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

Javier Ruiz*1, Laura Prieto* and Diana Astorga*.

*Department of Coastal Ecology and Management, Instituto de Ciencias Marinas de Andalucía, Consejo Superior de Investigaciones Científicas, Avda Republica Saharaui 2, 11519 Puerto Real, Cádiz, Spain

1Corresponding Author:
Javier Ruiz
Departamento de Ecología y Gestión Costera
Instituto de Ciencias Marinas de Andalucía (ICMAN-CSIC)
Avda Republica Saharaui 2
11519 Puerto Real (Cádiz)
SPAIN
Tel: 34-956-832612
Fax: 34-956-834701
javier.ruiz@icman.csic.es
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.

Key words: jellyfish, medusa, Mediterranean, *Cotylorhiza tuberculata*, Bayesian framework, Mar Menor, coastal lagoon.
1. INTRODUCTION

The Mar Menor is a large (135 km²) 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 80s (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 90s. 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 scyphozoaa (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 scyphozoan species, e.g. *Aurelia aurita* (Lucas 2001) or *Chrysaora quinquecirrha* (Purcell et al. 1999), cold waters prevent strobilation (Kikinger 1992). However, in contrast to other scyphozoan, *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 scyphozoan 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.

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 \( T_w \) (ºC):

\[
dP/dt = m(T_w)P
\]  

[1]

Polyp mortality by cold temperature is negligible for waters above 16ºC (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 4ºC (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 16ºC, as evident after baseline fitting equation 2 to the three points.

\[
m = \begin{cases} 
0.016T_w - 0.256 & \text{if } 4 \leq T_w < 16^\circ C \\
0 & \text{if } T_w \geq 16^\circ C 
\end{cases}
\]  

[2]
The connection between $m$ and $T_w$ in equation 2 is used to create a prior for the fraction of the polyp population remaining after a winter ($r_i$). Equation 2 is integrated over the winter months between years $i$ and $i+1$ to calculate the prior:

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

were $m$ 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,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):

\[
\frac{HC_w}{C_t U_{10} C_{pa}} \approx 1 \text{ month}
\]

where \( H \) is water column depth (~4 m average in the lagoon), \( C_w \) 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 ms\(^{-1}\) 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 \((T_{air}^{\text{Fourier}})\) that are coherent as a proxy for \( T_w \) (Fig. 3b).

The lethal effect of cold water during winter \((r_i)\) was, therefore, modelled through \( T_{air}^{\text{Fourier}} \) (Fig. 4a,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 \((S_{\text{winv}})\) 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 \( S_{\text{winv}} \) 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 \( T_{air}^{Fourier} \geq 18^\circ C \) minus 9 weeks of ephyra stage. This duration is presented in Fig. 4.b.

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 \( (J^{t,0}) \) evolves by somatic growth according to the following expression:

\[
\sum_{k=1}^{k=j} J^{t-1,k} G^{k,j}
\]  

\[5\]
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):

\[
(t/20) \left[ e^{a+bD_j} / \left( 1 + e^{a+bD_j} \right) \right]
\]

[6]

where \(a\) and \(b\) are parameters of the logistic curve for gear selectivity (Supporting Information 1), \(D_j\) the diameter (cm) of medusae in size class \(j\) and 20 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:

\[
J^{t,j} = (t/20) \left[ e^{a+bD_j} / \left( 1 + e^{a+bD_j} \right) \right] \sum_{k=1}^{20} J^{t-1,k} G^{k,j}
\]

[7]

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

\[
\eta_i = N(\eta_{i-1}^{i-1} - F^{t-1,i}, S_{med})
\]

[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 $F'_{2005} = 0$ for every $t$.

2.3 BENTHIC-PELAGIC COUPLING

The number of polyps at week $t$ of summer $i$, $\rho'_i$, is figured out depending on medusa biomass, the proportion of planulae-carrying females, $L$, and a parameter $\alpha$:

$$\rho'_i \sim N(\rho'^{-1}_i + \alpha L \omega'_i \eta'_i, S_{pol})$$

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

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

The biomass $(\omega'_i \eta'_i)$ is derived from an estimation of the average weight $(\omega'_i, \text{ in grams})$ obtained from equation 7 and the relationship weight=0.071$D^3$ (Supporting Information 3). This weight-length relationship is close to weight=0.08$D^{3.1}$, 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 $\alpha$ in equation 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 ($\alpha$) 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. Equation 9 summarizes all the factors above into a single parameter ($\alpha$) for which $a$ posteriori probability distribution is obtained after implementation of the Bayesian framework.

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

$$\eta_{i+1}^1 \sim N \left( r, \sum_{i} \rho_i^t, S_{\text{int}} \right)$$

[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 to 2006. Fishing vessels
7-10 meters length and $>$40 horse power (HP) worked by pairs in numbers that varied
by year (5, 7, 7, 8, 7, 0 and 6 pairs for years 2000 to 2006). Effort also varied with these
pair numbers although efficiency did not greatly change owing to the same fleet being
hired every season. The fleet always worked in a limited area (the lagoon) and under an
administrative contract to devote the working week to extract medusae as the unique
target species. Consequently, this effort is less prone to the complexities of fishing fleets
for which efficiency evolves over years and where species selection as well as economic
criteria decide when, where and what to fish (Maunder et al. 2006). Weekly capture per
unit effort ($cpue_i$, 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 $cpue_i$ equals medusa abundance in
the lagoon divided by a catchability coefficient ($q$) which does not vary over time:

$$ cpue_i \sim N(\eta_i/q, S_{cpue}) $$

[12]

where $S_{cpue}$ is the standard deviation accounting for errors in the observation of $cpue_i$
data. $S_{cpue}$ and $q$ posterior probability distribution are obtained after implementation of
the Bayesian approach. Low medusa numbers in 2005 rendered unnecessary the
eextraction 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
omenclature 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 (\(\alpha\) and \(q\)) plus sources of error (\(S_r\), \(S_{winr}\),
\(S_{med}\), \(S_{pol}\) and \(S_{cpue}\)).

Vague priors were implemented for these parameters. Thus, a uniform distribution was
selected for \(\alpha\) in a domain between zero and a maximum production of \(~10^8\) 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: \(S_r\), \(S_{winr}\) \(S_{med}\), \(S_{pol}\) 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).

Besides parameters and errors, an additional prior is necessary for \( \eta_{2000}^1 \) to initiate the process model. The time-series starts with zero polyps \((\rho_{2000}^1 = 0)\) 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 \( \eta_{2000}^1 \) 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 \( \eta_{2000}^1 \).prior as \( N(56 \times 10^6, S_{win}) \).

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:

\[
A \text{POSTERIORI} \propto p(\alpha, q, S_r, S_{win}, S_{med}, S_{pol}, S_{CPUE}, ..., \eta_i, \rho_i, ...) \times p(..., cpue_i, ..., | \alpha, q, S_r, S_{med}, S_{pol}, S_{CPUE}, ..., \eta_i, \rho_i, ...)
\]

[13]

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). The uniform priors for $\alpha$ and $q$ become unimodal posteriors. The Gamma prior given to the precisions become either unimodal ($S_{pol}$ and $S_{scpue}$) or a very different to posterior. Thus, the Gamma (0.001, 0.001) could not be distinguished from the y-axis if superimposed on the plot of $S_p$, $S_{wint}$ or $S_{med}$. 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 $T_{\text{Fourier}}^{\text{air}}$ 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 equation 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,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$^{-1}$ (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,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.

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 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 suggest 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 at 2006 even though there are adequate environmental conditions for high growth. This four-step sequence is similar to regime shifts involving exploited fishes, where the stock upholds strong fishing pressures for years except under conditions of extreme vulnerability to climatic fluctuations (Bakun
and Weeks 2006; deYoung B 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 are 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 to 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 to 2006 since the significant changes of the benthic community that may
have affected components such as fish or nudibranchs occurred in the 80s (Verdile-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 \textit{C. tuberculata} population along the analyzed 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 \textit{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 \textit{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 provide a pattern that can straightforwardly (as temperature does) explain the variance of \textit{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 Fig. 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\(^{-1}\) 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 \(\mu\text{M}\) 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 scyphozoan models (Pauly et al. 2009).

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 summarised 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 life-cycles 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.
ACKNOWLEDGMENTS

This work was funded by the projects P06-RNM-02393 and P07-RNM-02976 from the Junta de Andalucía and by SESAME (FP6-036949). Meteorological data were provided by the Agencia Estatal de Meteorología.

REFERENCES


Lyman, J.M., Good, S.A., Gouretski, V.V., Ishii, M., Johnson, G.C., Palmer, M.D.,
465, 334-337.

North Sea jellyfish and links to the North Atlantic Oscillation. *Limnology and
Oceanography*, 49, 637-643.

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: *Dynamics of Marine Ecosystems: Biological-

Interpreting catch per unit effort data to assess the status of individual stocks and

of Fisheries Aquatic Sciences*, 56, 1078-1086.

the Total Catch. *Journal of the American Statistical Association*, 87(420), 962-968.


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

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$C_w$</td>
<td>Specific heat of seawater</td>
<td>$\text{Jm}^{-3}\text{K}^{-1}$</td>
</tr>
<tr>
<td>$C_t$</td>
<td>Coefficient for heat transfer</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$U_{10}$</td>
<td>Air velocity at 10 m above sea level</td>
<td>$\text{Ms}^{-1}$</td>
</tr>
<tr>
<td>$C_{pa}$</td>
<td>Specific heat of air</td>
<td>$\text{Jm}^{-3}\text{K}^{-1}$</td>
</tr>
<tr>
<td>$H$</td>
<td>Lagoon average depth</td>
<td>m</td>
</tr>
<tr>
<td>$T_{air}$</td>
<td>Air temperature at San Javier airport</td>
<td>°C</td>
</tr>
<tr>
<td>$T_{air,\text{Fourier}}$</td>
<td>Fourier-filtered air-temperature</td>
<td>°C</td>
</tr>
<tr>
<td>$T_w$</td>
<td>Temperature of lagoon water</td>
<td>°C</td>
</tr>
<tr>
<td>$t$</td>
<td>Time</td>
<td>Weeks</td>
</tr>
<tr>
<td>$i$</td>
<td>Time</td>
<td>Years</td>
</tr>
<tr>
<td>$m$</td>
<td>Temperature-dependent mortality-rate of polyps</td>
<td>Day$^{-1}$</td>
</tr>
<tr>
<td>$r_i$</td>
<td>Proportion of polyps remaining after winter $i$</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$\eta_i^t$</td>
<td>Stochastic number of medusa in week $t$ of year $i$</td>
<td>Number</td>
</tr>
<tr>
<td>$\rho_i^t$</td>
<td>Stochastic number of polyps in week $t$ of year $i$</td>
<td>Number</td>
</tr>
<tr>
<td>$j_{i-j}^t$</td>
<td>Proportion of medusae in size class $j$ at week $t$ of ephyra stage</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$G_{k-j}^t$</td>
<td>Matrix containing the proportion of size $k$ transported to class $j$ after a week of growth</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$\omega_i^t$</td>
<td>Stochastic medusa weight in week $t$ of year $i$</td>
<td>g</td>
</tr>
<tr>
<td>$F_i^t$</td>
<td>Medusa landing in week $t$ of year $i$</td>
<td>g</td>
</tr>
<tr>
<td>$L_i^t$</td>
<td>Proportion of planula-carrying females</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Parameter for weekly production of viable offspring</td>
<td>Number $g^{-1}$</td>
</tr>
<tr>
<td>$q$</td>
<td>Catchability</td>
<td>Fishing Weeks</td>
</tr>
<tr>
<td>$D$</td>
<td>Medusa diameter</td>
<td>cm</td>
</tr>
<tr>
<td>$W$</td>
<td>Medusa weight</td>
<td>g</td>
</tr>
<tr>
<td>CPUE</td>
<td>Capture per unit effort</td>
<td>$\text{g Weeks}^{-1}$</td>
</tr>
<tr>
<td>$S_{\text{med}}$</td>
<td>Standard deviation of $\eta_i^t$ model</td>
<td>Number</td>
</tr>
<tr>
<td>$S_{\text{pol}}$</td>
<td>Standard deviation of $\rho_i^t$ model</td>
<td>Number</td>
</tr>
<tr>
<td>$S_{\text{cpue}}$</td>
<td>Standard deviation of cpue observational model</td>
<td>$\text{g Weeks}^{-1}$</td>
</tr>
<tr>
<td>$S_{\text{wint}}$</td>
<td>Standard deviation of winter survival model</td>
<td>Number</td>
</tr>
<tr>
<td>$S_r$</td>
<td>Standard deviation for the fraction of polyp winter mortality owing to cold water</td>
<td>Dimensionless</td>
</tr>
</tbody>
</table>
FIGURE LEGENDS

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

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 4ºC was derived from equation 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 $T_{air}^{Fourier}$, 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) $T_{air}^{Fourier}$ (ºC). 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 $T_{air}^{Fourier}$.

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 $\eta_i^1$.

Fig. 6. Posterior probabilities of the model parameters and error sources.
**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 to 2006. Vertical bars (right axis) are the weekly landing data from Consejería de Agricultura y Pesca (Región de Murcia).

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

**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 equation 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.

**Figure 11.** Nutrient and light bottom-up control of primary production in the lagoon. a) Rain fall 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.
Figure 1
Figure 2
Figure 3
Figure 4
Figure 5
Figure 6
Figure 7

Biomass (tons) vs. Landing (tons) for the years 2000 to 2006.
Figure 8

Diameter (cm)
SUPPORTING INFORMATION LEGENDS

S1. Proportional cumulative catches as a function of medusa diameter. Dots are all data available from different samplings of the fishery in years 2000 to 2006, where individuals were classified as belonging to <5, 5-10 or >10 cm size classes. The line is a least square fit ($r^2 = 0.81$) of the logistic curve, $\frac{e^{a+bdD}}{1+e^{a+bdD}}$, see Eq. 6, to these data with coefficients $a$ and $b$ equal to -2.78 and 0.40 respectively.

S2. Proportion of planula-carrying females vs. diameter. The line is a least square fit ($r^2 = 0.97$) of the logistic curve, $0.6413\frac{e^{c+ddD}}{1+e^{c+ddD}}$. Means of parameters c and d are -8.3302 and 0.4961, and their standard deviations 3.6731 and 0.2175 respectively. Data from Consejería de Agricultura y Pesca, Región de Murcia, for year 2004.

S3. Medusa weight vs. diameter. Dots are measured diameter vs. weight data for *Cotylorhiza tuberculata* (data from Consejería de Agricultura y Pesca, Región de Murcia, for year 2004). Line is the equation $W = 0.071D^{3.0}$.