

Climate-driven population size fluctuations of jellyfish (*Chrysaora plocamia*) off Peru

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Abstract There is a general concern that jellyfish populations are increasing throughout marine ecosystems worldwide, mainly due to environmental (e.g., climate drivers) and anthropogenic forces (e.g., overfishing and eutrophication), or interactions among them. To identify drivers of jellyfish populations in the heavily fished northern Humboldt upwelling system (NHUS), we examined linkages between a 43-year-long annual time series (1972–2014) of the biomass of the scyphomedusae *Chrysaora plocamia* and several forcing factors: the Peruvian Oscillation Index, the Regime Indicator Series and commercial landings of Peruvian anchovy. We found that *C. plocamia* biomass fluctuated with climate drivers, but not with anchovy landings (a proxy of fishing pressure). Jellyfish biomass was high and variable during the warm El Viejo regime in the 1970s and 1980s, with peaks connected to intra-regime El

Niño Southern Oscillation (ENSO) events. By contrast, no peaks occurred during warming events in the cold La Vieja regime in the late 1990s and 2000s when jellyfish biomass was very low or below detection; however, at the end of the study period, biomass rose slightly. The fishing pattern in the NHUS is just the opposite of those that previously have been attributed to removing small pelagic fish. We suggest that environmental factors and prey availability act synergistically to generate observed population size variability of this medusa in the NHUS.

Introduction

Jellyfish (medusae and ctenophores) abundance fluctuations have been recorded in different marine ecosystems worldwide (Purcell 2005, 2012; Condon et al. 2013), giving a general impression that jellyfish blooms are becoming larger and more frequent in the global ocean. Jellyfish population sizes typically show dramatic inter-annual variability, but whether jellyfish populations have increased worldwide is less clear (Condon et al. 2012; Purcell 2012). A recent global effort suggests that populations exhibit worldwide oscillations over decadal time scales with a slight, rising trend in abundance

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since the 1970s (Condon et al. 2013). Variability in jellyfish population size and bloom frequency has been attributed to environmental and anthropogenic factors such as climate change, overfishing, ocean sprawl, eutrophication, biological invasions and hypoxia, as well as synergistic interactions among them (Purcell et al. 2007; Duarte et al. 2012; Miller and Graham 2012; Purcell 2012; Bayha and Graham 2014; Decker et al. 2014; Uye 2014). Climate forcing can affect ecosystem structure promoting shifts in temperature, circulation, stratification, nutrient input and oxygen contents among others (Doney et al. 2012) and, when operating along ocean basins, have been correlated with jellyfish abundance in several northern Atlantic, Pacific and Mediterranean ecosystems (Goy et al. 1989; Cargo and King 1990; Lynam et al. 2005, 2010; Purcell 2005; Purcell and Decker 2005; Brodeur et al. 2008; Molinero et al. 2009; Kogovšek et al. 2010; Robinson and Graham 2013). Climate forcing has been shown to affect ctenophore growth and reproduction (Jaspers et al. 2011; Robinson and Graham 2014) and early life-cycle processes, such as strobilation in scyphozoan medusae (Purcell et al. 1999b; Purcell 2007), through their effects of local temperature, salinity and plankton production cycles (Stenseth and Mysterud 2002).

Fisheries harvests have also been proposed to drive variability of jellyfish abundance in heavily fished ecosystems (e.g., Bakun and Weeks 2006; Richardson et al. 2009). Overfishing can produce modifications of marine ecosystems by altering biodiversity and taxa abundance across multiple trophic levels (Cury et al. 2000; Reid et al. 2000; Worm et al. 2006), sometimes leading to a process known as “fishing down the marine food web” where fisheries sequentially exploit resources at ever-decreasing trophic levels (Pauly et al. 1998). Overfishing of small pelagic planktivorous fish has been hypothesized to enhance jellyfish production by releasing zooplanktivorous jellyfish from competition for shared prey resources (Parsons and Lalli 2002; Lynam et al. 2011; Robinson et al. 2014). In some heavily fished ecosystems, the massive removal of small pelagic fishes has been linked with major jellyfish outbreaks (Purcell et al. 1999a; Bakun and Weeks 2006; Daskalov et al. 2007; Roux et al. 2013). However, evidence supporting this hypothesis is not conclusive as the paucity of long-term (>20 year), quantitative jellyfish time series, particularly in the Southern Hemisphere, has hampered the ability to identify the roles climate, and harvesting of small pelagic fish plays in regulating jellyfish bloom frequency and size in some of the most intensely fished ecosystems in the world (Brotz et al. 2012; Condon et al. 2012).

One of these ecosystems is the northern Humboldt upwelling system (NHUS) off Peru. As one of the most productive ecosystems in the world ocean, it supports one of the largest single-species fisheries (Peruvian anchovy, *Engraulis ringens*) (Chavez et al. 1999, 2008; Pennington

et al. 2006), as well as populations of the large scyphomedusa *C. plocamia* (in Quiñones 2008; Quiñones et al. 2010). Biological productivity in NHUS varies on inter-annual and inter-decadal time scales, with fluctuations primarily driven by the El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) (Bakun 1998; Chavez et al. 2003, 2008). Fluctuations in *C. plocamia* abundance over time have recently been described by Mianzan et al. (2014) who suggests that peaks occur during ENSO events within the “El Viejo” warm regime. To test the hypothesis that climate forces and fisheries harvest drive variations in *C. plocamia* biomass in the NHUS, we examined the relationship between jellyfish biomass, two climate indexes, and commercial landings of the forage fish, *E. ringens*, over the past four decades.

Materials and methods

Jellyfish time series

A 43-year time series (1972–2014) of jellyfish biomass (kg) was constructed from bycatch data taken during purse seine ($N = 20$) and pelagic trawl ($N = 70$) surveys conducted by the Instituto del Mar del Perú (IMARPE). Surveys targeted the Peruvian anchovy (*Engraulis ringens*) and Pacific sardine (*Sardinops sagax*). No cruises were performed in 1989. In all other years, cruises were performed two or three times per year, mostly during austral spring and summer. The area surveyed was along the Peruvian coast, between the borders of Ecuador (03°23'S, 80°18'W) and Chile (18°21'S, 70°22'W) and up to 100 nautical miles offshore. Only cruises conducted between September and May were used to construct the jellyfish time series because the occurrence of jellyfish starts in the austral spring and medusae are observed through late autumn (Quiñones 2008).

Trawl and purse seine nets were towed through the upper 100 m of the water column. Both gear types were operated during day and night. *Chrysaora plocamia* are pelagic animals that occur in the near surface layers (Mianzan et al. 2014); therefore, data from pelagic nets (both trawling and purse seines) were considered to provide representative estimates of jellyfish abundance. A total of 12,091 hauls were analyzed (Fig. 1), resulting in an average effort of 295 hauls per year. The average bell diameter of *C. plocamia* individuals is 50 cm (Quiñones 2008); thus, they are large enough to be retained in trawl and purse seine nets with mesh sizes of 13 mm. Jellyfish catches were weighed on board and catches <1 kg were considered as zeros.

Jellyfish biomass was standardized to the volume filtered by the net ($\text{kg } 1000 \text{ m}^{-3}$). Volume filtered (m^3) was

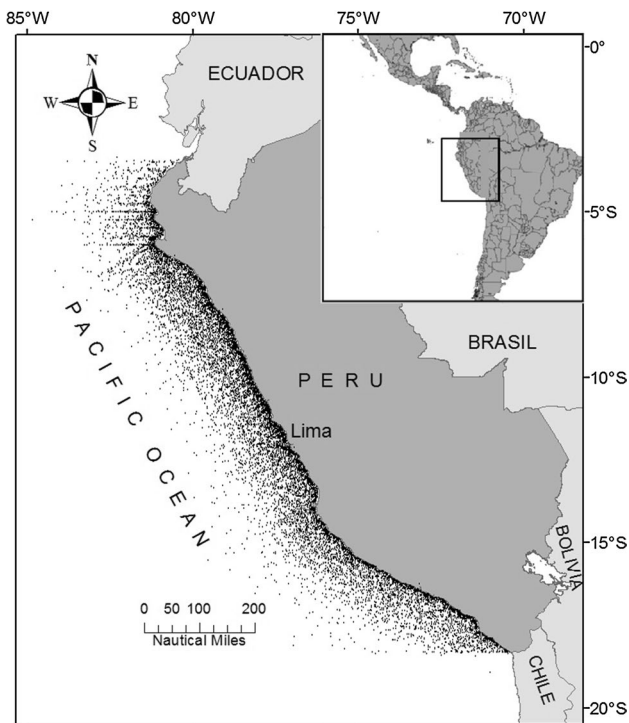


Fig. 1 Sampling effort of research cruises targeting pelagic resources, small black dots ($N = 12,091$), carried out from 1972 to 2013

estimated separately for pelagic trawl and purse seine nets. For pelagic trawl nets, the mean net open area (m^2), estimated by Eq. 1, was multiplied by the distance trawled (m). The width of pelagic trawl net openings ranged from 12 to 20 m, and the height of net openings ranged from 9 to 15 m. Distance trawled was estimated using the initial and final latitude and longitude coordinates of the trawl.

$$\begin{aligned} \text{net open area} (m^2) &= \left(\frac{\pi}{4} \times \text{net height} \right) \\ &\times \text{net width} \\ &= \left(\frac{\pi}{4} \times \text{net height} \right) \times \text{net width} \end{aligned} \quad (1)$$

For purse seine nets, volume filtered was estimated, assuming that the net was a cylinder (Eq. 2). The radius (r) of the net was derived from net perimeter (m) (Eq. 3). Purse seine net perimeters ranged from 520 to 700 m, and net heights ranged from 84 to 100 m.

$$\text{Volume filtered} (m^3) = (\pi \times r^2) \times \text{net height} \quad (2)$$

$$r = \left(\frac{\text{net perimeter}}{2} \right) \div \pi \quad (3)$$

Jellyfish were not identified to the species level during the 1970s and 1980s surveys. To quantify jellyfish biomass for these decades, ten scientists participating as research chiefs on those cruises were interviewed. Interviews included questions about species identity using photographs of the most common jellyfish bycatch taxa in the area and the animal sizes. Ninety percent of jellyfish identified were *C. plocamia*.

Climate forcing

The Oceanic Niño Index (ONI) is estimated on the basis of sea surface temperature (SST) anomalies in the El Niño 3.4 region (5° – 5° S, 170° – 140° W), and it is commonly employed to define El Niño and La Niña episodes (Smith et al. 2008). However, the ONI does not necessarily reflect local warming events (WEs) occurring in the Peruvian coast. We employed yearly estimations of the Peruvian Oscillation Index (POI) to describe environmental variability at inter-annual scales (Montecinos et al. 2003). The POI represents the coastal SST variations in Peru and is positively correlated with the ONI and the PDO and thus reflects conditions in the eastern tropical Pacific (Montecinos et al. 2003). Because jellyfish are present from September to May, we averaged POI values along a “jellyfish biological year.” For example, the year 2012 covers from September 2011 to May 2012. The phases of ENSO episodes were taken according to the ONI (onset = -0.5 , peak = 0 and offset = $+0.5$). An ENSO episode is different from a WEs because an ENSO episode originates in the Central Pacific, while a WEs event could originate in the East or West Pacific, and its effect is local. WEs cannot be detected in the Central Pacific, but they have important ecological consequences in the Peruvian coast (Zuta et al. 1976).

The Regime Indicator Series (RIS3) was employed to describe environmental variability at inter-decadal scales (Chavez et al. 2003; Kamykowski 2012). This series was constructed according to alternating fluctuations in sardine and anchovy populations over their ranges in Japan, California, Peru and South Africa. RIS3 data cover the period 1972–2009 (Kamykowski 2012).

Fishing pressure

Fishing intensity was estimated using annual landings (10^6 tons per year; $mt \text{ yr}^{-1}$; FAO 2013) and the annual number of fishing trips (IMARPE) made by the industrial anchovy fishery for the years 1972 to 2012. This fleet exerts the highest fishing effort in NHUS, and its activity overlaps in space and time with *C. plocamia* occurrence. Landings of other small pelagic species such as sardines, jack and chub

mackerels were not included since their distributions do not overlap with *C. plocamia* (Valdivia, pers. comm.).

Data Analysis

To explore the effects of POI, RIS3 and anchovy fisheries on jellyfish biomass, a generalized additive model (GAM; Hastie and Tibshirani 1986) approach was implemented. Data were included from 1972 to 2009, since time series data were all available in this time frame. GAMs robustly describe nonlinear correlations that may exist between fisheries and the environment (Brander 1994; Bigelow et al. 1999; Venables and Dichmont 2004) and have previously been used to model jellyfish abundance in relation to climate (Brodeur et al. 2008; Eriksen et al. 2012; Decker et al. 2013).

GAMs are relatively robust to the effects of autocorrelation (Segurado et al. 2006). However, to ensure the validity of model assumptions the presence of autocorrelation in the jellyfish time series was tested using a Durbin–Watson test. First-order temporal autocorrelation was not present ($DW = 1.767$, $p = 0.185$), and thus, we did not build models that account for autocorrelation.

The underlying probability distribution employed was selected using Akaike information criterion (AIC) following Burnham and Anderson (2002) and applied by Damalas et al. (2007). The probability distribution from the model with the highest Akaike weight was used. A constant of 1 was added to the response variable (Jellyfish Biomass) to allow transformation of the data for logarithmic models (Lo et al. 1992; Mitchell et al. 2014), and the “gamma” parameter of the GAM function was set at 1.4 following Wood (2006) to reduce overfitting. The full model examined thus takes the following form:

$$(\text{Jelly} - \text{Biomass} + 1) \sim s(\text{RIS3}) + s(\text{POI}) + s(\text{Anchovy Landings}) \quad (4)$$

We employed cubic regression splines with an added shrinkage component (Wood 2006; Decker et al. 2013; Photopoulou et al. 2014) to represent the possible nonlinear effects of the predictors because of their improved stability (Venables and Dichmont 2004). Smoothness parameters were estimated by generalized cross-validation (GCV), similar to previous work (Brodeur et al. 2008; Eriksen et al. 2012; Decker et al. 2013). Given the size of the data set, the number of smoother knots (k) was limited to 4 to avoid overfitting (Brodeur et al. 2008; Decker et al. 2013). Covariates were deemed statistically insignificant at p value > 0.05 .

The “mgcv” package in the free statistical software R (R Development Core Team, version 3.1.1, 2014, USA) was used for statistical analysis.

An additional comparative analysis between the strong ENSO events of 1982–1983 and 1997–1998 was carried

out to test the jellyfish response during strong ENSO events within a warm and a cold regime, respectively.

Results

The *C. plocamia* time series show two periods of high abundance (Fig. 2a). During the first period (1972–1989), jellyfish show several strong oscillations ranging from zero to mean annual values higher than $12 \text{ kg } 1000 \text{ m}^{-3}$. A dramatic decrease took place at the beginning of the second period (ca. 1989), and jellyfishes were extremely scarce or absent for the next 20 years, though a slight abundance recovery happened at the end of the series (2009–2014). This two-stage pattern matches inter-decadal warm–cold climate fluctuations known as El Viejo and La Vieja regimes (Fig. 2d), respectively. Both regimes are clearly seen within the RIS3, which show a positive El Viejo regime in the early to mid-1970s until early 1990s and then a negative La Vieja regime between 1990s and 2000s. The same two-stage pattern is shown in anchovy landings and fishing trips (Fig. 2b), with the lesser values during the warm El Viejo regime (1970s–1980s) characterized by positive values of the RIS3 and an increase in anchovy landings during the cold La Vieja regime (1990s–2000s) characterized by negative values of the RIS3.

Jellyfish biomass peaked during the strong ENSO events of 1982–1983 and 1986–1987 and warm event of 1976 during the El Viejo regime, with mean annual values of positive stations (i.e., not considering zeros) reached 5.7, 12.4 and $5.6 \text{ kg } 1000 \text{ m}^{-3}$, respectively. Five ENSO events can be detected in the POI series (Fig. 2c): two strong events in 1982–1983 (POI = +13.2) and 1997–1998 (POI = +10.8), and three moderate ones in 1972 (POI = +2.5), 1987 (POI = +3.4) and 1991–1993 (POI = +4.9). In addition, four WEs occurred in 1976 (POI = +2.0), 1979 (POI = +0.4), 1993 (POI = +1.1) and 2012 (POI = +0.1). Although the yearly POI value for 1976 (a year with high jellyfish abundance) was not extreme, anomalies during some months were very high (+2.6 June; +3.1 July; +3.3 August). No peaks in jellyfish biomass occurred during the ENSO events nor WEs throughout La Vieja regime (e.g., 1991–1992 or 1997–1998). At the end of the time series (2009–2014), a slight recovery of *C. plocamia* was noticed (Fig. 2a).

GAM modeling

We chose the gamma distribution with the inverse link function after comparing Akaike weights (w_i) and evidence ratios (ER) of all candidate models (Table 2). This distribution has previously been selected to model the reproductive biology of fisheries based on the reduction in the

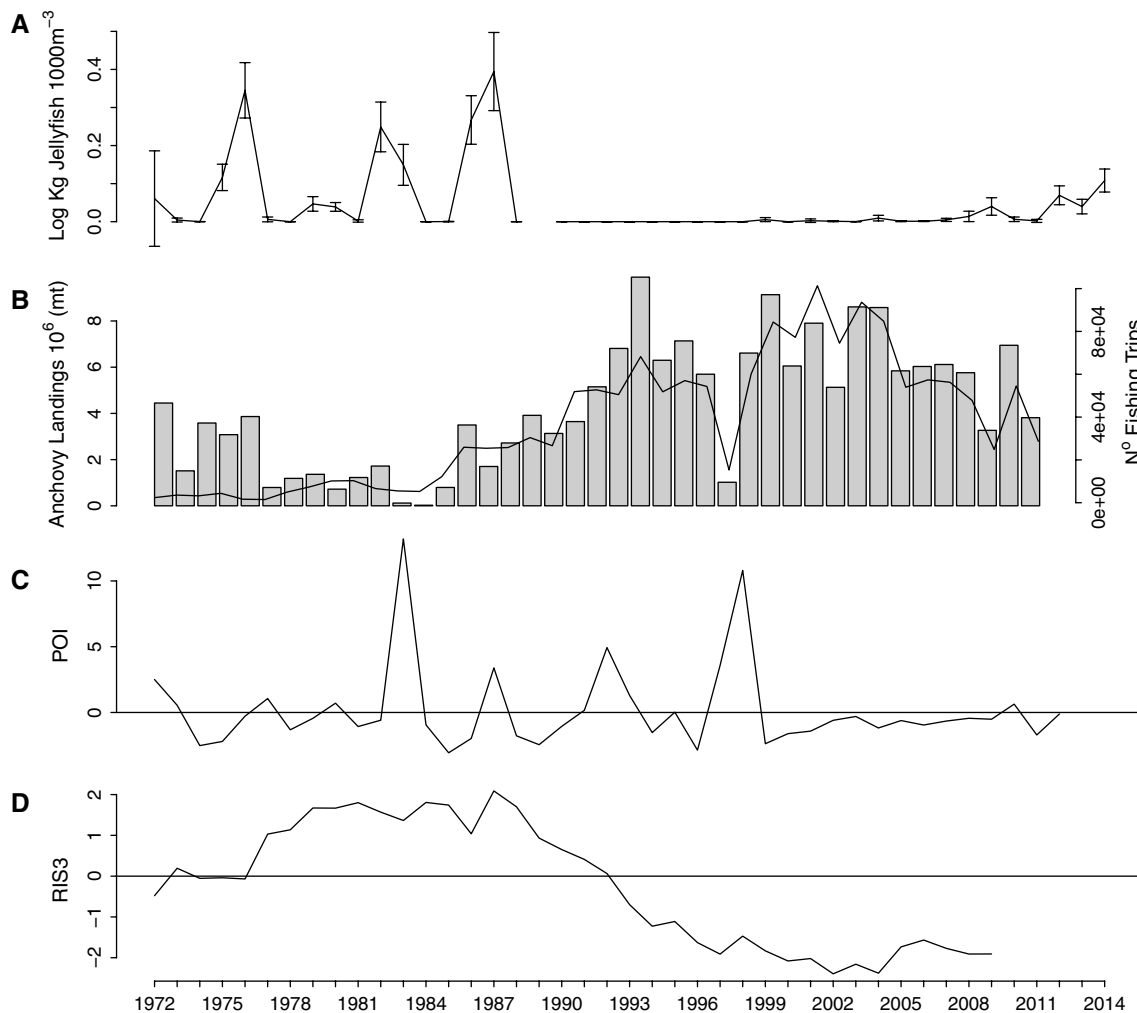


Fig. 2 Time series of jellyfish (*Chrysaora plocamia*) abundances for the period 1972–2013 expressed as kg jellyfish 1000 m⁻³; abundances were log-transformed (a); Anchovy (*Engraulis ringens*) land-

ings expressed in million tons, and number of fishing trips (1972–2011) (b); Peruvian Oscillation Index (POI) time series (1972–2012) (c) and Regime Indicator Series (RIS3) (1972–2009) (d)

generalized cross-validation value (GCV) (Flores et al. 2015). GAM modeling indicated anchovy fishery landings were not a significant predictor of jellyfish biomass (p value > 0.05) and were excluded from further analysis (Table 3). RIS3 and POI were both significant predictors of jellyfish biomass between 1972 and 2009 (p value < 0.05). Following diagnostics (Wood 2006; Figure S1), the model was a relatively good fit and no over or under-smoothing was detected using the “gam.check” function following the “mgcv” package literature (Pointin and Payne 2014).

GAMs were plotted and visually analyzed for trends (Fig. 3). To maintain identifiability in the model, smoothing functions were averaged to 0 (Wood and Augustin 2002). As the inverse link function interacts with the predictors (x_1, \dots, x_k) such that $g(\mu_i) = 1/\mu_i$, where $\mu(x)$ is the mean of the gamma distribution, GAM smoothing of explanatory variables indicates that jellyfish biomass increases as

RIS3 and POI increase and, in the case of POI, plateaus after the POI reach a value of 5. The RIS3 and POI indices are scaled such that positive (e.g., warm) and negative (e.g., cool) climate anomalies are above and below 0, respectively. Thus, jellyfish biomass increased during warming inter-decadal and inter-annual climate events (e.g., El Viejo and El Niño, respectively). These outcomes suggest that jellyfish biomass is positively correlated with the climatic variables included in the model.

Discussion

Jellyfish–climate relationships

A suite of environmental conditions (e.g., SST, salinity, currents and vertical mixing) and atmospheric variability

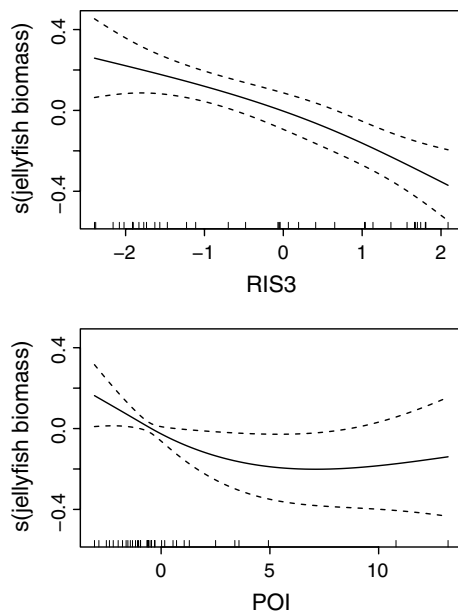


Fig. 3 GAM smooths of significant predictors of jellyfish (*Chrysaora plocamia*) biomass in Peru, 1972–2009, using the gamma distribution and the inverse link function. Dashed lines indicate 95 % confidence interval, and rug plot shows the density of data points included in the model

(e.g., wind patterns) may benefit jellyfish in certain circumstances (Purcell 2005; Purcell et al. 2007; Brodeur et al. 2008; Gibbons and Richardson 2009). These include *Cyanea capillata* and *Aurelia aurita* in the Barents Sea and in the northwest region of the North and the Irish Seas (Lynam et al. 2005, 2011; Eriksen et al. 2012). As seen here in the NHUS, scyphomedusae abundances in several ecosystems were greater during warmer years. However, it is not always true that jellyfish outbreaks occur during warm years. In the Northern California Current, *Chrysaora fuscescens* and *Aequorea* sp. abundances were positively correlated with cool boreal spring–summer conditions or negative anomalies of the Pacific Decadal Oscillation (Lenarz et al. 1995; Purcell 2012; Suchman et al. 2012). During the cold La Vieja regime, jellyfish abundance was very low or below detection despite the occurrence of two ENSO events (1991–1993 and 1997–1998; Fig. 2), showing that the biophysical conditions associated with ENSO events are not adequate to trigger jellyfish biomass increase. The distribution of *C. plocamia* (encompassing the Pacific and Atlantic coasts of southern South America) shows that this species prefers temperate rather than subtropical or tropical waters (Mianzan et al. 2014); consequently, other factors besides temperature should be involved in producing the population size fluctuations. The information regarding the effects of environmental variability on the asexual reproduction of jellies is scarce; recent work suggests that some jellies develops multiple cohorts throughout the medusa season,

suggesting the continuous production of ephyrae from polyps (Ceh et al. 2015). Favorable environmental conditions can lead to increased strobilation in many jellyfish species (Purcell 2007; Boero et al. 2008; Purcell et al. 2009; Holst 2012), leading to greater abundances of medusae. Favorable conditions driven by inter-decadal and inter-annual climate regimes most likely trigger increased production of medusae, and thus, greater biomass of *C. plocamia* was observed earlier in our time series.

At broader or decadal stages in the southeast Pacific Ocean, climate and productivity of coastal and open ocean ecosystems have varied over periods of about 50 years. In the mid-1970s, the Pacific changed from a cool “anchovy regime” (El Viejo) to a warm “sardine regime” (La Vieja). A return back to an “anchovy regime” occurred in the middle to late 1990s. The NHUS is the region where ENSO, and climate variability in general, is most notable (Chavez et al. 2003, 2008). Natural environmental rhythms affect several biological components of this ecosystem such as phytoplankton, zooplankton and small pelagic fish (Alheit and Niquen 2004; Ayón et al. 2008). High jellyfish abundances occurred within the El Viejo regime (warm and “sardine dominated”) since 1975 until early to mid-1990s, and the low abundances or absence of jellyfish during the La Vieja regime (cool and “anchovy dominated”) that began in the early 1990s. However, the temporal pattern of jellyfishes shows also higher frequency fluctuations during the El Viejo regime. At the end of the time series, jellyfish slightly recovers, together with the return back of sardine in artisanal fisheries of Peru.

Jellyfish populations are typically regulated by bottom-up processes (West et al. 2009; Purcell 2012) since predation on jellyfish tends to be opportunistic rather than obligatory (Purcell and Arai 2001; Arai 2005). Time series of *C. plocamia* abundances show that they peaked only during ENSO or warm events that occurred throughout El Viejo regime. A comparison between strong ENSO events occurring within El Viejo (ENSO 1982–83) and La Vieja (ENSO 1997–98) illustrates that both had a similar physical input (McPhaden et al. 2011) including oxygen minimum zone (OMZ), depth (Gutierrez et al. 2011) and phytoplankton composition (Ochoa et al. 1985; Sánchez et al. 2000). However, the zooplankton assemblage was dominated by different groups (Table 1). During the 1982–1983 ENSO event, small gelatinous zooplankton such as doliolids, siphonophores, hydromedusae and larvaceans dominate (Santander and Carrasco 1985; Carrasco and Santander 1987). In contrast, during 1997–1998 ENSO event, the zooplankton assemblage was dominated by copepods; small gelatinous zooplankton were present but only at reduced densities (Bonicelli 2008). It is known that other species of the genus *Chrysaora* may prefer gelatinous prey (Purcell 1991), *C. quindecirrha* in the Chesapeake Bay is a large consumer

of the ctenophore *Mnemiopsis leidyi* (Purcell and Decker 2005). *C. fuscescens* in the north Pacific (Suchman et al. 2008) and *C. melanaster* in the Bering Sea (Brodeur et al. 2002) consume euphausiid eggs and gelatinous zooplankton, respectively. In the NHUS, the contrast in prey fields could be the reason, at least in part, for differences in jellyfish abundances between El Viejo and La Vieja regimes (Tables 2, 3).

Since *C. plocamia* has a metagenetic life cycle (i.e., with benthic polyps), conditions at the sea floor need to be examined. During the 1982–1983 ENSO event, densities of benthic organisms were six times greater than during the 1997–1998 ENSO event (Tarazona et al. 1985). Favorable conditions for the benthos could have enhanced polyp abundance and ephyra production, overwhelming the effects of increased competition for space and food; indeed, there is existing evidence from other *Chrysaora* species showing increased asexual reproduction in warm waters (Purcell et al. 1999b; Holst 2012).

The abundance variability of jellyfish with a metagenetic life cycle cannot be fully understood if the scyphistomae ecology is not taken into consideration (Prieto et al. 2010; Lucas et al. 2012). However, the finding and study of scyphistomae in their natural environment are extremely difficult (Lucas et al. 2012). Similarly, little information is available for *C. plocamia* (Mianzan et al. 2014), and their polyps are only known from laboratory experiments (Riascos et al. 2013). Nevertheless, it is possible that at least part of the observed variability is related to the ecology of the benthic stage, especially considering the strong impact of the regime shifts on the benthos of the NHUS.

Fishing

Fishing pressure seems not to have the same consequences for NHUS jellyfish as those in other, heavily fished ecosystems (Fig. 2), as evidenced by GAM modeling. NHUS industrial fishery landings and annual trips were increased by a factor of three in the last two decades (1990s and 2000s), a period of almost total absence of jellyfish. Conversely, the period of the highest jellyfish abundance in the 1970s and 1980s was characterized by relatively low fishing pressure. These findings contrast links made between jellyfish proliferation and an increase in fishing pressure in other regions. Large-scale perturbations in the food web caused by fishing are suggested to increase jellyfish population growth through the reduction in competitors and top predators (Richardson et al. 2009). In the Benguela Current, it was suggested that jellyfish overtook small pelagic fish as a consequence of overfishing (Lynam et al. 2006; Roux et al. 2013). Dominant pelagic fishes like the sardine (*Sardinops sagax*) were replaced by the bearded goby (*Sufflogobius bibarbus*) and jellyfish (*Chrysaora*

Table 1 A comparison of oceanographic conditions during two strong, eastern Pacific El Niño Southern Oscillation (ENSO) events within El Viejo and La Vieja regimes that deeply impacted the Peruvian coast McPhaden et al. (2011)

	El Niño during El Viejo 1982–1983 (warm event during warm period)	El Niño during La Vieja 1997–1998 (warm event during cold period)	References
Oxygen minimum zone	The upper border of the OMZ deepened until 300 m	The upper border of the OMZ deepened until 300 m	Gutierrez et al. (2011)
Phytoplankton	Dominant diatoms were severely reduced and then replaced by tropical dinoflagellates at the beginning of the event	At the beginning of the ENSO, the dominant diatoms were reduced and then replaced by tropical dinoflagellates	Ochoa et al. (1985); Sánchez (2000)
Zooplankton	Decrease in copepod abundance (17 %) compared to neutral years Increases in giant chaetognaths, appendicularians, hydromedusae, doliolids and siphonophores Zooplankton biovolumes were dominated by micro-gelatinous organisms	Copepod-dominated assemblage (79 %) Gelatinous zooplankton were minor contributors to the assemblage: appendicularians (6 %) and chaetognaths (2 %)	Santander and Carrasco (1985); Carrasco and Santander (1987); Bonicelli (2008)
Benthos	Strong increase in species diversity and biomass in regions that previously were anoxic and without macrofauna Extension of the vertical distribution of several macroinfaunal species	Macrobenthos densities were up to six times smaller than those during the 1982–1983 event	Tarazona et al. (1985, 2001)

Table 2 Akaike information criteria (AIC) results, Akaike weights and evidence ratios (ER) for probability distributions of GAMs for predictors of jellyfish biomass in Peru, 1972–2009. Only full mod-

els were compared for consistency. Evidence ratios were calculated in comparison with the model with the highest Akaike weight

Error distribution	Link function	AIC	Delta (Δ_i)	Akaike weights (w_i)	ER
Gaussian	Identity	159.914	85.505	2.68E ¹⁹	3.69E ¹⁸
Gaussian	Log	119.519	45.101	1.58E ¹⁰	6.24E ⁹
Gamma	Inverse	74.409	0	0.988	1
Gamma	Log	83.315	8.905	0.0151	85.860

Table 3 GAM results of environmental and ecological predictors relating to jellyfish biomass in Peru, 1972–2009, using the gamma distribution and the inverse link function

Predictor	Estimated degrees of freedom	F	p value
RIS3	1.145	5.289	0.017
POI	1.135	7.944	0.004
Anchovy landings	2.578	2.626	0.070

fulgida and *Aequorea forskalea*) (Flynn et al. 2012). The increase in the jellyfish *Aurelia aurita*, *Cyanea nozakii* and *Nemopilema nomurai* in Chinese coastal waters has been attributed to overfishing, among other factors (Dong et al. 2010). Outbreaks of *Aurelia aurita* and *Cyanea capillata* in the North Sea occurred following the decline of herring stocks (Lynam et al. 2005). Trophic cascades and jellyfish outbreaks in the Black Sea have been reported as a consequence of overfishing (Daskalov and Mamedov 2007). Thus, while increases in jellyfish abundance may result from overfishing in some ecosystems (Bakun and Weeks 2006; Lynam et al. 2006; Richardson et al. 2009; Utne-Palm et al. 2010; Jensen et al. 2012), it does not appear to be the case in the NHUS, where consistent with previous research; the importance of climatic and oceanographic variation on jellyfish abundance is demonstrated in the Irish Sea (Lynam et al. 2011), Bering Sea (Decker et al. 2013) and Hawaii (Chiaverano et al. 2013), and our results suggest that climate regime, rather than fishing, driven shifts in food web structure may be a greater driver of jellyfish abundance in the NHUS.

Prey availability

Environmentally driven changes in the in the NHUS pelagic food web have been hypothesized to underlie the observed shifts in regime indicator species such as sardines and anchovies (Ayón et al. 2011). During warm episodes or regimes (e.g., ENSO and El Viejo), dinoflagellates, heterotrophic flagellates and small zooplankton dominate (Ochoa et al. 2010; Ayón et al. 2011) as a consequence of reduced nutrient inputs to the ecosystem (Bertrand et al. 2004).

Conversely, the high productivity of ENSO neutral years or the cold regime promotes the dominance of large phytoplankton like diatoms and zooplankton such as euphausiids (Ochoa et al. 2010; Ayón et al. 2011). Information on gelatinous taxa in the NHUS is scarce during either regime. One study indicates that small gelatinous taxa (i.e., siphonophores, tunicates and ctenophores), which would be presumably prey for *C. plocamia*, were present in the NHUS during the La Vieja ENSO event of 1997 (Pagés et al. 2001). Currently, there are no diet studies of *C. plocamia* during an ENSO year within a warm El Viejo regime; however, during those periods pelagic gelatinous organisms and benthic macro benthos were both abundant (Table 1) and could act synergistically to trigger the jellyfish blooms due to the increase in prey availability for polyps and medusa.

Drivers responsible for jellyfish population peaks probably involve increased productivity at time scales relevant to their annual production cycles (Condon et al. 2013). Numerous jellyfish aggregations are possible a consequence of prey availability (Purcell 2003); indeed, jellyfish prey on a broad range of zooplankton, including copepods, other gelatinous taxa, meroplankton and fish eggs (Suchman et al. 2008). A recent study shows that the eggs of the Peruvian anchovy (*E. ringens*) and copepods constituted nearly 90 % of the diet of *C. plocamia* in northern Chile (Riascos et al. 2014); however, this study was performed in a cold period within a La Vieja regime (November 2010–March 2011). Consequently, these results are not representative of *C. plocamia* diet during peak abundance in warm El Viejo regimes.

Because fishing effects are different in the NHUS than other ecosystems, where reduction in piscivorous fish by overfishing results in a jellyfish increase (Parsons and Lalli 2002; Purcell 2012), in the NHUS other factors could probably play a role, trophic interactions between scyphomedusae and small jellies could probably explain better this situation. Trophic cascades throughout the plankton food web have been exemplified in Chesapeake Bay where *Chrysaora quinquecirrha* reduces ctenophores and results in more zooplankton (Purcell and Decker 2005); unfortunately, no time series of small jellies are available in the NHUS, despite the fact that we have seen several small

jellies species in the gut content analysis of *C. plocamia* (Quiñones unpublished data); the sample size was really small and was performed only in a short period of time, and consequently, this trophic interactions remains unknown in the area; however, we cannot discard the potential importance of the trophic interactions in the jellyfish variability in the NHUS.

Conclusion

The population fluctuations of *C. plocamia* in the NHUS were related to ENSO and warm events that occurred during El Viejo warm regime, but not to commercial landings of anchovy. Water temperature *per se* does not seem enough to explain fluctuations because during strong ENSO events within the La Vieja regime, jellyfish were scarce or absent. Moreover, judging from its geographical distribution, *C. plocamia* seems to prefer temperate rather than warmer, subtropical or tropical waters. The NHUS is one of the ecosystems most heavily fished in the world, with pelagic fisheries targeting forage fishes. Despite fishing intensity, low *C. plocamia* biomass when fishing effort was high allows us to reject the hypothesis that harvests of planktivorous fishes in the NHUS enhance *C. plocamia* abundance. We propose an alternative hypothesis where climate-driven environmental factors and food availability act synergistically to produce the observed variability in jellyfish population size in the NHUS. Peaks in large jellyfish abundance during the El Viejo regime could be explained by the dominance of small gelatinous plankton (supposedly their preferred food), favorable conditions for their benthic polyps and a more prolonged period of warm water temperatures during ENSO events, giving more time for planula settlement and polyp growth and development. Finally, the rising trend of jellyfish abundance at the end of the series (2009–2014) could be indicative of a coming regime shift to El Viejo warm regime.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human participants and animals consent No human experimentation was involved in this research. The animals (jellyfish) used in this study were at low taxonomical resolution and were captured as bycatch in the pelagic scientific research cruises.

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