Spatial patterns of large jellyfish *Chrysaora plocamia* blooms in the Northern Humboldt Upwelling System in relation to biological drivers and climate

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In the Northern Humboldt Upwelling System (NHUS), one of the most productive ecosystems in the world, the large jellyfish *Chrysaora plocamia* exhibits high inter-annual variability in population size, often resulting in massive blooms. In this study, we examined the geographic patterns *C. plocamia* in the NHUS and their spatial overlap with ichthyoplankton, zooplankton, and chlorophyll *a* concentration (Chl *a*) during two El Niño (EN) years (1982–1983 and 1986–1987), and a neutral year (2014). During EN years, the spatial extent of *C. plocamia* medusae was larger than in the neutral year. In 1982–1983, medusae were concentrated mainly in the central-southern and southern regions of Peru, where they were associated with zooplankton, sardine larvae, and Chl *a*. In 1986–1987, medusae occurred in the northern and southern regions and spatially overlapped with sardine larvae and Chl *a*, and with zooplankton and anchoveta larvae, respectively. In 2014, medusae occurred mainly in the northern region, where they were associated with zooplankton, Chl *a*, and anchoveta eggs and larvae. Our results indicate strong EN effects on the distribution and abundance of *C. plocamia*, which can have consequences for zooplankton and ichthyoplankton abundance, as well as fisheries, in the NHUS.

Keywords: *Chrysaora plocamia*, El Niño, ichthyoplankton, Perú, scyphomedusae, spatial patterns, zooplankton

Introduction

Jellyfish (medusae, ctenophores, and siphonophores) are important components of coastal and oceanic marine ecosystems worldwide (Lucas *et al.*, 2014). Large medusae in particular, have

received special attention due to the capacity of a few species to suddenly increase in population size, often resulting in mass occurrences or blooms in marine ecosystems worldwide (Purcell, 2012; Condon *et al.*, 2013). Recent studies have linked mass

occurrences of jellyfish with climatic fluctuations (Purcell, 2005), overfishing (Lynam *et al.*, 2006), pollution, habitat modification, and the translocation of species (Richardson *et al.*, 2009; Purcell, 2012; Duarte *et al.*, 2013). However, the mechanisms behind the formation of these mass occurrences remain poorly understood (Duarte *et al.*, 2013; Gibbons and Richardson, 2013), perhaps due to the scarcity of long-term datasets of jellyfish (Purcell, 2012). Previous long-term studies indicate that jellyfish abundance often co-varies with climate variability at inter-annual and -decadal scales (e.g. Goy, 1989; Lynam *et al.*, 2005a; Purcell, 2005; Brodeur *et al.*, 2008a; Chiaverano *et al.*, 2013; Quiñones *et al.*, 2015). However, our understanding of the environmental processes that influence jellyfish distribution is limited (see Brodeur *et al.*, 2008a, 2014). The potential long term, climate-driven direct and indirect effects on the spatial distribution of jellyfish is almost unknown in most marine ecosystems (see Brodeur *et al.*, 2008a).

Climate-driven distributional shifts of marine taxa can affect species interactions (Kordas *et al.*, 2011). Numerous studies have shown that jellyfish have the potential to consume large amounts of planktonic prey, including fish eggs and larvae (Purcell, 2003; Meredith *et al.*, 2016; Zeman *et al.*, 2016). Hence, efforts have been made towards understanding how environmental (biotic and abiotic) variation is related to the distribution of jellyfish and their overlap with the early life stages of commercially exploited fishes (Purcell, 2003). Spatial overlap between large jellyfish and adult and larval commercially targeted fishes has been reported in several ecosystems, including the Northern California Current (Brodeur *et al.*, 2008a,b, 2014) and in the Barents Sea (Eriksen, 2015). Large jellyfish have also been reported to overlap spatially with sardine and anchovy spawning areas within the North Sea (Lynam *et al.*, 2005b), the Northern Benguela Current System (Flynn *et al.*, 2012), and the North Western Mediterranean Sea (Tilves *et al.*, 2016), suggesting that jellyfish aggregations feed on sardine and anchovy larvae. In addition, other biological factors were correlated with the spatial distribution of scyphozoan jellyfish, including other gelatinous zooplankton taxa (Brodeur *et al.*, 2002; Purcell and Decker, 2005; Costello *et al.*, 2012), Chl *a*, and primary productivity (Schroeder *et al.*, 2014).

The Northern Humboldt Upwelling System (NHUS) is one of the most productive marine ecosystems, supporting the largest single-species fishery in the world (by weight) based on the Peruvian anchoveta (*Engraulis ringens*) (Pennington *et al.*, 2006). Ecosystem function in the NHUS is periodically altered by inter-annual (ENSO cycle) and inter-decadal climate regimes, producing changes from a cool "anchoveta regime" (La Vieja) to a warm "sardine regime" (El Viejo) (Chavez *et al.*, 2003). Such climate variability has also been linked to blooms of the large jellyfish *Chrysaora plocamia* (Quiñones *et al.*, 2015), where biomass has increased during El Niño (EN) years within both a warm "sardine regime" in the 1970 s and 1980 s and a cool "anchoveta regime" in the late 2010s (Quiñones *et al.*, 2015). When abundant, *C. plocamia* become regular by-catch of industrial purse-seine fisheries, which negatively affects the local fishing industry by producing economic losses because processors refuse catches with high jellyfish by-catch (Quiñones *et al.*, 2013).

Although the relationship between environmental factors and temporal variability of *C. plocamia* populations has been established (Quiñones *et al.*, 2015), where *C. plocamia* biomass fluctuated with climate drivers at inter-annual and inter-decadal scales, but not with anchovy landings (a proxy of fishing pressure). The potential direct and indirect effects of environmental (biotic and abiotic) variation on the spatial patterns of *C. plocamia* medusae remain unknown. Such information is particularly needed for the NHUS because of the potential impact of jellyfish blooms on the early stages of commercially exploited fish. In this study, we analysed data from three massive bloom years identified from 45 years of pelagic survey data off Peru to establish the distributional patterns of *C. plocamia* medusae, ichthyoplankton, zooplankton, and chlorophyll *a* concentration (Chl *a*) during 2 EN years (1982–1983 and 1986–1987) and a neutral year (2014), To evaluate the potential effect of biotic environmental and climate variability on the distribution of large jellyfish in this highly productive and commercially important system. In the neutral year 2014, abundance of *C. plocamia* medusae was higher than other neutral years; however, the extent of spatial distribution remained unchanged (Quiñones, pers. obs.)

Methods
Study area and data

The area of study extended across Peruvian waters from 03°23'S to 18°21'S and 200–280 km km offshore (to a depth about 100 m), covering ∼500 000 km^2 (Figure 1). The study area was divided into four regions: Northern (04°S–09°S), Central-Northern (09°S–12°S), Central-Southern (12°S–15°S), and Southern (15°S–18°S) (Figure 1). Three periods of *C. plocamia* blooms were selected for analysis: 1982–1983 (extraordinary EN year), 1986–1987 (strong EN year), and 2014 (neutral year) (Figure 1). In each of these periods, *C. plocamia* abundance was at least 400% higher than the mean abundance of a 45-year data series (see Quiñones *et al.*, 2015).

All data used in this study were collected from fishery-independent surveys conducted by the Instituto del Mar del Peru (IMARPE) at the same locations in space and time (Figure 1) during spring and summer of each selected period. Parallel survey transects were performed every 20–30 km perpendicular to the coast. Medusae of *C. plocamia* (log kg wet weight—WW 1000 m^{-3}) were sampled using trawl and purse seine nets that were towed within the upper 100 m of the water column. Both gear types were operated during day and night. Jellyfish biomass (kg—WW) was standardized by the volume filtered (m^3), which was calculated separately for each sampling gear. The mean net open area (m^2) and volume filtered (m^3) was estimated using the net height and width for the trawl nets, and the net height and perimeter for the purse seiners (see Quiñones *et al.*, 2015 for specific details and formulations). Biomass of *C. plocamia* medusae was averaged within digitized sample grid cells used by IMARPE to assess the Peruvian anchoveta fishery, this grid cells were being used since the 1970s and are 18 × 55 km (Gutiérrez and Peraltilla 1999). Each grid cell was categorized into the following upper bounds of abundance: 0, 0.01, 0.1, 1.0, 10, and 100. Chl *a* (μg l^{-1}) was obtained from water samples collected at fixed oceanographic stations every 9–18 km using Holm-Hansen *et al.* (1965). Zooplankton was collected by performing vertical tows (50 m in depth to the surface) using a Hensen net with a 0.33 m^2 mouth area and 300 μm mesh size. Each research cruise lasted between 40 and 50 days; sampling stations were located every 7 km within the first 55 km from the coast and every 9 km from 55 to 280 km offshore. Zooplankton samples were fixed with 2% formaldehyde and zooplankton biovolume (ml per sample) was determined at the time of collection using the displacement method (Kramer *et al.*, 1972). Abundance of eggs and larvae of Peruvian anchoveta
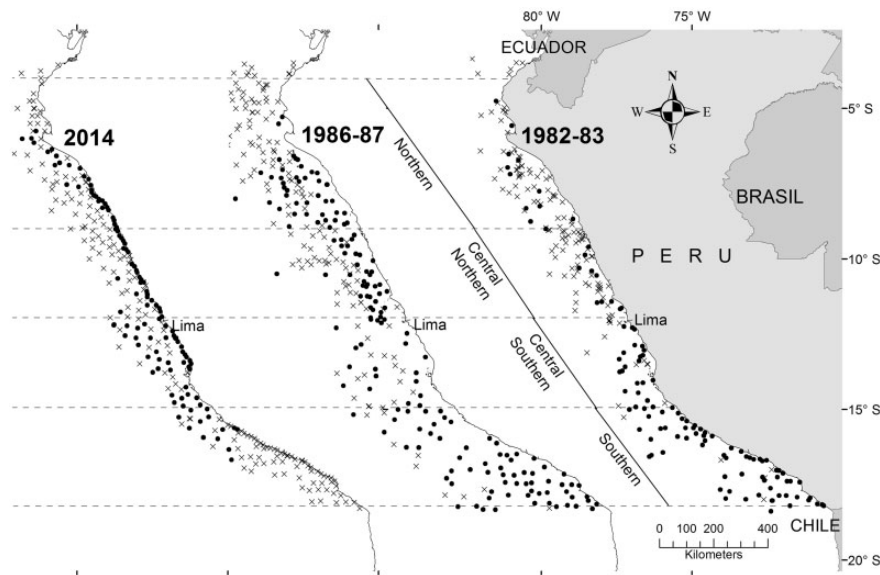
Figure 1. Study area of the three selected periods with large jellyfish (*C. plocamia*) blooms in the NHUS. From left to right EN year 1982–1983, EN year 1986–1987, and the neutral year 2014. Presence and absence of C. plocamia medusae in hauls are represented by the solid dots and crosses, respectively.

and sardine (*Sardinops sagax sagax*) were obtained by counting eggs and larvae per sampling station and standardizing values to obtain number of eggs and larvae per m^2 (see Santander, 1987).

Data analysis

All biological explanatory variables were log-transformed and outliers were replaced by the maximum value of the remaining range because kriging estimators are sensitive to the presence of a few unusually large or small values (Armstrong and Boufassa, 1988). Biological variables were then interpolated for each year using ordinary kriging to increase spatial resolution (Lloyd, 2006). Ordinary kriging is a flexible interpolation method that can accommodate changes in the mean value of the surface conducted in ArcGIS 10.1 (ESRI, 2011). However, for the 1982–1983 period, sardine eggs, anchoveta larvae, and anchoveta eggs were excluded from further analyses because values and spatial coverage were low, while in 1986–1987 sardine eggs and anchoveta eggs were excluded for the same reasons. Similarly, sardine egg and larval abundance were not included in further analyses for 2014 because sardine biomass has been severely reduced in Peru since 2000 (FAO FishStats, 2011).

Spatial distributional patterns of *C. plocamia* medusae were examined by using the Getis-Ord Hot Spot analysis (ESRI, 2011), which calculates a GiZScore statistic for gridded and categorized abundance. The resultant z-scores and *p*-values refer to the level of clustering, with low values indicating locations where abundance is relatively low (cold spots) and high values indicating locations where abundance is relatively high (hot spots) (Scott and Warmerdam, 2005). A grid cell hot/cold spot was considered when the *SD* was ≥ 1.96 of the GiZScore. Spatial relationships were modelled using the "Polygon Contiguity Edges Technique" because grid cells were similar in size and shape (ESRI, 2011). This analysis was performed separately for each of the selected years. Hot Spot size categories were defined as: small (>5000 km^2), medium (15 000–30 000 km^2), large (15 000–30 000 km^2), and very large ($>30 000$ km^2).

To identify biological variables that best explain variation in the distribution of *C. plocamia* abundance across time periods, we fit a series of geographically weighted regressions (GWRs) in ArcGIS 10.1 (ESRI, 2011). GWR provides a method to analyse spatial data by incorporating spatial autocorrelation and non-stationarity in regression coefficients. GWR calculates regression coefficients for each location by incorporating information from the dependent and explanatory variables of features falling within a defined distance of each location and is expressed in the following formula:

$$Y_i = \beta_{0,i} + \sum_{k=1}^{p} \beta_{k,i} X_{k,i} + \epsilon$$

where Y_i is the response (jellyfish abundance log kg 1000 m^{-3}) at location i, $\beta_{0,i}$ is the intercept parameter at location i, $\beta_{k,i}$ are the location specific regression coefficients of explanatory variable $X_{k,i}$ (i.e. Chl *a*, zooplankton volume, abundance of sardine larvae and anchoveta eggs and larvae) at location i, and ϵ is the residual error. The distance from each location was selected via Aikake Information Criterion for small sample sizes (AICc), which tries to identify the optimal fixed distance or optimal adaptive number of neighbours. The kernel technique, a tool that calculates the density of features in a neighbourhood around those features, was set as adaptive in order the make the distance bandwidth change according to the spatial density of the jellyfish. Separate GWRs were fit for each biological variable and the biological variables that best explained variation in *C. plocamia* abundance were selected by comparing adjusted R^2 and AICc values. The biological variables that best explain variation in jellyfish abundance were then visualized in a spatial overlap map.

The degree of spatial overlap of *C. plocamia* with biological variables was estimated using the geostatistical methods described in Brodeur *et al.* (2008a, 2014). A Moran's I test was performed for spatial autocorrelation where the inverse euclidean distance method and a distance threshold of 40 km were employed. Data were determined to be significantly autocorrelated at *p*-values

≤ 0.05. Continuous coverage layers (point data) of *C. plocamia* medusa abundance and the selected biological variables were produced using the Geostatistical Analyst technique in ArcMap 10.1 (ESRI, 2011). Given our geographical distance in sample stations, coverage maps are not intended to represent small scale processes but rather to elucidate broad-scale patterns in the spatial distribution of *C. plocamia* and the tested biological variables (Brodeur *et al.* 2008a). Predicted values were grouped into 3 classes to illustrate areas where *C. plocamia* and each biological variable were absent (abundance = 0), present (biomass > 0), and highly abundant (abundance ≥ 75th percentile) for the 1982–1982, 1986–1987, and 2014 time periods. Then polygon maps were produced to estimate where *C. plocamia* and each selected variable overlapped at any level (both values > 0) and where they had the highest overlap (presence and > 75th percentile). The area within each polygon feature was then expressed in square kilometers (km^2) by means of the "calculate geometry technique" in ArcMap 10.1 and the percent overlap area was calculated by dividing the area of the polygon feature where distributions of jellyfish (present or highly abundant) and each explanatory variable (present or highly abundant) overlapped by the total area surveyed (km^2) × 100 (Brodeur *et al.*, 2014). In addition, a latitudinal spatial overlap analysis was performed between *C. plocamia* and each biological variable per each year tested, considering the four regions of the study area.

Results

Distribution of *C. plocamia* medusae

During the 1982–1983 period, the bulk (>70%) of *C. plocamia* medusae were distributed within 75 km from the coast, with individuals occurring up to 185 km offshore in lower abundances (Figure 2). Mean abundance per grid cell was 3.5 (SD: 1.5) kg 1000 m^{-3} in 1982–1983, ranging from 1.7 to 7.8 (n = 467). During the 1986–1987 period, medusae were distributed further offshore, reaching up to 280 km from the coast. Approximately 50% of medusae were distributed within 75 km, with 32% and 12% of medusae in waters between 75 to 185 and 185 to 280 km, respectively (Figures 2 and 3a). In 1986–1987, mean abundance

per grid cell was 4.4 (SD: 4) kg 1000 m^{-3}, ranging from 1 to 43.2 (n = 835). In 2014, the distribution of medusae was relatively constrained to the coast, with the majority (∼68%) distributed within 35 km, 23% was recorded between 75 and 110 km, and ∼9% were recorded between 110 and 185 km offshore (Figures 2 and 3a). In 2014, mean abundance per grid cell was 1.8 (SD: 0.8) kg/1000 m^3, ranging from 1 to 7.6 (n = 366).

During the 1982–1983 period, 6% of the *C. plocamia* medusae were distributed in the Northern region of the study area, 28% in the Central-Northern region, ∼21% in the Central-Southern region, and 44% in the Southern region (Figure 3b). In 1986–1987, 6% of the medusae were registered in the Northern region, ∼31% in the Central-Northern region, ∼19% in the Central-Southern region, and 44% in the Southern region (Figure 3b). In 2014, ∼10% of the medusae were distributed in the Northern region, ∼41% in the Central-Northern region, 38% in the Central-Southern and ∼11% in the Southern region (Figure 3b). In both 1982–1983 and 1986–1987 periods, *C. plocamia* abundance was greatest in the Southern region, while in 2014 the peak of abundance was recorded in the Central-Northern region (Figure 3b). Spatial coverage maps of *C. plocamia* medusae and biological variables are presented in the Supplementary Figures S1–S3.

Three hot spots *C. plocamia* were identified in the NHUS during 1982–1983 (Figure 4). The largest hot spot (18 414 km^2) was located in the northern/central-northern of the study area at 08°–10°S within 90 km from the coast. A medium size hot spot (10 938 km^2) was located off the southern coast between 15° and 16°S within 75 km from the coast and a small hot spot (2981 km^2) was located off the central coast of Peru at 12°S within 35 km of the coast (Figure 4). In 1986–1987, two hot spots were identified, a very large hot spot (32 542 km^2) located along the southern coast between 16° and 18°S and up to 55–75 km from the coast and a medium size hot spot (11 601 km^2) located along the northern coast (07°–08°S) within 55 km from the coast (Figure 4). In 2014, only a medium hot spot of *C. plocamia* (12 260 km^2) was identified along the northern coast between 08° and 09°S within 35 km from the coast (Figure 4). In 2014,
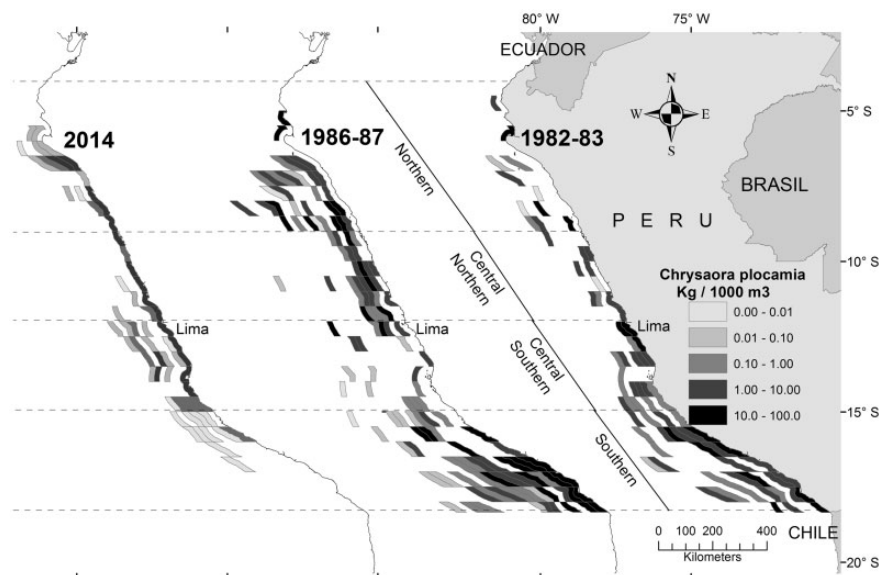
Figure 2. Grid-cells distribution of *C. plocamia* medusae in the NHUS (off Peru) during warm EN years (1982–1983 and 1986–1987) and a neutral year (2014). Abundance is expressed in log kg jellyfish 1000 m^{-3}.
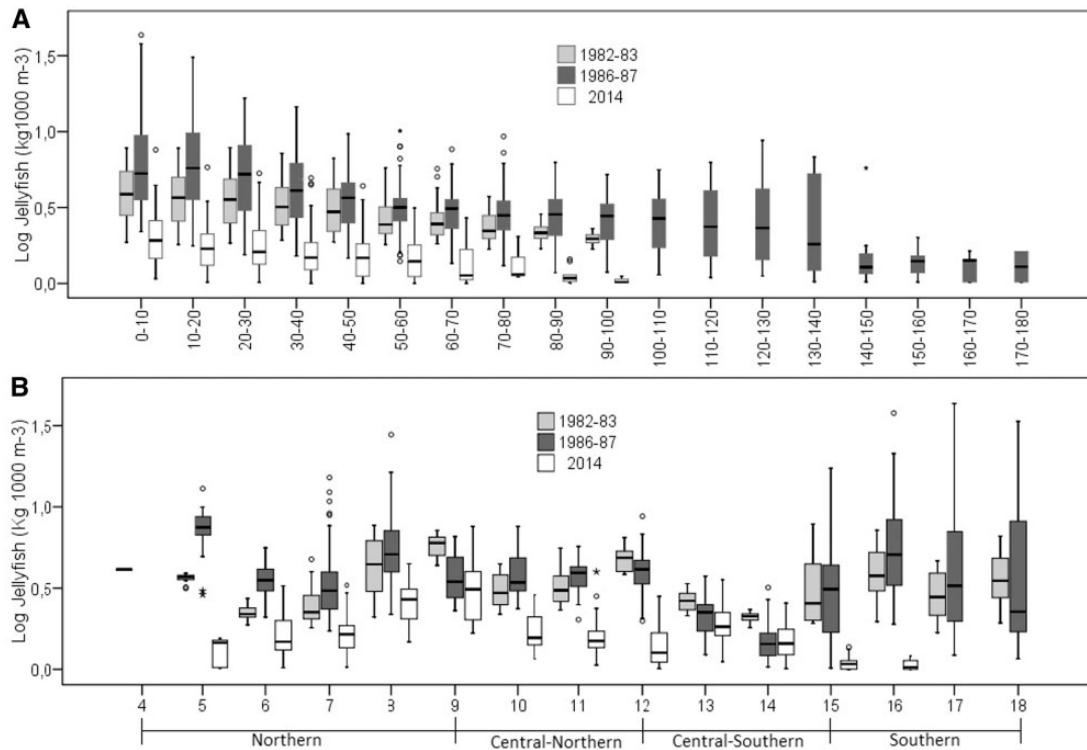
Figure 3. Jellyfish (*C. plocamia*) abundance (log kg jellyfish 1000 m^{-3}) in relation to distance to the coast (x-axes) (a) and latitudinal degree (x-axes) (b) for EN year 1982–1983, EN year 1986–1987, and the neutral year 2014.
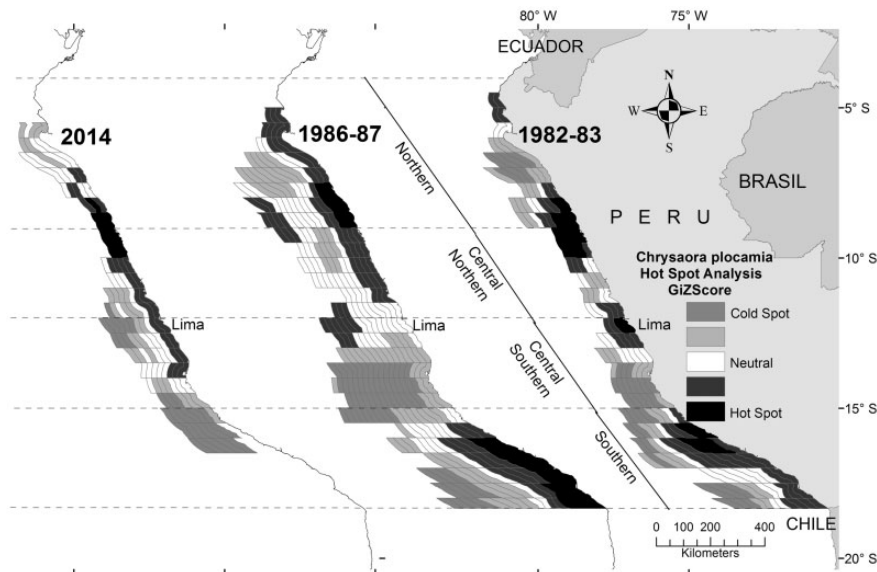
Figure 4. Distribution of "hot spots" (GIZ Score > 2.9; black polygons) of *C. plocamia* medusae abundance in the NHUS (off Peru) during warm EN years (1982–1983 and 1986–1987) and a neutral year (2014). Abundance is expressed in log kg jellyfish 1000 m^{-3}.

C. plocamia did not exhibit high abundances in the south of the study area, contrary to the medium sized hot spots identified in 1982–83 and 1986–1987 (Figure 4).

Spatial overlap with biological variables
The GWR analyses indicated that in 1982–1983 and 1986–1987, the variable that best correlated abundance of *C. plocamia* was Chl *a*, followed by zooplankton biovolume, and abundance of sardine and anchoveta larvae (Table 1). In contrast, in 2014, *C. plocamia* abundance was best explained by abundance of anchoveta eggs, followed by zooplankton volume, Chl *a* and anchoveta larvae (Table 1). The geostatistical analysis indicated that in 1982–1983, *C. plocamia* displayed the highest spatial overlap with sardine larvae (55.2%), followed by zooplankton volume

Table 1. Summary of the results from the GWR between the dependent variable (*C. plocamia*) and the explanatory variables.

Year	1982–1983		1986–1987		2014	
	r^2-adjusted	AICc	r^2-adjusted	AICc	r^2-adjusted	AICc
Chl *a*	0.942*	−563	0.905*	−668	0.743*	−334
Zooplankton	0.876*	−465	0.689*	−300	0.802*	−356
Sardine larvae	0.719*	−325	0.623*	−253		
Sardine eggs	0.251	−169	0.352	−670		
Anchoveta larvae	0.152	−147	0.649*	−263	0.716*	−317
Anchoveta eggs	0.530	−250	0.431	−108	0.819*	−356.2

The asterisks (*) indicate selected variables (higher r^2-adjusted and lower AICc).

(31.5%), and Chl *a* (31.5%). For 1986–1987 the highest overlap was with zooplankton volume (39.2%), followed by sardine larvae (37.2%), anchoveta larvae (37%), and Chl *a* (33.8%). For 2014 the highest overlap was with zooplankton volume (37.3%), followed by anchoveta eggs (33.2%), Chl *a* (29.4%), and anchoveta larvae (28%) (Figure 5).

Within years and areas of high medusa and biological variable values (≥75th percentile), spatial overlap between *C. plocamia* and biological variables varied with latitude (Table 2). In 1982–1983, *C. plocamia* and sardine larvae exhibited the highest spatial overlap in the northern areas (17.6%), while medusae displayed high spatial overlap with Chl *a* (9.5%) and zooplankton (10.1%) in the southern areas. In 1986–1987, medusae displayed the highest spatial overlap with Chl *a* (20.2%) and sardine larvae (17.2%) in the northern areas, and with zooplankton (12.7%) and anchoveta larvae (10.6%) in the southern areas. In 2014, *C. plocamia* showed the highest overlap with Chl *a* (25.9%) in the northern area and with anchoveta eggs and larvae (21.4%) in the central and northern areas (Figure 5; Table 2).

Discussion

The spatial distribution of *C. plocamia* medusae varied considerably between climatic periods, suggesting that environmental conditions play a critical role in determining the spatial pattern of abundances of these large jellyfish in the NHUS. At the same time, the environmental conditions that normally benefit jellyfish occurrence and abundance in certain areas may be detrimental to other biological variables. If this happens, some spatial segregation could be occurring (Brodeur *et al.*, 2014). The massive blooms of *C. plocamia* reported in EN years 1982–1983 and 1986–1987 were mainly distributed within the first 75 km from the coast and were even present up to 280 km offshore. Conversely, blooms during a neutral year (2014) were primary restricted to the coastal areas within 35 km from the coast. During both EN periods, oceanographic conditions were similar and consisted of highly stratified waters and a strong thermal gradient (IMARPE, 1988; Gutiérrez *et al.*, 2011), elevated sea surface temperature (SST), SST anomalies, and a pronounced deepening of the thermocline (Arntz and Tarazona, 1990; IMARPE, 1988). A prolonged deepening of the thermocline can prevent the upwelling of cold, nutrient-rich waters, which results in a reduction of diatoms and an increase in flagellate species (Ochoa *et al.*, 2010) because diatoms sink in highly stratified waters (Smetacek, 1985). Flagellates are common prey for mesozooplankton, which

represents the main prey for most jellyfish; consequently increased in flagellate abundance can lead to increased jellyfish abundance (Parsons and Lalli, 2002; Richardson *et al.*, 2009). Previous research in the NHUS suggests that high prey availability, mainly ichthyoplankton and gelatinous zooplankton, can trigger jellyfish population growth (Quiñones *et al.*, 2015). Therefore, such shifts in plankton community composition likely have a role in the extended distribution of *C. plocamia* during both EN years 1982–1983 and 1986–1987. How environmental factors affect the distribution of *C. plocamia* medusae under cold La Niña (LN) conditions (1975, 2007, and 2013) is less clear. However, during LN years 2007 and 2013, *C. plocamia* was almost absent from open waters, and were mainly restricted below the thermocline in enclosed areas. (Quiñones, pers. obs.).

Variability in pelagic planktonic assemblages may partially explain the restriction of *C. plocamia* blooms to coastal waters in 2014. During this year, zooplankton was less abundant in offshore waters, with a lower percentage of gelatinous organisms (IMARPE, unpublished data). Jellyfish of the genus *Chrysaora* feed on a wide array of prey, including gelatinous zooplankton (Brodeur *et al.*, 2002; Purcell and Decker, 2005; Costello *et al.*, 2012) and reduced offshore prey availability likely limited the offshore expansion of *C. plocamia* in 2014. The hot spots of *C. plocamia* medusae during EN years 1982–1983 and 1986–1987 are also likely a reflection of patches of potential prey items in high abundance (e.g. sardine and anchoveta larvae, meso zooplankton), while the only one hot spot detected in 2014 is perhaps a consequence of low food availability in offshore waters. For example, hot spot analyses indicated that *C. plocamia* medusae was most abundant in areas of the NHUS where biological variables (sardine larvae, anchoveta eggs and larvae, zooplankton volume, Chl *a*) were most abundant. Medusae displayed the greatest spatial overlap with sardine larvae during both EN years 1982–1983 and 1986–1987, while in 2014 the highest spatial overlap was with anchoveta eggs. Variation in the spatial overlap between *C. plocamia* medusae and anchoveta eggs and sardine larvae suggests a possible diet change resulting from climate-driven regime shifts, from anchoveta to sardine in the NHUS (Chavez *et al.*, 2003). For example, anchovy eggs are the most common prey item of *C. plocamia* in northern Chile during cool anchoveta years (Riascos *et al.*, 2014). However, their diet preferences during neutral (warm) years remain unclear. There are several reports on overlap and predation of some medusa on ichthyoplankton. *Pelagia noctiluca* in the Northwest Mediterranean overlaps with larval European anchovy (*Engraulis encrasicolus*), its most frequently ingested prey item (Tilves *et al.*, 2016). In addition, medusae of *C. quinquecirrha* in Barnegat Bay, New Jersey disproportionately consume fish eggs and larvae (Meredith *et al.*, 2016), overlapping in space and time (P. Bologna, pers. comm.). In the Northern California Current, anchovy eggs (*Engraulis mordax*) are the most consumed prey item by medusae of *C. fuscescens* (Zeman *et al.*, 2016), and there is a high spatial overlap between these medusae and adult anchovies (Brodeur *et al.*, 2008b, 2014). Furthermore, a strong positive selection for ichthyoplankton (fish eggs and larvae) has been observed in *C. fuscescens* off the coast of Oregon, USA (Zeman *et al.*, 2016) and by *C. quinquecirrha* in the Chesapeake Bay, USA (Purcell *et al.*, 1994).

Zooplankton volume had an important degree of spatial overlap with *C. plocamia* medusae in the NHUS. During the 1982–1983 EN year, zooplankton assemblages were dominated by gelatinous zooplankton, mainly consisting of chaetognaths,
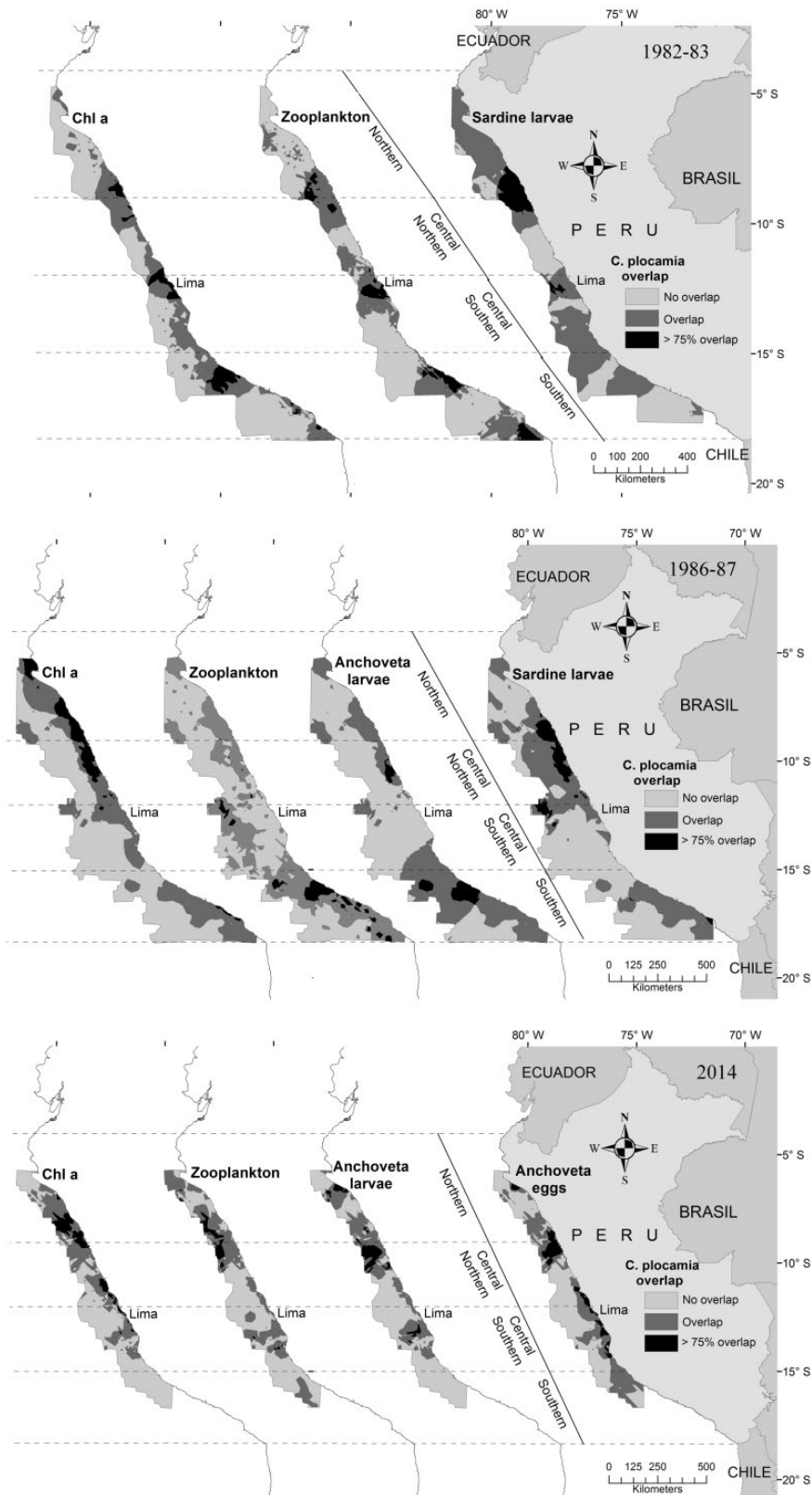
Figure 5. Study area showing the spatial overlap between *C. plocamia* medusae and the biological (explanatory) variables during warm EN years (1982–1983 and 1986–1987) and a neutral year (2014). The distribution of the explanatory variable tested is depicted in light grey. Total overlap between *C. plocamia* and a given explanatory variable is represented in dark grey, while the area of maximum overlap (>75th percentile of biomass of both combined jellyfish and explanatory variable) is shown in black.

Table 2. Overlap circumscribed by the high *C. plocamia* concentration areas (≥75%) (black areas in Figure 5) and the biological variables per geographic latitudinal area.

Year/variables 1982–1983	Chl *a* Overlap (km²)	%	Zooplankton Overlap (km²)	%	Sardine larvae Overlap (km²)	%	Anchoveta larvae Overlap (km²)	%	Anchoveta eggs Overlap (km²)	%
Northern	2735	4.7	3697	6.4	10213*	17.6*				
Central-Northern	2250	6.1	2141	5.8	6608	18.0				
Central-Southern	4676	9.6	5818	12.0	2096	4.3				
Southern	10547*	9.5*	11182*	10.1*	0	0.0				
Total	**20 208.1**	**8.0**	**22 837.9**	**9.0**	**18 917.8**	**8.4**				
1986–1987										
Northern	18417*	20.4*	64	0.1	8797*	9.7*	0.0	0.0		
Central-Northern	13219*	16.4*	1067	1.3	13905*	17.2*	4203	5.2		
Central-Southern	502	0.4	2757	2.4	4367	3.9	0	0.0		
Southern	1755	1.1	19537*	12.7*	1363	0.9	16270*	10.6*		
Total	**33 893.0**	**7.7**	**23 425.1**	**5.3**	**28 431.8**	**6.5**	**20 472.6**	**4.7**		
2014										
Northern	11 662*	25.9*	5534	12.3			1779	3.9	3365	7.5
Central-Northern	5853	12.3	4303	9.1			10173*	21.4*	10017*	21.4*
Central-Southern	1500	2.4	940	1.5			2317	3.7	4985	8.1
Southern	0	0.0	0.0	0.0			0.0	0.0	0.0	0.0
Total	**19 015.3**	**10.3**	**10 776.0**	**5.9**			**14 268.8**	**7.8**	**18 367.6**	**10.0**

Areas of high overlap (> 10, 000 km²) are marked with an asterisk (*), as well as high percentages of overlap.

doliolids, siphonophores, hydromedusae, and larvaceans (Carrasco and Santander, 1987; S. Carrasco, pers. comm.). During the 1986–1987 EN year, zooplankton was primarily composed of small copepods and gelatinous taxa, such as doliolids, pteropods, and larvaceans (IMARPE, 1988). During 2014 on the other hand, small hydromedusae (Trachymedusae and Narcomedusae) were more abundant than in previous years (P. Ayón, pers. obs.). Previous research indicates that species of the genus *Chrysaora* feed on gelatinous zooplankton, among other taxa. For instance, medusae of *Chrysaora quinchecirrha* in the Chesapeake Bay, USA feed on the ctenophore *Mnemiopsis leydyi* (Purcell and Decker, 2005; Costello *et al.*, 2012), and medusae *C. melanaster* in the Bering Sea feed on gelatinous macrozooplankton when available (Brodeur *et al.*, 2002). Although the diet of *C. plocamia* off Peru has not been examined extensively, decapod zoeae, fish eggs, and hydromedusae can be found in their guts during warm years like 2017 (Aller, 2017). Therefore, the high abundance of gelatinous zooplankton prey in the NHUS may play as well an important role in the distribution of *C. plocamia* observed in this system. Similarly, there was high overlap between *C. plocamia* and Chl *a* in the NHUS. Previous studies have shown scyphomedusae and ctenophore concentrations can be correlated with concentrations of Chl *a* (Kideys *et al.*, 2008). The apparent influence of Chl *a* on the distribution of *C. plocamia* however, likely represents an indirect effect, since jellyfish feed on mesozooplankton taxa that in turn feed directly on diatoms and flagellates (Parsons and Lalli, 2002; Chiaverano *et al.*, 2013).

The spatial overlap between *C. plocamia* medusae and biological drivers exhibited a clear latitudinal component. Overlap between jellyfish and fish eggs and larvae was consistently greatest within the northern part of the study area (7–10°S) in all study periods. Such trends are likely due to the consistent location of spawning for fish in upwelling ecosystems (Bakun, 2006a; Acha *et al.*, 2015) given the selection for areas with particular water dynamics that promote egg and larval retention (Bakun, 2006b). Although highly productive, areas of upwelling can also be highly advective, transporting eggs and larvae offshore (Acha *et al.*, 2015). Minimal overlap between *C.*

plocamia and ichthyoplankton in the Central-Southern area is likely a result of high advection and poor larval habitat for pelagic fish given high wind anomalies from 1979 to 2010 and the presence of an intense upwelling-core at ∼13°S–16°S (Rahn and Garreaud, 2014). Hot spots in the Southern area (15°–18°20'S) in 1982–1983 and 1986–1987 however, were highly associated with high zooplankton volume. This area also has a relatively strong annual cycle of heat content (Takahashi, 2005). Temperature is positively correlated with jellyfish production in the NHUS (Quiñones *et al.*, 2015) and likely explains local productivity in this area.

Most scyphozoan medusae, such as *C. plocamia*, are produced and released from benthic polyps. Hence, there appears to be a direct relationship between polyp abundance and medusa population size (Schiariti *et al.*, 2014). To date, *C. plocamia* polyps have not been observed in the wild, but obtained through artificial fertilization under laboratory conditions. Riascos *et al.*, (2013) showed that under simulated EN conditions from northern Chile, *C. plocamia* exhibited a rapid polyp recovery after an initial decrease in somatic growth. However, polyp survival was considerably lower under EN-like (22.3°C) thermal conditions compared with neutral-like (14.3°C) to La Niña-like (12.5°C) thermal conditions. Their results appear to not support our findings, most likely due to differences in environmental conditions between both areas of study. In our study, off of the coast of Peru, sea surface temperatures during the tested EN can easily reach 28–30°C, and primary productivity and food availability are considerably higher than in northern Chile (Bakun and Broad, 2003; Pennington *et al.* 2006). Thus, it is likely that *C. plocamia* polyp populations in Peru experience different environmental conditions than those in Chile, leading to different responses in terms of polyp productivity, medusa distribution and abundance. Future studies will help to elucidate these potential discrepancies.

Conclusions

These results and those by Quiñones *et al.*, (2015), allow us to propose two environmentally driven scenarios that can lead to jellyfish blooms in the NHUS. First, both *C. plocamia* abundance

and spatial distribution are expected to increase during warm EN years most likely as a consequence of increased food availability during the warm El Viejo regime (high concentration of sardine larvae in the north and anchovy larvae in south together with zooplankton abundance) and suitable oceanographic conditions (high SST, strong thermal gradient and deeper thermocline) that can potentially promote medusae growth and increase production. This scenario is represented by the 1982–1983 and 1986–1987 EN years, during which the spatial overlap of *C. plocamia* was greatest with potential prey items like sardine and anchoveta larvae and zooplankton in areas associated with sardine and anchoveta spawning and zooplankton production (Bakun and Broad, 2003; Alheit and Niquen, 2004). Second, during neutral (or slightly warm) years, high abundance of *C. plocamia* medusae will likely be restricted to coastal waters. This scenario is represented by 2014, where *C. plocamia* was higher than other neutral years, however the same spatial pattern was observed. In this year, *C. plocamia* distribution was limited most likely as a consequence of relatively less favourable environmental conditions, such as reduced prey availability in offshore areas and changes in the trophic structure of the NHUS leading to maximal shelf (coastal) retention of ichthyoplankton and prey concentration (Brochier *et al.*, 2011). For both scenarios, blooms of *C. plocamia* are expected to be distributed along oceanographic features associated with the retention of ichyoplankton and thermal gradients that promote jellyfish production.

Understanding the spatial distribution of *C. plocamia* medusae, and the environmental effects on it in the NHUS can be highly beneficial for fisheries in this commercially important area. The spatial patterns presented and the scenarios proposed here may be used to assist the anchoveta fishery fleet in avoiding areas of high concentration of *C. plocamia* medusae and minimize jellyfish bycatch, which can lead to important economic losses (Quiñones *et al.*, 2013). Alternatively, the identification of large jellyfish hot spots can also assist the establishment of a jellyfish fishery to support the demand from Asians markets (Brotz *et al.*, 2017). Last, spatial patterns of jellyfish abundance, as well as their spatial overlap with commercial fish eggs and larvae, could be used to assist in ecosystem-based fishery management approaches for the NHUS, and other highly productive, commercially important marine systems worldwide.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the article.

References

Acha, E. M., Piola, A., Iribarne, O., and Mianzan, H. 2015. Ecological Processes at Marine Fronts: Oases in the Ocean. Springer Cham, Heidelberg; New York; Dordrecht; London. 66 pp.

Alheit, J., and Niquen, M. 2004. Regime shifts in the Humboldt Current ecosystem. Progress in Oceanography, 60: 201–222.

Aller, 2017. Descripción de la dieta de la medusa *Chrysaora plocamia* (Lesson, 1830) en la bahía Independencia, Perú. Tesis para el grado de licenciatura de la Universidad Científica del ur, Lima, Perú. 50 pp.

Armstrong, M., and Boufassa, A. 1988. Comparing the robustness of ordinary kriging and lognormal kriging: outlier resistance. Mathematical Geology, 20: 447–457.

Arntz, W. E., and Tarazona, J. 1990. Effects of El Niño 1982-83 on benthos, fish and fisheries off the South American Pacific coast. Elsevier Oceanography Series, 52: 323–360.

Bakun, A., and Broad, K. 2003. Environmental 'loopholes' and fish population dynamics: comparative pattern recognition with focus on El Niño effects in the Pacific. Fisheries Oceanography, 12: 458–473.

Bakun, A. 2006a. Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. Scientia Marina, 70: 105–122.

Bakun, A. 2006b. Wasp-waist populations and marine ecosystem dynamics: navigating the predator pit topographies. Progress in Oceanography, 68: 271–288.

Brochier, T., Lett, C., and Fréon, P. 2011. Investigating the 'northern Humboldt paradox from model comparisons of small pelagic fish reproductive strategies in eastern boundary upwelling ecosystems. Fish and Fisheries, 12: 94–109.

Brodeur, R. D., Sugisaki, H., and Hunt, G. L. Jr, 2002. Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. Marine Ecology Progress Series, 233: 89–103.

Brodeur, R. D., Decker, M. B., Ciannelli, L., Purcell, J. E., Bond, N. A., Stabeno, P. J., Acuna, E., *et al.* 2008a. The rise and fall of jellyfish in the Bering Sea in relation to climate regime shifts. Progress in Oceanography, 77: 103–111.

Brodeur, R. D., Suchman, C. L., Reese, D. C., Miller, T. W., and Daly, E. A. 2008b. Spatial overlap and trophic interactions between pelagic fish and large jellyfish in the northern California Current. Marine Biology, 154: 649–659.

Brodeur, R. D., Barcelo, C., Robinson, K. L., Daly, E. D., and Ruzika, J. J. 2014. Seasonal and interannual variability in the spatial overlap between forage fishes and the large medusa *Chrysaora fuscescens* in the northern California Current region. Marine Ecology Progress Series, 510: 167–181.

Brotz, L., Schiariti, A., López-Martínez, J., Álvarez-Tello, J., Hsieh, Y. H. P., Jones, R. P., Quiñones, J., *et al.* 2017. Jellyfish fisheries in the Americas: origin, state of the art, and perspectives on new fishing grounds. Reviews in Fish Biology and Fisheries, 27: 1–29.

Carrasco, S., and Santander, H. 1987. The El Niño Event and its influence on the zooplankton off Peru. Journal of Geophysical Research, 92: 14405–14410.

Costello, J. H., Bayha, K. M., Mianzan, H. W., Shiganova, T. A., and Purcell, J. E. 2012. Transitions of *Mnemiopsis leidyi* (Ctenophora: lobata) from a native to an exotic species: a review. Hydrobiologia, 690: 21–46.

Chavez, F. P., Ryan, J., Lluch-Cota, S. E., and Niquen, M. 2003. From Anchovies to Sardines and Back: multidecadal Change in the Pacific Ocean. Science, 299: 217–221.

Chiaverano, L. M., Holland, B. S., Crow, G. L., Blair, L., Yanagihara, A. A., and Hays, G. C. 2013. Long-term fluctuations in circalunar beach aggregations of the box jellyfish *Alatina moseri* in Hawaii, with links to environmental variability. PloS One, 8: e77039.

Condon, R. H., Duarte, C. M., Pitt, K. A., Robinson, K. L., Lucas, C. H., Sutherland, K. R., and Mianzan, H. W. 2013. Recurrent jellyfish blooms are a consequence of global oscillations. Proceedings of the National Academy of Sciences of the United States of America, 110: 1000–1005.

Duarte, C. M., Pitt, K. A., Lucas, C. H., Purcell, J. E., Uye, S. I., Robinson, K., Brotz, L., *et al.* 2013. Is global ocean sprawl a cause of jellyfish blooms? Frontiers in Ecology and the Environment, 11: 91–97.

Eriksen, E. 2015. Do scyphozoan jellyfish limit the habitat of pelagic species in the Barents Sea during the late feeding period? ICES Journal of Marine Science, 73: 217–226.

ESRI, 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA.

FAO, 2011. Fisheries and aquaculture software. FishStatJ - software for fishery statistical time series. In: FAO Fisheries and Aquaculture Department [online]. Rome. Updated 21 July 2016 (cited 4 August 2017). http://www.fao.org/fishery/statistics/software/fishstatj/en

Flynn, B. A., Richardson, A. J., Brierley, A. S., Boyer, D. C., Axelsen, B. E., Scott, L., Moroff, N. E., et al. 2012. Temporal and spatial patterns in the abundance of jellyfish in the northern Benguela upwelling ecosystem and their link to thwarted pelagic fishery recovery. African Journal of Marine Science, 34: 131–146.

Gibbons, M. J., and Richardson, A. J. 2013. Beyond the jellyfish joy-ride and global oscillations: advancing jellyfish research. Journal of Plankton Research, 35: 929–938.

Goy, J., Morand, P., and Etienne, M. 1989. Long term fluctuation of *Pelagia noctiluca* (Cnidaria, Scyphomedusa) in the western Mediterranean Sea. Prediction by climatic variables. Deep-Sea Research, 36: 269–279.

Gutiérrez, M., and Peraltilla, S. 1999. Aplicación de un Sistema de Información Geográfica y de la carta electrónica iso-paralitoral en las evaluaciones hidroacústicas de la biomasa de recursos pesqueros en el mar peruano. Informe Instituto del Mar del Perú, 146: 25–29.

Gutiérrez, D., Bertrand, A., Wosnitza-mendo, C., Dewitte, B., Purca, S., Peña, C., Chainegau, A., et al. 2011. Sensibilidad del sistema de afloramiento costero del Perú al cambio climático e implicancias ecológicas [Climate change sensitivity of the Peruvian upwelling system and ecological implications]. Revista Peruana Geoatmosférica, 3: 1–24.

Holm-Hansen, O., Lorenzen, C. J., Holmes, R. W., and Strickland, J. D. 1965. Fluorometric determination of chlorophyll. ICES Journal of Marine Science, 30: 3–15.

IMARPE, 1988. Informe del Crucero 8610-12 a bordo del BIC Humboldt y BIC SNP-1 "Prospección pesquera de los recursos pelágicos anchoveta, sardina, jurel y caballa". Instituto del Mar del Perú, 20. pp.

Kideys, A. E., Roohi, A., Eker-Develi, E., Mélin, F., and Beare, D. 2008. Increased chlorophyll levels in the southern Caspian Sea following an invasion of jellyfish. Research Letters in Ecology, 185642: 1–4.

Kordas, R. L., Harley, C. D., and O'Connor, M. I. 2011. Community ecology in a warming world: the influence of temperature on interspecific interactions in marine systems. Journal of Experimental Marine Biology and Ecology, 400: 218–226.

Kramer, D., Kalin, M., Stevens, E. G., Thrailkill, J. R., and Zweifel, J. R. 1972. Collecting and processing data on fish eggs and larvae in the California Current region. NOAA Technical Report NMFS Circ-370, 38 pp.

Lloyd, C. D. 2006. Local Models for Spatial Analysis. CRC Press, Belfast. 244 pp.

Lucas, C. H., Jones, D. O., Hollyhead, C. J., Condon, R. H., Duarte, C. M., Graham, W. M., Robinson, K. L., et al. 2014. Gelatinous zooplankton biomass in the global oceans: geographic variation and environmental drivers. Global Ecology and Biogeography, 23: 701–714.

Lynam, C. P., Brierley, A. S., and Hay, S. J. 2005a. Jellyfish abundance and climate variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. Journal of the Marine Biological Association of the United Kingdom, 85: 435–450.

Lynam, C. P., Heath, M. R., Hay, S. J., and Brierley, A. 2005b. Evidence for impacts by jellyfish on North Sea herring recruitment. Marine Ecology Progress Series, 298: 157–167.

Lynam, C. P., Gibbons, M. J., Axelsen, B. A., Sparks, C. A. J., Coetzee, J., Heywood, B. G., and Brierley, A. S. 2006. Jellyfish overtake fish in a heavily fished ecosystem. Current Biology, 16: R492–R493.

Meredith, R. W., Gaynor, J. J., and Bologna, P. A. 2016. Diet assessment of the Atlantic Sea Nettle *Chrysaora quinquecirrha* in Barnegat Bay, New Jersey, using next-generation sequencing. Molecular Ecology, 25: 6248–6266.

Ochoa, N., Taylor, M. H., Purca, S., and Ramos, E. 2010. Intra-and interannual variability of nearshore phytoplankton biovolume and community changes in the northern Humboldt Current system. Journal of Plankton Research, 32: 843–855.

Parsons, T. R., and Lalli, C. M. 2002. Jellyfish population explosions: revisiting a hypothesis of possible causes. La Mer, 40: 111–121.

Pennington, J. T., Mahoney, K. L., Kuwahara, V. S., Kolber, D. D., Calienes, R., and Chavez, F. P. 2006. Primary production in the eastern tropical Pacific: a review. Progress in Oceanography, 69: 285–317.

Purcell, J. E., Nemazie, D. A., Dorsey, S. E., Houde, E. D., and Gamble, J. C. 1994. Predation mortality of bay anchovy (*Anchoa mitchilli*) eggs and larvae due to scyphomedusae and ctenophores in Chesapeake Bay. Marine Ecology Progress Series, 114: 47–58.

Purcell, J. E. 2003. Predation on zooplankton by large jellyfish, *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*, in Prince William Sound, Alaska. Marine Ecology Progress Series, 246: 137–152.

Purcell, J. E. 2005. Climate effects on formation of jellyfish and ctenophore blooms: a review. Journal of the Marine Biology Association of the United Kingdom, 85: 461–476.

Purcell, J. E., and Decker, M. B. 2005. Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987–2000. Limnology and Oceanography, 50: 376–387.

Purcell, J. E. 2012. Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. Annual Review of Marine Sciences, 4: 209–235.

Quiñones, J., Monroy, A., Acha, E. M., and Mianzan, H. 2013. Jellyfish bycatch diminishes profit in an anchovy fishery off Peru. Fisheries Research, 139: 47–50.

Quiñones, J., Mianzan, H., Purca, S., Robinson, K. L., Adams, G. D., and Acha, M. 2015. Climate-driven population size fluctuations of jellyfish (*Chrysaora plocamia*) off Peru. Marine Biology, 162: 2339–2350.

Rahn, D. A., and Garreaud, R. D. 2014. A synoptic climatology of the near-surface wind along the west coast of South America. International Journal of Climatology, 34: 780–792.

Riascos, J. M., Paredes, L., Gonzales, K., Caceres, I., and Pacheco, A. S. 2013. The larval and benthic stages of the scyphozoan medusa *Chrysaora plocamia* under El Niño–La Niña thermal regimes. Journal of Experimental Marine Biology and Ecology, 446: 95–101.

Riascos, J. M., Villegas, V., and Pacheco, A. S. 2014. Diet composition of the large scyphozoan jellyfish *Chrysaora plocamia* in a highly productive upwelling centre off northern Chile. Marine Biology Research, 10: 791–798.

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

Santander, H. 1987. Relationship between anchoveta egg standing stock and parent biomass off Peru, 4°–14°S. *In* The Peruvian Anchoveta and Its Upwelling Ecosystems: Three Decades of Change, 1st edn, pp. 179–207. Ed. by D. Pauly, and I. Tsukayama, ICLARM Studies and Reviews, Manila. 351 0.

Schiariti, A., Morandini, A. C., Jarms, G., von Glehn Paes, R., Franke, S., and Mianzan, H. 2014. Asexual reproduction strategies and

blooming potential in Scyphozoa. Marine Ecology Progress Series, 510: 241–253.

Schroeder, R., Branco, J. O., Freitas, F., Jr., and Resgalla, C. Jr, 2014. Preliminary assessment of the jellyfish bycatch captured off southern and southeastern Brazil. Latin American Journal of Aquatic Research, 42: 288–300.

Scott, L., and Warmerdam, N. 2005. Extend crime analysis with ArcGIS spatial statistics tools. ArcUser Online, April–June 2005.

Smetacek, V. S. 1985. Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. Marine Biology, 84: 239–251.

Takahashi, K. 2005. The annual cycle of heat content in the Peru Current region. Journal of Climate, 18: 4937–4954.

Tilves, U., Purcell, J. E., Fuentes, V. L., Torrents, A., Pascual, M., Raya, V., Gili, J. M., *et al.* 2016. Natural diet and predation impacts of *Pelagia noctiluca* on fish eggs and larvae in the NW Mediterranean. Journal of Plankton Research, 38: 1243–1254.

Zeman, S. M., Brodeur, R. D., Daly, E. A., and Sutherland, K. R. 2016. Prey selection patterns of *Chrysaora fuscescens* in the northern California Current. Journal of Plankton Research, 38: 1433–1443.

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