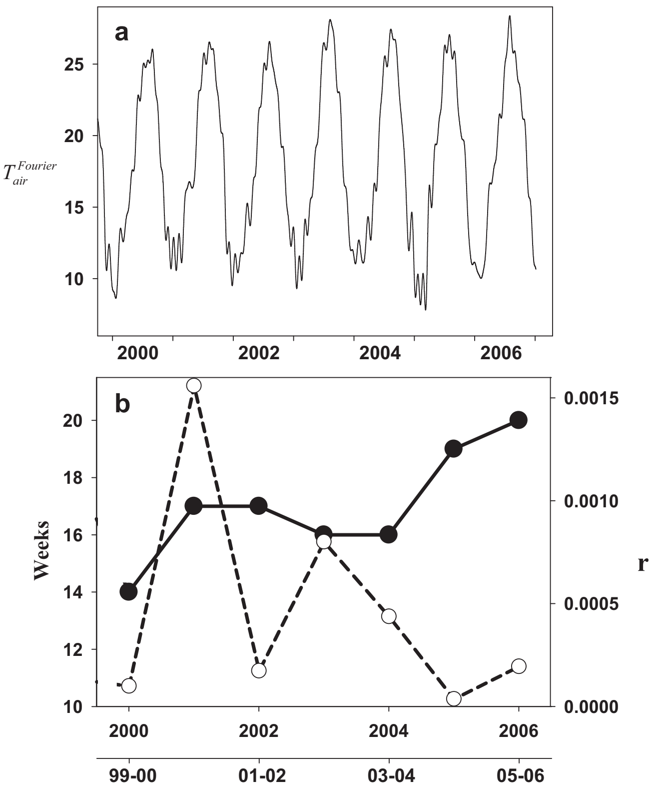

Fig. 4. Thermal regime in the lagoon. (a) $T_{\mathrm{air}}^{\mathrm{Fourier}}$ (°C). (b) Duration of the summer for medusa growth (solid symbol and line, left axis) and fraction of the polyp population remaining after winter (empty symbol, broken line and right axis; lower bottom scale indicates winter years) derived from $T_{\mathrm{air}}^{\mathrm{Fourier}}$.

winter (r_i). Eq. (2) is integrated over the winter months between years i and $i+1$ to calculate the *prior*:

$$r_i \sim N\left(-\frac{1}{P_i}\int mPdt, S_r\right) \tag{3}$$

where m is a function of T_w and P_i is the initial polyp population. S_r is the standard deviation accounting for the process error for which *a posteriori* probability distribution is obtained after implementation of the Bayesian framework. Water temperature of the lagoon is unknown during the years simulated by the model except for some monthly records from the Eurogel European project during 2003 and 2004. There are, nevertheless, historical data of air temperature (T_{air}) from a nearby meteorological station at San Javier airport. Monthly means of sea surface temperatures (AVHRR) outside the lagoon were also obtained from the Jet Propulsion Laboratory web site (ftp://podaac.jpl.nasa.gov) for a coastal fringe of 25 km width between capes Palos and La Nao (Fig. 3). Although temperature fluctuates more in air than in seawater, air–water differences are not as large within the lagoon as in the open Mediterranean. In coherence with air temperature, the temperature range is wider within the lagoon and the seasonal heating–cooling start earlier than in waters outside (Fig. 3a and b). The enclosed and shallow nature of the lagoon makes its thermal regime less dependent of oceanographic processes at the western Mediterranean and more connected to atmospheric fluctuations.

A timescale for the thermal response of the lagoon to changes in air temperature can be roughly estimated from the sensible heat flux equation (Gill, 1982):

$$\frac{HC_w}{C_t U_{10} C_{pa}} \approx 1\,\text{month} \tag{4}$$

where H is water column depth (~4 m average in the lagoon), C_w is the specific heat of seawater (4.2E6 J m^{-3} K^{-1}), C_t is a dimensionless coefficient for heat transfer (~0.001, Gill, 1982), U_{10} is air velocity at 10 m above sea level (assumed ~5 m s^{-1} for this time scale estimation) and C_{pa} is the specific heat of air (1298 J m^{-3} K^{-1}). Consistent with the output of equation 4, Fourier filtering from T_{air} the variance at frequencies higher than one month results in values ($T_{\mathrm{air}}^{\mathrm{Fourier}}$) that are a reasonable proxy for T_w (Fig. 3b).

The lethal effect of cold water during winter (r_i) was, therefore, modelled through $T_{\mathrm{air}}^{\mathrm{Fourier}}$ (Fig. 4a and b) although also incorporating the uncertainty of using a proxy for T_w. This uncertainty was included in the model by considering an additional error source (S_{wint}) in those processes (see equations below) to transfer the number of polyps throughout winter i (first and last winters, $i = 1$ and $i = 7$, correspond to the winter between years 1999–2000 and 2005–2006 respectively). The posterior probability distribution of S_{wint} is obtained after implementation of the Bayesian analysis.

2.2. Process model for the pelagic phase

Polyps surviving the winter strobilate ephyrae at the subsequent summer when temperature rises over 18 °C. Laboratory experiments strongly indicate that the vast majority of polyps strobilate when temperature rises over 18 °C (Prieto et al., 2010), therefore polyp numbers drop to zero every early summer. Ephyrae grow in two phases (Kikinger, 1992). In an early stage, ephyrae grow slowly and ~9 weeks are required to reach a diameter of ~3 cm. After the ephyra stage, growth accelerates to average rates of ~3.6 ± 1 cm/week that vary little with environmental conditions in different years (Kikinger, 1992). Since 18 °C is the strobilation temperature (Prieto et al., 2010) and *C. tuberculata* are unable to survive the fast transition between autumn and winter, the operational summer duration for medusa growth can be considered as the number of weeks with $T_{\text{air}}^{\text{Fourier}} \geq 18\,^{\circ}\text{C}$ minus 9 weeks of ephyra stage. This duration is presented in Fig. 4b.

Sharp thermal control on strobilation (Prieto et al., 2010) results in coherent cohorts that make feasible the uncoupled modelling of population size structure and numerical abundance (Carlotti and Sciandra, 1989; Fennel, 2001). Owing to the probabilistic nature of the model implemented here, a normal distribution for growth rates, $N(3.6, 1)$, rather than point estimates was applied to predict organism sizes during the summer. Following Ruiz (1997) approach to transfer mass along the size spectrum, these growth rates were integrated during one week to define a transfer matrix, $G^{k,j}$, which contains the proportion of size k transported to class j after a week of growth. Thus, the proportion of medusae in size class j at week t after ephyra stage ($J^{t,j}$) evolves by somatic growth according to the following expression:

$$\sum_{k=1}^{k=j} J^{t-1,k} G^{k,j} \tag{5}$$

Somatic growth is not the only process affecting population size structure. Other components such as damage caused by waves or motor boats as well as fishing gear selectivity also modify sizes. Mechanical damage inhibits medusae growth (Kikinger, 1992) and fishing preferentially eliminates larger sizes (Millar, 1992). These effects impact organism sizes as summer progresses according to a logistic curve whose parameters depend on gear selectivity (Millar, 1992):

$$\left(\frac{t}{20}\right)\left[\frac{e^{a+bD^j}}{1+e^{a+bD^j}}\right] \tag{6}$$

where a and b are parameters of the logistic curve for gear selectivity (Supporting information 1), D^j is the diameter (cm) of medusae in size class j and 20 is the longest summer (weeks) in the series (Fig. 4b). The proportion of medusae in size class j at week t after ephyra stage is thus modelled as the combination of the size increments associated to somatic growth and the accumulated damage generated by fishing and mechanical impacts:

$$J^{t,j} = \left(\frac{t}{20}\right)\left[\frac{e^{a+bD^j}}{1+e^{a+bD^j}}\right]\sum_{k=1}^{k=j} J^{t-1,k} G^{k,j} \tag{7}$$

Given the absence of lagoon predators for medusae, their number in week t of year i (η_i^t) is considered to decrease mainly by fishing (F_i^t) as:

$$\eta_i^t \sim N(\eta_i^{t-1} - F_i^{t-1}, S_{med}) \tag{8}$$

where S_{med} is the standard deviation accounting for the process error for which *a posteriori* probability distribution is obtained after implementation of the Bayesian approach. Low medusa numbers in 2005 rendered unnecessary its extraction and $F_{2005}^t = 0$ for every t.

2.3. Benthic–pelagic coupling

The number of polyps at week t of summer i, ρ_i^t, is figured out depending on medusa biomass, the proportion of planulae-carrying females, L, and a parameter α:

$$\rho_i^t \sim N(\rho_i^{t-1} + \alpha L \omega_i^t \eta_i^t, S_{pol}) \tag{9}$$

The proportion of planulae-carrying females is size dependent (Supporting information 2):

$$L = 0.6413\left[\frac{e^{c+dD}}{1+e^{c+dD}}\right]$$
$$c \sim N(-8.3302, 3.6731), \quad d \sim N(0.4961, 0.2175) \tag{10}$$

The biomass ($\omega_i^t \eta_i^t$) is derived from an estimation of the average weight (ω_i^t, in g) obtained from Eq. (7) and the relationship weight = $0.071D^3$ (Supporting information 3). This weight–length relationship is close to weight = $0.08D^{3.1}$, found by Kikinger (1992) for weight–length data of *C. tuberculata* in Vlyho Bay. S_{pol} is the standard deviation accounting for the process error for which posterior probability distribution is obtained after implementation of the Bayesian approach.

The incorporation of parameter α in Eq. (9) follows other attempts to model the production of viable offspring by pelagic metazoans as a function of reproductive biomass (Oguz et al., 2008; Ruiz et al., 2009). Rather than fully resolving all steps involved in the production of polyps from spawning biomass, the process is represented through only one parameter that transforms the amount of medusa biomass into a rate of polyp production. Thus, polyp production is considered proportional to spawning biomass with a factor (α) that accounts for the sex ratio in the population (~0.5), the investment in egg creation per unit mass and the quota of that investment resulting in healthy planulae that become polyps. Experimental results indicate no mortality under the full range of physical conditions faced by planulae during summer in the lagoon (Prieto et al., 2010). Therefore, their endurance to adverse environments makes unnecessary to include this phase in the model. Eq. (9) summarizes all the factors above into a single parameter (α) for which *a posteriori* probability distribution is obtained after implementation of the Bayesian framework.

Last week of summer i accumulates a number of polyps, $\sum_t \rho_i^t$, that becomes after winter the number of medusae for the first week of next year, η_{i+1}^1:

$$\eta_{i+1}^1 \sim N\left(r_i \sum_t \rho_i^t, S_{wint}\right) \tag{11}$$

Therefore, the model is a simple alternating sequence where medusae produce polyps during summer and the fraction of these that survive the winter strobilate and become the medusae that will grow in the lagoon the subsequent summer.

2.4. Observational model

Pelagic nets designed *ad hoc* to be trawled by a pair of vessels through the shallow lagoon was the procedure to extract medusae during years 2000–2006. Fishing vessels 7–10 m length and >40 horse power (HP) worked by pairs in numbers that varied by year (5, 7, 7, 8, 7, 0 and 6 pairs for years 2000–2006). Effort also varied with these pair numbers although efficiency did not greatly change owing to the same fleet being hired every season. The fleet always worked in a limited area (the lagoon) and under an administrative contract to devote the working week to extract medusae as the unique target species. Consequently, this effort is less prone to the complexities of fishing fleets for which efficiency evolves over years and where species selection as well as economic criteria decide when, where and what to fish (Maunder et al., 2006). Weekly capture per unit effort ($cpue_i^t$, grams per week and fishing pair) was then calculated as landing divided by the number of operating pairs. The model connecting observations to the latent variables (medusa abundance) assumes that $cpue_i^t$ equals medusa

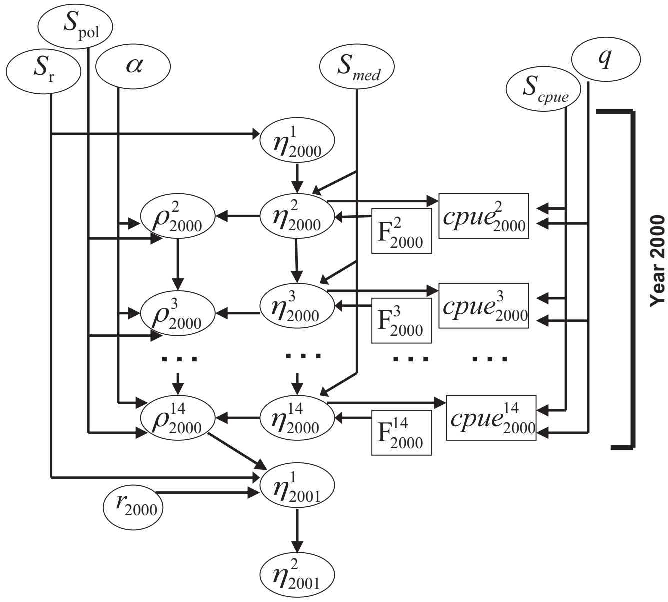

Fig. 5. Directed acyclic graph of the model. The figure exemplifies the first year of the time series (2000). Subsequent years repeat this structure starting with η^1_i.

abundance in the lagoon divided by a catchability coefficient (q) which does not vary over time:

$$cpue^t_i \sim N\left(\frac{\eta^t_i}{q}, S_{cpue}\right) \tag{12}$$

where S_{cpue} is the standard deviation accounting for errors in the observation of $cpue^t_i$ data. S_{cpue} and q posterior probability distribution are obtained after implementation of the Bayesian approach. Low medusa numbers in 2005 rendered unnecessary the extraction of medusae and no observational model is implemented for that year.

2.5. *Directed acyclic graph, prior distributions and sampling the posterior probabilities*

A directed acyclic graph (DAG) representation of the model is shown in Fig. 5. Data are shown as rectangles while oval nodes depict stochastic variables. Table 1 describes nomenclature for the symbols in Fig. 5 and equations above. The DAG incorporates the effect of man and environment on the dynamics of *C. tuberculata* benthic and pelagic stages over 7 years with only two parameters (α and q) plus sources of error (S_r, S_{wint}, S_{med}, S_{pol} and S_{cpue}).

Vague priors were implemented for these parameters. Thus, a uniform distribution was selected for α in a domain between zero and a maximum production of $\sim 10^8$ polyps per medusa gram. This upper limit greatly overestimates the highest capacity expected for medusae to produce polyps during one week if embryogenesis lasts one day and all produced planulae fix as viable polyps (Kikinger, 1992). The value of q can be interpreted as the number of weeks a vessel pair needs to deplete medusa biomass in the lagoon. Based on this interpretation, a very wide domain was given to a uniform prior that ranges between 1 and 10^3. We follow the rationale of Millar and Meyer (2000) and used non-informative priors for the errors: S_r, S_{wint}, S_{med}, S_{pol} and S_{cpue}. The Bayesian analysis usually incorporates these errors as the inverse of the variance, *i.e.* the precision, and approximates their non-informative priors by Gamma (0.001, 0.001) functions to avoid improper distributions (Millar and Meyer, 2000). Although this choice has received criticism for hierarchical models (Gelman, 2006), we found that it resulted in more stable sampling within JAGS as well as in posteriors that were able to reflect the influence of data (see Fig. 6).

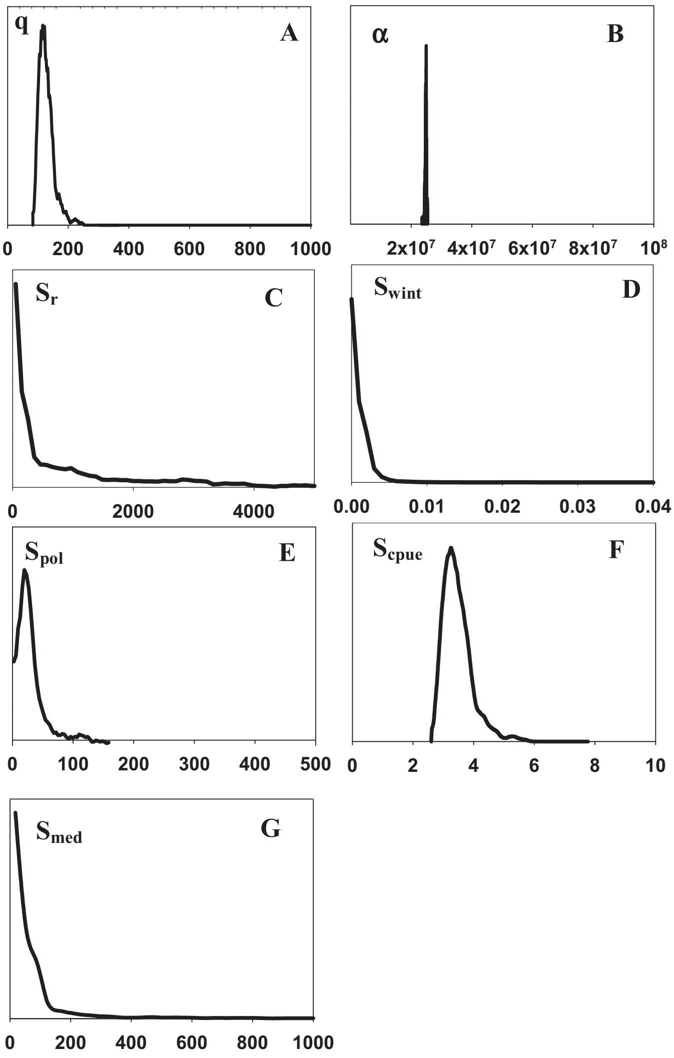

Fig. 6. Posterior probabilities of the model parameters and error sources.

Besides parameters and errors, an additional prior is necessary for η^1_{2000} to initiate the process model. The time-series starts with zero polyps ($\rho^1_{2000} = 0$) since strobilation has just occurred in the first week of summer 2000. Therefore, only a prior for medusa abundance in this week is needed. No *a priori* numeric information exists to set this prior but values coherent with subsequent catches typically result in realistic posteriors for the stocks (Ibaibarriaga et al., 2008). Too high a value of η^1_{2000} increases medusae every year towards unrealistic numbers, whereas too low a value causes the model to collapse since it cannot accommodate the fishing losses. Both extremes were diagnosed and the mid-point between them set as the mean to define η^1_{2000} prior as $N(56 \times 10^6, S_{wint})$.

The Bayesian approach estimates the parameters by updating their prior probability with the likelihood of the observations. Bayes' theorem makes the posterior probability of the parameters proportional to the product of the priors and the likelihood:

$$\begin{aligned} \textit{A POSTERIORI} \propto\ & p(\alpha, q, S_r, S_{\mathrm{wint}}, S_{med}, S_{pol}, S_{CPUE}, \ldots, \eta^t_i, \rho^t_i, \ldots) \\ & \times p(\ldots, cpue^t_i, \ldots \mid \alpha, q, S_r, S_{med}, S_{pol}, S_{cpue}, \\ & \ldots, \eta^t_i, \rho^t_i, \ldots) \end{aligned} \tag{13}$$

Table 1
Symbols used for the parameters and variables implemented in the model.

Symbol	Description	Units
C_w	Specific heat of seawater	$\mathrm{J\,m^{-3}\,K^{-1}}$
C_t	Coefficient for heat transfer	dimensionless
U_{10}	Air velocity at 10 m above sea level	$\mathrm{m\,s^{-1}}$
C_{pa}	Specific heat of air	$\mathrm{J\,m^{-3}\,K^{-1}}$
H	Lagoon average depth	m
T_{air}	Air temperature at San Javier airport	°C
$T_{\mathrm{air}}^{\mathrm{Fourier}}$	Fourier-filtered air-temperature	°C
T_w	Temperature of lagoon water	°C
t	Time	weeks
i	Time	years
m	Temperature-dependent mortality-rate of polyps	$\mathrm{day^{-1}}$
r_i	Proportion of polyps remaining after winter i	dimensionless
η_i^t	Stochastic number of medusa in week t of year i	number
ρ_i^t	Stochastic number of polyps in week t of year i	number
$j^{t,j}$	Proportion of medusae in size class j at week t after ephyra stage	dimensionless
$G^{k,j}$	Matrix containing the proportion of size k transported to class j after a week of growth	dimensionless
ω_i^t	Stochastic medusa weight in week t of year i	g
F_i^t	Medusa landing in week t of year i	g
L_i^t	Proportion of planula-carrying females	dimensionless
α	Parameter for weekly production of viable offspring	number $\mathrm{g^{-1}}$
q	Catchability	fishing weeks
D	Medusa diameter	cm
W	Medusa weight	g
$cpue$	Capture per unit effort	g $\mathrm{weeks^{1}}$ fishing $\mathrm{pair^{-1}}$
S_{med}	Standard deviation of η_i^t model	number
S_{pol}	Standard deviation of ρ_i^t model	number
S_{cpue}	Standard deviation of cpue observational model	g $\mathrm{weeks^{1}}$ fishing $\mathrm{pair^{-1}}$
S_{wint}	Standard deviation of winter survival model	number
S_r	Standard deviation for the fraction of polyp winter mortality owing to cold water	dimensionless

Explicit formulation of this joint probability density function is extremely laborious because of the need to construct the full conditional of different stages in the model during the different years. We implemented the whole Bayesian model in version 1.0.3 of JAGS (freely available at http://www-fis.iarc.fr/~martyn/software/jags/). The software avoids this tedious formulation as it is designed to construct complex posteriors for the user and to sample them by means of Gibbs numerical techniques.

Slow convergence is a chronic issue in state-space models owing to the high correlation of variables in the time series (Rivot et al., 2004). To ensure convergence three chains were initiated by JAGS with 10^3 burn-in period plus 10^6 iterations. All parameters were randomly initiated by JAGS in the first chain. To force over dispersion, extreme high and low values for q were selected from the posterior of the first chain as initial values for the other two chains. Convergence was then diagnosed following Gelman and Rubin statistics (Brooks and Gelman, 1998) for the parameters.

3. Results

Posteriors are less dispersed than priors and evidence the information added by data to the initial beliefs of the model parameters (Fig. 6). Posteriors for the dynamics of medusa biomass, as simulated with the combined process and observational models, are coherent with fishing data at the seasonal scale (Fig. 7a–g). Both landing data and simulation outputs increase through August and September, when somatic growth allows accumulation of a large biomass of medusae in the lagoon. The seasonal coherence illustrates the capacity of the model to capture the timing of ephyra liberation and of medusa growth. This is the result of the tight control that temperature exerts on the strobilation process (Prieto et al., 2010) and also indicates that $T_{\mathrm{air}}^{\mathrm{Fourier}}$ is a useful proxy of T_w. This can also be contrasted with information on the size structure of the medusa population (available during ten weeks in 2004) that has not participated in model construction. This structure is coherent though more dispersed than expected from Eq. (7) (Fig. 8a–j). Although somatic growth can potentially proceed to sizes >30 cm at rates of 3.6 cm/week (Kikinger, 1992), data indicate a stagnation beyond mid August.

The model provides further evidence for an overall decrease in somatic growth of *C. tuberculata* in the lagoon. The tight control that temperature exerts on ephyra onset and the high post-strobilation mortality of polyps (Prieto et al., 2010) make a unique cohort of medusa every year. The number of medusae in this cohort cannot be lower than the individuals landed in that year. That number growing up to >30 cm at its potential rate of 3.6 cm/week results in an accumulation of medusa biomass impossible to control by fishing. Fig. 9a and b exemplifies this for year 2002 when fishing seems to have been very effective in reducing the medusa population. A somatic growth of 3.6 cm/week (Fig. 9a) implies a growth of biomass many times the landing rates, rendering negligible the effect of fishing and resulting in unrealistic medusa stocks.

Administration and operators of the fishing program must have perceived the impact of landing medusae as significant, otherwise the high cost of operating the capture program was not justified. Fig. 7 also suggests this although it distinguishes the periods before and after the dramatic drop of abundance in year 2005. Before 2005, the simulations suggest a decrease in ephyra numbers in the year after a summer of high fishing losses (Fig. 10a and b). However, the ephyra collapse in year 2005 is not connected to an extreme peak of fishing losses in 2004. Also, the lack of captures in 2005 does not result in a peak of ephyrae in 2006. Summer 2005 was the second longest growth period in the series (Fig. 4b) without fishing losses (Fig. 7f); thus, the lack of a sufficient number of ephyrae carried over from 2004 must be the cause of low medusa numbers that year. The duration of summer in 2004 (Fig. 4b) and medusa biomass (Fig. 7e) suggest a potentially high polyp production, thus the low number of ephyrae must be due to high polyp mortality in the winter of 2004–2005.

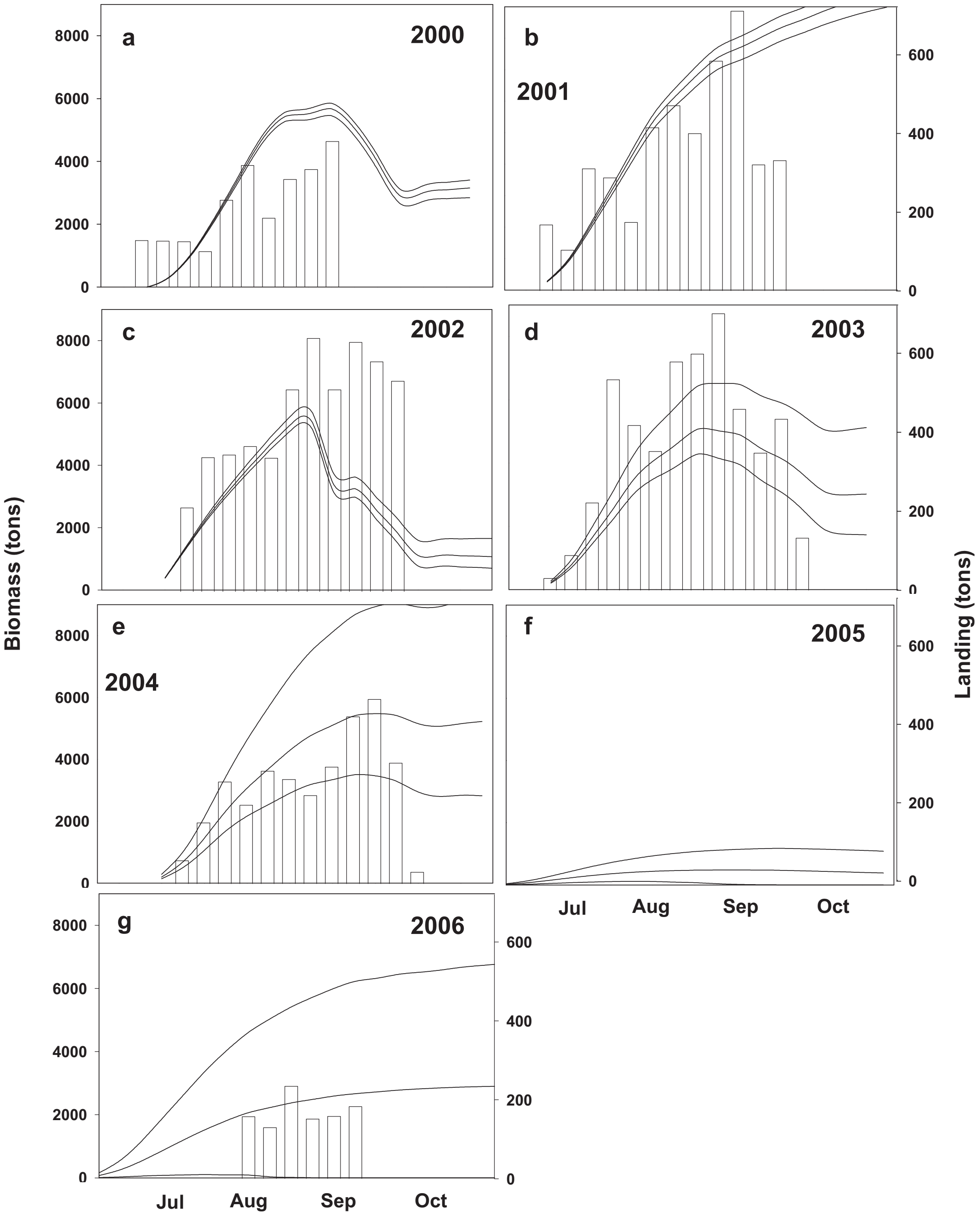

Fig. 7. Medusa biomass and landings. Lines represent the mean as well as the 5 and 95 percentile of the weekly resolved model during years 2000–2006. Vertical bars (right axis) are the weekly landing data from Consejería de Agricultura y Pesca (Región de Murcia).

4. Discussion

Results presented here demonstrate a neat connection between physical forcing and *C. tuberculata* population dynamics. Thermal forcing of the life-cycle produces results coherent with seasonal and inter-annual observations. This is facilitated by the tight control temperature exerts on *C. tuberculata* strobilation and mortality, as well as by the closed nature environment inhabited by this population. The semi-enclosed lagoon minimizes uncertainties originating from population changes due to early-stage advection or adult migration (Johnson et al., 2001; Gordon and Seymour, 2009). These elements hamper the attempts to simulate population dynamics of other metazoans in open waters (Hilborn and Walters, 1992).

The coherent example of *C. tuberculata* in the Mar Menor provides a useful perspective on the mechanisms involved in the dynamics of scyphozoan populations at larger scales. Although the factors responsible for increasing outbursts of scyphozoa are probably diverse, complex and partly site specific, they are usually associated with an overall degradation of marine ecosystems (Arai, 2001; Mills, 2001). In the case of the Mar Menor, deterioration of the benthic ecosystem occurred during the last two decades (Pérez-Ruzafa et al., 2002), liberating polyp and medusa from bottom-up and top-down controls (Pauly et al., 2009). Without these controls, fluctuations in scyphozoan populations at seasonal and inter-annual scales are largely driven by the physical environment, *e.g.* in the case of *C. tuberculata* the relationship between

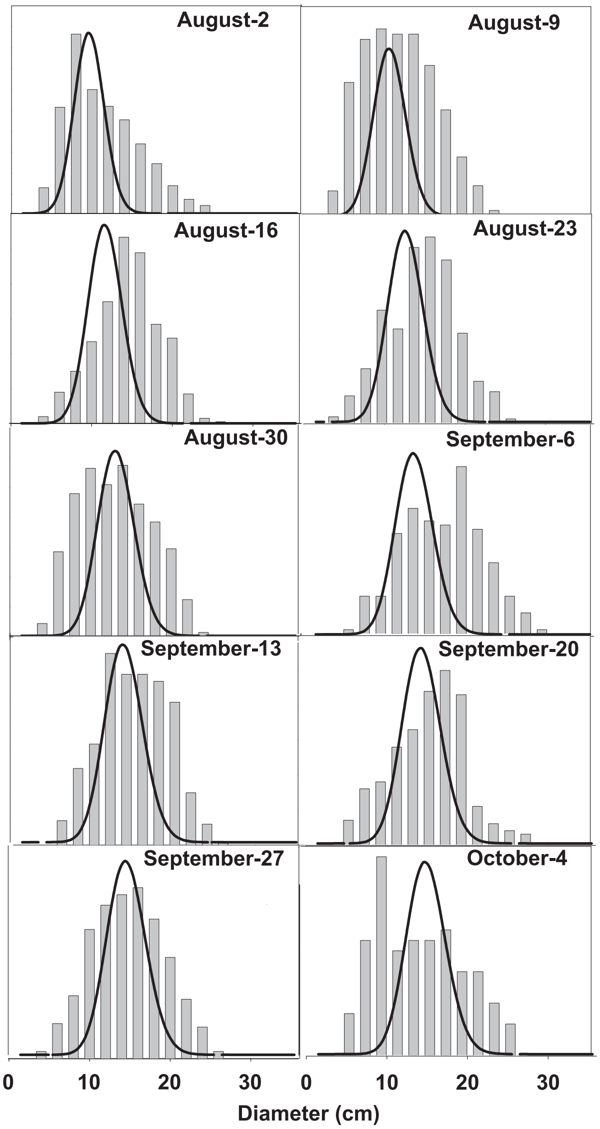

Fig. 8. Size structure of the medusa population for year 2004. *Y*-axis is relative frequency for data (bars) and simulations (line). a–j stand for the weeks from August 2 to October 10.

polyp survival and winter temperatures. This is akin to the climate vulnerability of fish populations in ecosystems under severe over exploitation (Perry et al., 2010). In the case presented here the physical environment had a dramatic fluctuation in the winter between 2004 and 2005. This particular winter is notable for the occurrence of very low $T_{\text{air}}^{\text{Fourier}}$ (Fig. 4a). These sustained low temperatures substantially decreased *r*, leading to the lowest value for the whole time series (Fig. 4b). Although the subsequent winter (between 2005 and 2006) did not show manifest temperature drops (Fig. 4a) and the summer was long (Fig. 4b), the medusa population was not particularly large in 2006 (Fig. 7g). As in 2005, the simulations point to insufficient ephyrae at the start of summer (Fig. 10a). However, in this case it appears to be the low spawning biomass of the previous year (Fig. 7f), and not an adverse environment, what is responsible for the low ephyra numbers and medusa biomass. Therefore, the model suggests the following sequence of events: (1) an adverse environment dramatically decreases polyp numbers in winter 2004–2005, (2) this environmentally driven mortality results in low ephyrae at the start of summer 2005, (3) few ephyrae produce low medusa biomass that year and (4) modest spawning biomass in 2005 results in low ephyrae and biomass

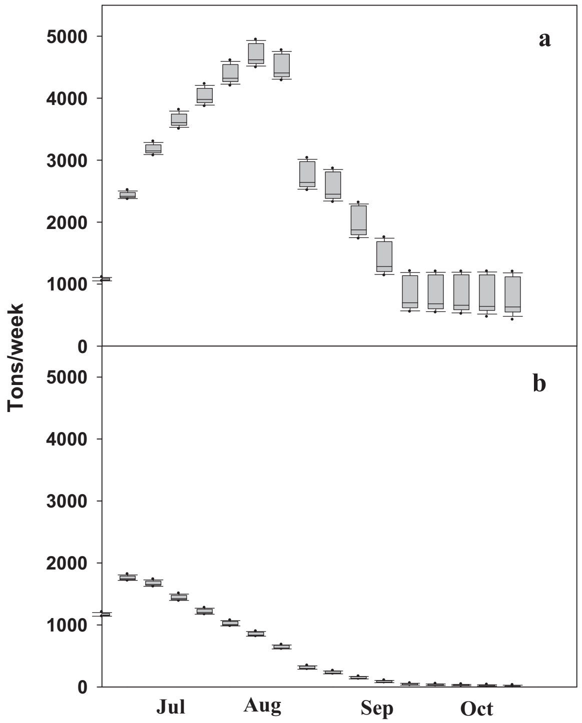

Fig. 9. Instantaneous accumulation of medusa biomass at year 2002. The number is obtained after considering the evolution of medusa number as in Fig. 6c but growing under no mechanical damage (a) or according to Eq. (7) (b). Box limits and whiskers indicate respectively the 25–75 and the 10–90 percentile limits.

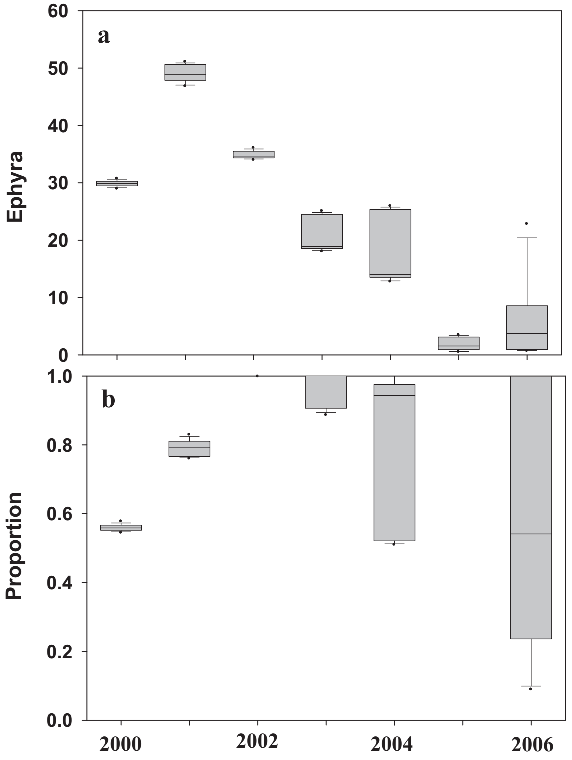

Fig. 10. Ephyra abundance and impact of fishing on the population. (a) Number of ephyrae (in millions) at the start of the summer. (b) Proportion of fished individuals. Box limits and whiskers indicate respectively the 25–75 and the 10–90 percentile limits.

at 2006 even though there are adequate environmental conditions for high growth. This four-step sequence is similar to regime shifts involving exploited fish, where the stock upholds strong fishing pressures for years except under conditions of extreme vulnerability to climatic fluctuations (Bakun and Weeks, 2006; deYoung et al., 2008). When climatic variability brings adverse conditions for the exploited species the population collapses and no further recovery occurs despite the onset of favourable environment conditions (Barange, 2003). No large program of medusa extraction has been implemented after 2006, suggesting that the regime shift in the lagoon has persisted some years after the collapse shown in Fig. 7.

Other extensive analysis of the human and environmental factors driving the outburst of jellyfish in the Irish Sea, Lynam et al. (2011) also found an initial triggering connected to ecosystem disturbances created by over fishing and a subsequent control of abundance mainly explained by long term tendencies in sea surface temperature. According to Lynam et al. (2011), this connection between physical forcing and jellyfish abundance can emerge from a direct control of the life cycle or through indirect mechanisms involving climate modifications of the trophic interactions in the ecosystem. Both mechanisms do not mutually exclude and probably add in a synergic non-linear manner. The results presented here only resolve the direct effect of temperature and indicate that it alone explains the onset and decay of *C. tuberculata* in Mar Menor. In coherence with the Bayesian simulation of dynamical systems, the unresolved variance connected to trophic interactions is computed by the model as an increase in uncertainty. These unresolved mechanisms possible hamper the simulations to entirely match the landing patterns during years 2002–2004, what the model translates into a progressive increase of uncertainty in this period (Fig. 7). However, these trophic interactions cannot explain the four-step sequence of events described above for the onset and decay of *C. tuberculata* in Mar Menor. No abrupt shift of potential predators for *C. tuberculata* early stages is mentioned in the lagoon for the years 2000–2006 since the significant changes of the benthic community that may have affected components such as fish or nudibranchs occurred in the 1980s (Verdiell-Cubedo et al., 2008). Therefore, the rapid collapse in year 2005 cannot be connected with a sudden onset of top-down control of the population. Bottom-up control of the trophic flow cannot either explain the fluctuations of *C. tuberculata* population along the analysed years. As Fig. 11a–c shows, critical depth very rarely becomes shallower than the average lagoon depth. This prevents the existence of long phases where primary production is limited by light availability in the water column, as frequently occurs in the deep sea during winter (Mann and Lazier, 2006). Therefore, the success/failure of *C. tuberculata* recruitment in the lagoon cannot be explained through their phenology match/mismatch with a light-induced spring-bloom and the trophic cascades this generates through the food web. The match/mismatch of early stages with the spring bloom is considered to control the recruitment of many commercial fish species (Cushing, 1990). Similarly, it is difficult to think that a bottom-up mechanism associated with nutrient availability controls the fluctuations of *C. tuberculata* landings in Fig. 7. Input of nutrients to the lagoon is controlled by the drainage of watersheds and enhanced during precipitation events (Velasco et al., 2006; García-Pintado et al., 2007). Fig. 11 shows those events during the period of analysis. Neither their time distribution nor the accumulated value of precipitation during the rain season provides a pattern that can straightforwardly (as temperature does) explain the variance of *C. tuberculata* landings in Mar Menor.

Trophic flows can, nevertheless, have had a role in the size structure of the medusa population during summer since Figs. 8 and 9 indicate a stagnation beyond mid August. Kikinger (1992) suggests a reduction in somatic growth of medusae related to mechanical damage by waves and motor boats. Intense recreational boating during the summer period and a wind-driven energy that is not diluted in a deep water-column make feasible this damage. Nevertheless, although the growth of 3.6 cm/week calculated by Kikinger (1992) is very consistent among years (and, therefore, among trophic conditions), food constrain must also have a role in the limited size increments (Olesen et al., 1994; Scheneider and Behrends, 1994; Hansson, 1997; Ishii and Bamstedt, 1998; Lo and Chen, 2008). Nitrogen concentrations within the lagoon are below 0.5 μM during summer (Eurogel data) which limits primary production (Fasham et al., 1990). Although zooxanthellae do not significantly contribute to medusa energetic balance (Prieto et al., 2010), the amount of food particles available to *C. tuberculata* must be reduced during the oligotrophic summer. Additional knowledge on metabolism and ecological interactions is still needed to include these dynamical components in scyphozoa models (Pauly et al., 2009).

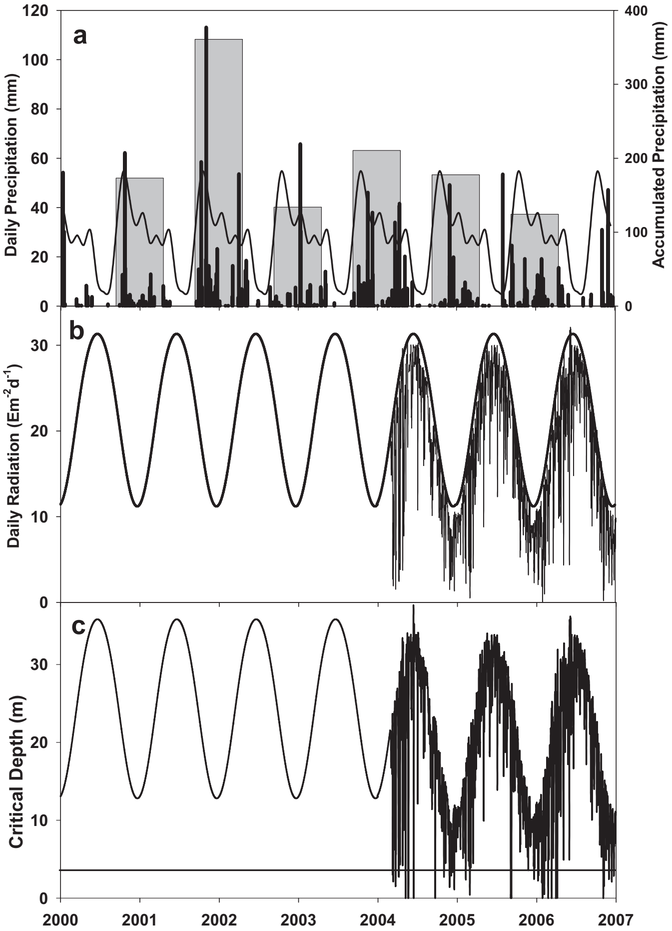

Fig. 11. Nutrient and light bottom-up control of primary production in the lagoon. (a) Rainfall at San Javier airport meteorological station. Black and grey bars are the daily and the yearly accumulated (during the hydrological year from September to August) precipitation respectively. The line shows the monthly climatology of precipitation for this station as provided by the Agencial Estatal de Meteorología. (b) Thick line is daily clear sky global radiation calculated from astronomical formulae (Brock, 1981) and thin line are the daily records at San Javier Stations when available (from 2004 onwards). (c) Minimum critical depth expected in the lagoon as derived from clear sky and daily records of global radiation above and a condition of maximum concentration of suspended solids and chlorophyll in the water column (10 mg/L and 10 μg/L respectively; Velasco et al., 2006). Horizontal solid line is the average depth of the lagoon.

Direct thermal forcing of *C tuberculata* life cycle seems enough to explain most of its rising and falling in Mar Menor. This direct forcing could also originate part of the correlation between different jellyfish species and sea surface temperature observed in the Irish or Barents seas (Lynam et al., 2011; Brodeur et al., 2008) as well as between the basin-scale abundance of these species and climatology indexes like El Niño (Raskoff, 2001; Dawson et al., 2001) or NAO (Molinero et al., 2008). The non-sophisticated response of the scyphozoan life cycle facilitates a direct transfer of climatology signals into fluctuations of the population dynamics once ecosystem resilience has been deteriorated.

Evidence for global scale degradation of coastal ecosystems is unquestionable (Halpern et al., 2008) thus suggesting that the physical environment is likely to increasingly control the dynamics of jellyfish at large scales. In parallel with ecosystem degradation, evidence of an overall warming of the oceans is also unquestionable (Lyman et al., 2010). In this context, a warming ocean must affect the life cycle of jellyfish and thus their global dynamics. The connection between climatic forcing and population response is straightforward in *C. tuberculata* and can be summarized with the simple rule "the warmer the better"; mild winters and long summers facilitate blooms. This relationship might change or have another sign for other species, which in turn may partially explain the contrasting trends observed for different scyphozoa (Purcell et al., 2007). However, it is clear that phase changes in jellyfish lifecycles are very sensitive to temperature and variations of less than 0.5 °C can trigger life cycle transitions that control their population dynamics (Prieto et al., 2010). As these variations are smaller than temperature changes observed in the upper ocean during recent decades (Domingues et al., 2008), it is likely that warming oceans have played some role in determining the observed global jellyfish trends. Finally, as a portend to the future, predicted increases in oceanic temperature (IPCC, 2007) are also large enough to suggest a potential for increasingly overall impact on jellyfish life cycles with consequences on global abundances.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2012.03.019.

References

Anderson, P.J., Piatt, J.F., 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecology-Progress Series 189, 117–123.

Arai, M.N., 2001. Pelagic coelenterates and eutrophication: a review. Hydrobiologia 451, 27–44.

Attrill, M.J., Wright, J., Edwards, M., 2007. Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. Limnology and Oceanography 52, 480–485.

Avian, M., 1986. Biological cycle of *Cotylorhiza tuberculata* (Macri 1778). Morphological aspects of the development from ephyra to young medusa. Nova Thalassia 8, 47–58.

Bakun, A., Weeks, S.J., 2006. Adverse feedback sequences in exploited marine systems: are deliberate interruptive actions warranted? Fish and Fisheries 7, 316–333.

Barange, M., 2003. Ecosystem science and the sustainable management of marine resources: from Rio to Johannesburg. Frontiers in Ecology and the Environment 1, 190–196.

Brock, T.D., 1981. Calculating solar radiation for ecological studies. Ecological Modelling 14, 1–19.

Brodeur, R.D., Decker, M.B., Ciannelli, L., Purcell, J.E., Bond, N.A., Stabeno, P.J., Acuna, E., Hunt Jr., G.L., 2008. Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts. Progress in Oceanography 77, 103–111.

Brooks, S.P., Gelman, A., 1998. General methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics 7, 434–455.

Carlotti, F., Sciandra, A., 1989. Population dynamics model of *Euterpina acutifrons* (Copepoda: Harpacticoida) coupling individual growth and larval development. Marine Ecology-Progress Series 56, 225–242.

Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. In: Blaxter, J.H.S., Southward, A.J. (Eds.), Advances in Marine Biology. Academic Press Limited, San Diego, pp. 250–313.

Dawson, M.N., Martín, L.E., Penland, L.K., 2001. Jellyfish swarms tourists and the Christ-child. Hydrobiologia 451, 131–144.

deYoung, B., Barange, M., Beaugrand, G., Harris, R., Perry, R.I., Scheffer, M., Werner, F., 2008. Regime shifts in marine ecosystems: detection prediction and management. Trends in Ecology and Evolution 23, 402–409.

Domingues., C., Church, M.J., White, A.N., Gleckler, J.P., Wijffels, J.S., Barker, E.P., Dunn, M.J.R., 2008. Improved estimates of upper-ocean warming and multidecadal sea-level rise. Nature 453, 1090–1094.

Fasham, M.J.R., Ducklow, H.W., McKelvie, S.M., 1990. A nitrogen-based model of plankton dynamics. Journal of Marine Research 48, 591–639.

Fennel, W., 2001. Modelling of copepods with links to circulation models. Journal of Plankton Research 23, 1217–1232.

García-Pintado, J., Martínez-Mena, M., Barberá, G.G., Albaladejo, J., Castillo, V.M., 2007. Anthropogenic nutrient sources and loads from a Mediterranean catchment into a coastal lagoon: Mar Menor, Spain. Science of the Total Environment 373, 220–239.

Gelman, A., 2006. Prior distributions for variance parameters in hierarchical models. Bayesian Analysis 3, 515–533.

Gibbons, M.J., Richardson, A.J., 2008. Patterns of pelagic cnidarian abundance in the North Atlantic. Hydrobiologia 616, 51–65.

Gill, A.E., 1982. Transfer of properties between atmosphere and ocean. In: Atmosphere–Ocean Interaction. Academic Press, London (Chapter 2) pp. 19–36.

Gordon, M.R., Seymour, J.E., 2009. Quantifying movement of the tropical Australian cubozoa *Chironex fleckeri* using acoustic telemetry. Hydrobiologia 616, 87–97.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappell, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., et al., 2008. A global map of human impact on marine ecosystems. Science 319, 948–952.

Hansson, L.J., 1997. Effect of temperature on growth rate of *Aurelia aurita* (Cnidaria, Scyphozoa) from Gullmarsfjorden, Sweden. Marine Ecology-Progress Series 161, 145–153.

Hilborn, R., Walters, C.J., 1992. Quantitative Fisheries Stock Assessment. Kluwer Academic Publishers, Boston, pp. 397–399.

Ibaibarriaga, L., Fernández, C., Uriarte, A., Roel, B., 2008. A two-stage biomass dynamic model for the Bay of Biscay anchovy: a Bayesian approach. ICES Journal of Marine Science 65, 191–205.

IPCC, 2007. In: Core Writing Team, Pachauri, R.K., Reisinger, A. (Eds.), Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, 104 pp.

Ishii, H., Bamstedt, U., 1998. Food regulation of growth and maturation in a natural population of *Aurelia aurita* (L.). Journal of Plankton Research 20, 805–808.

Johnson, D.R., Perry, H.M., Burke, W.D., 2001. Developing jellyfish strategy hypotheses using circulation models. Hydrobiologia 451, 213–221.

Kikinger, R., 1986. Development cycle of *Cotylorhiza tuberculata* (Scyphozoa: Rhizostomae). Nova Thalassia 8, 73–82.

Kikinger, R., 1992. *Cotylorhiza tuberculata* (Cnidaria: Scyphozoa). Life history of a stationary population. PSZNI Marine Ecology 13 (4), 333–362.

Lo, W.T., Chen, I.L., 2008. Population succession and feeding of scyphomedusae *Aurelia aurita*, in a eutrophic tropical lagoon in Taiwan. Estuarine Coastal and Shelf Science 76, 227–238.

Lucas, C., 2001. Reproduction and life history strategies of the common jellyfish *Aurelia aurita*, in relation to its ambient environment. Hydrobiologia 451, 229–246.

Lyman, J.M., Good, S.A., Gouretski, V.V., Ishii, M., Johnson, G.C., Palmer, M.D., Smith, D.M., Willis, J.K., 2010. Robust warming of the global upper ocean. Nature 465, 334–337.

Lynam, C.P., Hay, S.J., Brierley, S.A., 2004. Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. Limnology and Oceanography 49, 637–643.

Lynam, C.P., Lilley, M.K.S., Bastian, T., Doyle, T.K., Beggs, S.E., Hays, G.C., 2011. Have jellyfish in the Irish Sea benefited from climate change and overfishing? Global Change Biology 17, 767–782.

Mann, K.H., Lazier, J.R.N., 2006. In: Mann, K.H., Lazier, J.R.N. (Eds.), Dynamics of Marine Ecosystems: Biological–Physical Interactions in the Oceans. , third ed. Blackwell Publishing, Massachusetts, pp. 194–204.

Maunder, M.N., Sibert, J.R., Fonteneau, A., Hampton, J., Kleiber, P., Harley, S.J., 2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. ICES Journal of Marine Science 63, 1373–1385.

Meyer, R., Millar, R.B., 1999. BUGS in Bayesian stock assessment. Canadian Journal of Fisheries Aquatic Sciences 56, 1078–1086.

Millar, R.B., 1992. Estimating the size-selectivity of fishing gear by conditioning on the total catch. Journal of the American Statistical Association 87 (420), 962–968.

Millar, R.B., Meyer, R., 2000. Nonlinear state-space modelling of fisheries biomass dynamics using Metropolis-Hastings within Gibbs sampling. Applied Statistics 49, 327–342.

Mills, C.E., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions. Hydrobiologia 451, 55–68.

Molinero, J.C., Casini, M., Buecher, E., 2008. The influence of the Atlantic and regional climate variability on the long-term changes in gelatinous carnivore populations in the northwestern Mediterranean. Limnology and Oceanography 53 (4), 1456–1467.

Oguz, T., Salihoglu, B., Fach, B., 2008. A coupled plankton-anchovy population dynamics model assessing nonlinear control of anchovy stock and anchovy-gelatinous shift in the Black Sea. Marine Ecology-Progress Series 369, 229–256.

Olesen, N.J., Frandsen, K., Riisgard, H.U., 1994. Population dynamics growth and energetics of jellyfish *Aurelia aurita* in a shallow fjord. Marine Ecology-Progress Series 105, 9–18.

Omori, M., Nakano, E., 2001. Jellyfish fisheries in southeast Asia. Hydrobiologia 451, 19–26.

Pagès, F., 2001. Past and present anthropogenic factors promoting the invasion colonization and dominant by jellyfish of a Spanish coastal lagoon. CIESM Workshop Series 14, 69–74.

Pauly, D., Graham, W., Libralato, S., Morissette, L., Palomares, M.L.D., 2009. Jellyfish in ecosystems, online databases, and ecosystem models. Hydrobiologia 616, 67–85.

Pérez-Ruzafa, A., Gilabert, J., Gutiérrez, J.M., Fernández, A.I., Marcos, C., Sabah, S., 2002. Evidence of a planktonic food web response to changes in nutrient input dynamics in the Mar Menor coastal lagoon, Spain. Hydrobiologia 475/476, 359–369.

Perry, R.I., Cury, P., Brander, K., Jennings, S., Möllmanne, C., Planque, B., 2010. Sensitivity of marine systems to climate and fishing: concepts issues and management responses. Journal of Marine Systems 79, 427–435.

Prieto, L., Astorga, D., Navarro, G., Ruiz, J., 2010. Environmental control on phase transition and polyp survival of a massive-outbreaker jellyfish. PLoS One 5 (11), e13793.

Punt, A.E., Hilborn, R., 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. Reviews in Fish Biology and Fisheries 7, 35–63.

Purcell, J.E., Uye, S.I., Lo, W.T., 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Marine Ecology-Progress Series 350, 153–174.

Purcell, J.E., White, J.R., Nemazie, D.A., Wright, D.A., 1999. Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha*. Marine Ecology-Progress Series 180, 187–196.

Raskoff, K.A., 2001. The impact of El Niño events on populations of mesopelagic hydromedusae. Hydrobiologia 451, 121–129.

Richardson, A.J., Bakun, A., Hays, G.C., Gibbons, M.J., 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends in Ecology and Evolution 24 (6), 312–322.

Rivot, E., Prévost, E., Parent, E., Bagliniére, J.L., 2004. A Bayesian state-space modelling framework for fitting salmon stage structured population dynamic model to multiple time series of field data. Ecological Modelling 179, 463–485.

Ruiz, J., 1997. What generates daily cycles of marine snow? Deep-Sea Research I 44 (7), 1105–1126.

Ruiz, J., González-Quirós, R., Prieto, L., Navarro, G., 2009. A Bayesian model for anchovy: the combined pressure of man and environment. Fisheries Oceanography 18 (1), 62–76.

Scheneider, G., Behrends, G., 1994. Population dynamics and the trophic role of *Aurelia aurita* medusae in the Kiel Bight and western Baltic. ICES Journal of Marine Science 51, 359–367.

Velasco, J., Lloret, J., Millán, A., Marín, A., Barahona, J., Abellán, P., Sánchez-Fernández, D., 2006. Nutrient and particulate inputs into the Mar Menor lagoon (SE Spain) from an intensive agricultural watershed. Water, Air and Soil Pollution 176, 37–56.

Verdiell-Cubedo, D., Oliva-Paterna, F.J., Egea-Serrano, A., Torralva, M., 2008. Population biology and habitat associations of benthic fish species in the shallow areas of the mediterranean coastal lagoon (SE Iberian Peninsula). Scientia Marina 72 (2), 319–328.