Trends in abundance and phenology of *Aurelia aurita* and *Cyanea* spp. at a Skagerrak location, 1992–2011

Aino Hosia[1,3,*], Tone Falkenhaug[2], Lars-Johan Naustvoll[2]

[1]**Institute of Marine Research, PO Box 1870 Nordnes, 5817 Bergen, Norway**
[2]**Institute of Marine Research, Flødevigen, 4817 His, Norway**
[3]***Present address:* University Museum of Bergen, Natural History Collections, University of Bergen, 5007 Bergen, Norway**

ABSTRACT: Climate change is linked to changes in the distribution and phenology of plankton through several trophic levels, with potential impacts on pelagic food webs. Global warming and other anthropogenic stresses have also been implicated in proposed large-scale increases in jellyfish numbers. We have analyzed a 1992 to 2011 time series on occurrence of common scyphozoan jellyfish at a Skagerrak location for changes in their abundance and phenology, and attempted to relate these observations to environmental and climatic variables including temperature, salinity, chl *a* concentration, zooplankton prey biomass and the North Atlantic Oscillation index using generalized linear models (GLMs). *Cyanea* spp. abundances showed no significant trend during the study period. Their fluctuations were positively related to temperature and prey availability, with possible impacts on the polyp generation. The central tendency of annual *Cyanea* spp. abundance showed a borderline significant shift towards a later date, while zooplankton biomass showed the opposite trend, suggesting potential change in trophic match. *Aurelia aurita* abundance exhibited a considerable decline and 5-yr cyclicity, but neither pattern was explained by any of the investigated explanatory variables. Unidentified factors causing cyclicity may include predatory interactions or density-dependent processes, possibly involving the benthic stages. Observed changes in abundance may also be related to a possible regime shift in the Norwegian Skagerrak area around the turn of the millennia. Our results highlight the importance of considering changes in jellyfish abundances with regard to locality and species. Improved understanding of polyp ecology seems necessary for understanding fluctuations in jellyfish numbers.

KEY WORDS: Jellyfish · Scyphozoa · Time series · Zooplankton · Seasonality · Climate change · North Sea · Regime shift

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INTRODUCTION

Changing climate is affecting both the phenology and geographic distribution of planktonic organisms in the northeast Atlantic. In the North Sea, changes in the timing of occurrence and life history events have been observed through several trophic levels (e.g. Edwards & Richardson 2004). These shifts are not necessarily similar for all species in the pelagic community, and can thus alter the match/mismatch in the seasonal timing of species with trophic interactions (Edwards & Richardson 2004, Mackas et al. 2012). Distributions of many species are also moving northwards as a result of global warming (Beaugrand et al. 2009), changing the species composition of local plankton communities. These types of changes can considerably alter the structure and functioning of pelagic food webs (Edwards & Richardson 2004, Kirby & Beaugrand 2009, Alvarez-Fernandez et al. 2012).

Human activities can also promote increased jellyfish abundances (Purcell et al. 2007, Richardson et al.

2009). In addition to climate change, other suggested causes for increased jellyfish numbers — at least on a local scale — include overfishing, eutrophication, deteriorated light environments, species introductions and subsurface construction (reviewed in Purcell et al. 2007, Richardson et al. 2009). Shifts towards jellyfish dominance can have profound effects on the flow of carbon and nutrients and, subsequently, ecosystem structure and functioning (Pitt et al. 2009, Condon et al. 2011), the worst case scenario being a permanent regime shift (Richardson et al. 2009). Such shifts towards jellyfish as top predators have indeed been described (Lynam et al. 2006, Aksnes et al. 2009, Oguz et al. 2012) and deleterious jellyfish blooms are a common nuisance.

Nevertheless, the scarcity of long time series and reliable historical baseline data on jellyfish abundances makes it difficult to establish if large scale increases in jellyfish numbers are in fact taking place. A recent meta-analysis by Brotz et al. (2012) suggests that increases may be happening in many of the world's large marine ecosystems, while another synthesis by Condon et al. (2012) concludes that the currently available data cannot substantiate claims of global increases in jellyfish numbers. The most recent analysis of available time series found a weak overall increase in jellyfish numbers since the 1970s (Condon et al. 2013). More importantly, however, assumed persistent increases may be related to misidentified decadal oscillations in jellyfish numbers (Purcell et al. 2007, Condon et al. 2013).

In this paper, we analyze a 1992 to 2011 time series of local jellyfish abundances at Flødevigen Research Station on the Skagerrak Coast. We consider changes in both the phenology and the abundance of the locally most common scyphozoans, *Aurelia aurita* and *Cyanea* spp., and try to relate observed jellyfish abundances to environmental and climatic variables including chl *a* concentration, zooplankton prey biomass, temperature, salinity and the North Atlantic Oscillation index using generalized linear models (GLMs).

MATERIALS AND METHODS

Time series

The analyzed time series consists of jellyfish counts done from a pier at Flødevigen Research Station (58° 25' N, 8° 45' E), located in Flødevigen Bay on the Norwegian Skagerrak coast. The semi-exposed bay with an area of <1 km² and a maximum depth of 20 m is heavily influenced by the Norwegian Coastal Current (NCC) flowing westward along the Skagerrak coast, and plankton observations from the bay are considered a proxy for the abundance within the NCC (Dahl & Johannessen 1998). Jellyfish visible from the pier, over an area of ca. 100 m², were counted daily from 31 May 1992 to 19 January 2009, and thrice weekly since then (Fig. 1). Our analysis includes the data until the end of 2011. The observed
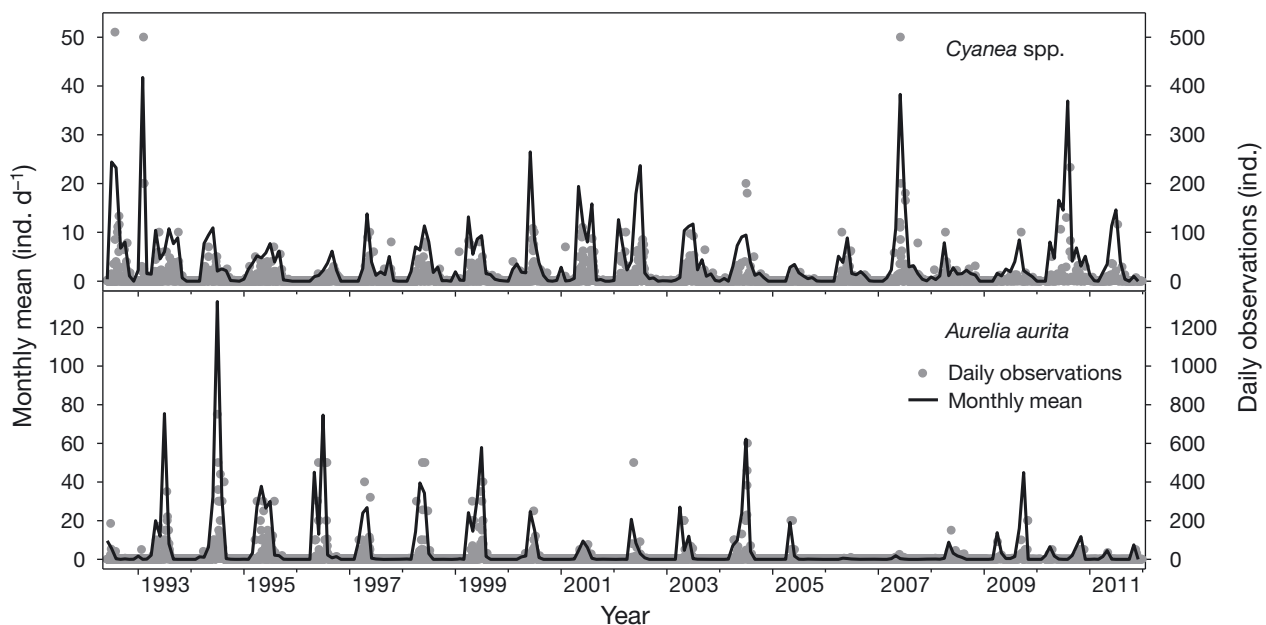

Fig. 1. Time series of jellyfish abundance. Grey dots indicate the number of individuals observed on a given day, the black line shows the observations averaged over the month. Note the different *y*-axes scales

jellyfish were identified as *Aurelia au-rita* or *Cyanea* spp. Observations on *Cyanea* spp. were not separated into the 2 species occurring in the area, *C. capillata* and *C. lamarckii*. The resulting daily data were checked for outliers, and 6 extreme observations of >1000 individuals were removed as possible typing mistakes (*Cyanea* spp: one observation from 1998; *A. aurita*: 2 from 1993 and 1998 and one from 1999). Two non-numeric ('many') *A. aurita* observations from 2007 were also removed. Ice cover prevented observations for large parts of February 2007 and could have interfered with the observation of earliest *Cyanea* spp. that year (see Fig. 2).

Data on temperature (*T*), salinity (*S*) and chlorophyll *a* concentration (*chla*) at 10 m (January 1992 to December 2011), as well as zooplankton biomass (dry wt, *zpl*) from a 50 to 0 m vertical haul with a 180 µm WP2 net (January 1994 to December 2011), came from a regular monitoring program at Arendal Station 2, ca. 1 nautical mile offshore from Flødevigen Research Station (58°23 N, 8°49 E; for details on the program, see Johannessen et al. 2012). Sampling frequency for these parameters was ca. twice monthly. The annual winter (December to March) station-based index of the North Atlantic Oscillation (NAO) was provided by the Climate Analysis Section, NCAR, Boulder, CO, USA (Hurrell 1995).
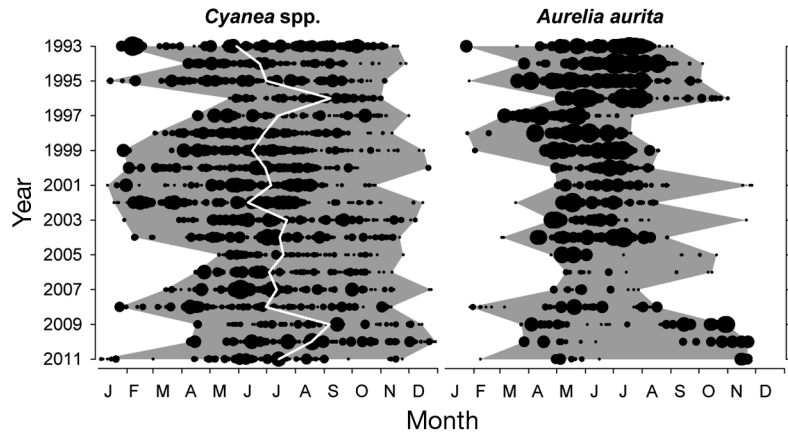

Fig. 2. Extraction of annual phenological variables from the time series. Black dots indicate dates with positive observations, the size of the bubble is relative to $\ln(1 + n)$, where n is the observed number of jellyfish. The left hand border of the gray area indicates the date of first observation, the right hand side that of the last observation. The width of the gray area is the span between first and last observations. The thick white line in the middle shows the central tendency *C* of the *Cyanea* spp. observations, calculated for the whole year (not shown for *A. aurita*)

Phenology

The following annual phenological variables were extracted from the daily data for both jellyfish species (Fig. 2): Dates of first and last occurrence, and the span (number of days) between these. The timing of the seasonal peak of jellyfish abundances, *zpl* and *chla* was estimated as central tendency (*C*), calculated as the month coordinate of the centre of gravity of the area below graphs of monthly mean abundances:

$$C = \frac{\sum_{i=1}^{12} mx_m}{\sum_{i=1}^{12} x_m} \qquad (1)$$

where x_m is the mean abundance in month *m* (Jan = 1,…, Dec = 12) (Colebrook & Robinson 1965). For species/groups exhibiting a single annual peak, *C* was calculated using the whole year. For groups with 2 seasonal peaks, *C* was also calculated separately for the first and last 6 months of the year. Standard

linear regression was used to estimate change over time in the phenological variables; residuals from these regressions showed no significant autocorrelation. Central tendencies of *zpl* calculated for the entire year ($y = 122.61 - 0.06x$, $R^2 = 0.67$, p < 0.001) as well as *chla* for the entire year ($y = 146.76 - 0.07x$, $R^2 = 0.22$, p = 0.036) and the first 6 mo of the year ($y = 107.10 - 0.05x$, $R^2 = 0.29$, p = 0.013) all showed a significant trend towards an earlier central tendency (Fig. 3), and were detrended by using the residuals from the linear regression against year in further analyses on annual time scale. Spearman correlations between the different phenological variables were also examined.

Modeling abundances

Jellyfish abundances were modeled at both monthly and annual time scales. Since the response variables in both cases are counts of individuals and exhibit overdispersion, GLMs with a negative binomial distribution and log link were used to model them (function *glm.nb*, R package 'MASS') (Venables & Ripley 2002). In both monthly and annual models, we tried to choose explanatory variables in a way that takes into account their possible impact also earlier in the life cycle (i.e. polyp stage). Collinearity between chosen explanatory variables was explored using Pearson correlations, pairplots and variance inflation factors (function *vif*, R package 'car') (Fox & Weisberg 2011), and strong collinearity was removed through selective elimina-
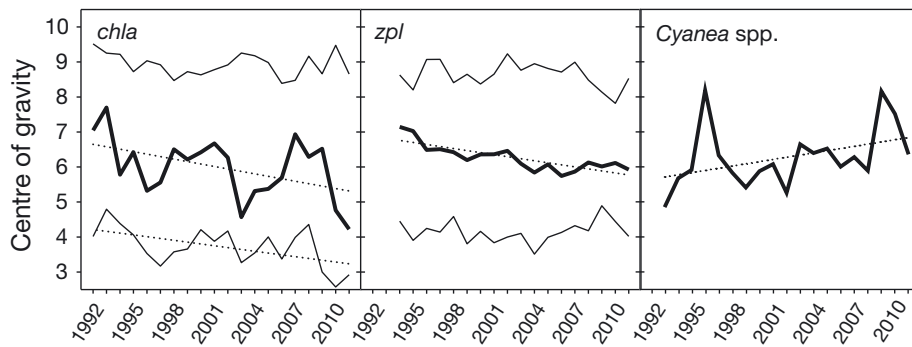
Fig. 3. Changes in the timing of the centers of gravity for chl *a* concentration (*chla*), zooplankton biomass (*zpl*) and *Cyanea* spp. observations. The thick lines in the middle represent the central tendency (*C*) calculated for the whole year, the thin lines show *C* calculated separately for the first 6 mo (lower line) and last 6 mo (upper line) of the year. Dotted lines indicate significant linear trends (borderline significant for *Cyanea* spp.)

tion of explanatory variables from the model prior to fitting. A full initial model including all the remaining explanatory variables was then fitted, and backward selection minimizing the Akaike's information criterion (AIC) was used to select the best model. Explanatory variables were dropped from the model one at a time in favor of the model with the lowest AIC. Explanatory variables were also dropped in favor of the simpler model if the difference in the AIC between the models was < 2. Model adequacy was assessed by examining the distribution and autocorrelation of residuals and comparing the observed and fitted values.

Monthly time scale

Since daily jellyfish observations may be affected by weather and wind conditions, the daily counts were aggregated into monthly observations (Fig. 1). Due to the change in sampling frequency, this was done by rounding the product of the daily average observation and the number of days per given month to the nearest integer.

Monthly averages were calculated for the environmental variables. For missing months within the environmental variables (4 cases for both *T* and *S*, 5 for *chla*, 8 for *zpl*), values were interpolated to create a regular time series for subsequent analyses (function *na.approx*, R package 'Zoo') (Zeileis & Grothendieck 2005). A single outlier in *S* (PSU ~18 in June 2002) was replaced with the corresponding monthly mean. A $\log_{10}(x + 1)$ transformation was applied to *chla* and *zpl*. The resulting monthly explanatory variables were deseasonalized using seasonal decomposition of time series by Loess (function *stl*, R package 'stats') (Cleveland et al. 1990). Standard linear regression was used to examine the resulting seasonally decomposed series for linear trends in time, and in case of significant trends (p < 0.05), the series in question was detrended by using residuals from the regression in subsequent analyses.

An initial model for the number of jellyfish observed on a given month (*J*) containing the following explanatory variables was fitted for both species separately:

$$J \sim Year \times Month + S + T + chla + zpl + S_{lag6} + T_{lag6} + chla_{lag6} + zpl_{lag6} + J_{lag1} + offset(logMonthdays) \quad (2)$$

The response variable *J* was neither deseasonalised nor detrended; instead, a *Year × Month* interaction with *Month* as a nominal variable was included in the model to account for seasonality, linear trends in time and changes in seasonality during the observed period. Lag6 indicates variables lagged by 6 mo, which were included to explore effects due to impacts occurring earlier in the life cycle. Due to autocorrelation within the explanatory variables, only a single lag was included, and this was chosen as large enough to exclude significant collinearity between the simultaneous and lagged variables. J_{lag1} is the response variable *J* lagged by 1 mo, and was included to account for first order temporal autocorrelation in the response variable. Logarithm of the number of days per month (*Monthdays*) was used as an offset.

Annual time scale

Since the observation frequency changed from daily to thrice weekly during the time series, a variable describing the expected number of jellyfish observations per annum (*E*), assuming daily observations, was calculated for both species separately as

$$E = PO_{\%} \times PO_{mean} \times 365 \quad (3)$$

where $PO_{\%}$ is the percentage of positive observations (i.e. observations with jellyfish present) and PO_{mean} is the average value (i.e. the number of jellyfish observed) of positive observations during the year. This expected number of annual observations was roun-

ded to the nearest integer and used for interannual comparisons of jellyfish abundance.

The annual explanatory variables *Year*, NAO, winter (mean from January to March) and summer (mean from July to September) temperature (T_W and T_S, respectively), salinity (S_W and S_S), chl *a* concentration ($chla_W$ and $chla_S$) and zooplankton biomass (zpl_W and zpl_S), as well as the central tendency of annual chl *a* concentration (C_{chla}) and zooplankton biomass (C_{zpl}) were considered for inclusion in the model. Standard linear regression was used to detrend annual variables prior to inclusion in the model: the only variable showing a significant linear change in time was NAO ($y = 371.33 - 0.19x$, $R^2 = 0.22$, p = 0.038), for which residuals from the linear regression were used in subsequent analyses. After controlling for collinearity between the explanatory variables (Table 1), the initial full model

$$E \sim Year + T_W + T_S + S_S + chla_S + zpl_S + zpl_W \quad (4)$$

was fitted for both species and subjected to backward selection.

Data exploration and statistical analyses were conducted with R v.2.9.1 (R Development Core Team 2009). Figures were plotted with R v.2.9.1 and Sigmaplot 11.0.

RESULTS

Phenology

Considering the entire study period, the average monthly abundances of *Cyanea* spp. tended to peak in June and have a wider spread than the *Aurelia aurita* observations peaking in July (Figs. 2 & 4). This overall pattern, however, changed during the period of observation, with the seasonal distribution of *A. aurita* seemingly unimodal prior to and bimodal after the extremely low abundances in 2006 and 2007 (Figs. 1, 2 & 4). During the latter period, *A. aurita* were virtually absent during the earlier peak month of July. *Cyanea* spp. abundance exhibited a borderline significant trend towards a later annual central tendency ($y = -118.147 + 0.062x$, $R^2 = 0.16$, p = 0.090), i.e. the bulk of the *Cyanea* spp. observations may occur successively later in the years during the study period (Figs. 2 & 3). Estimating a linear trend for the annual central tendency of *A. aurita* is meaningless
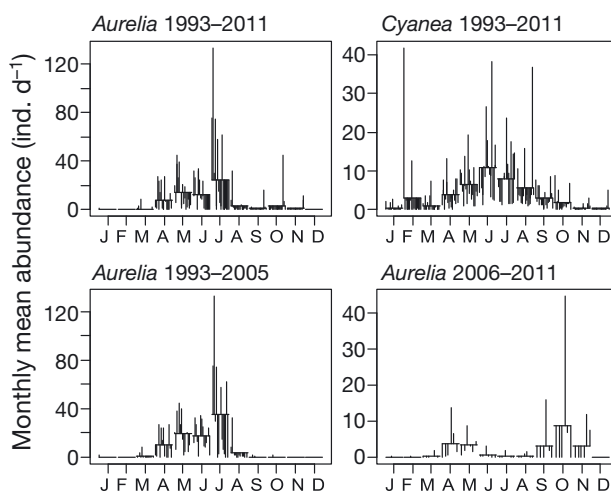

Fig. 4. Seasonal distribution of *Cyanea* spp. and *Aurelia aurita* as monthplots. The horizontal lines depict the monthly averages of observed individuals over the time period specified in the panel title, the vertical lines show the annual departures from that mean. *A. aurita* monthplots are shown for the entire period from 1993–2011 as well as for 1993–2005 and 2006–2011 in order to show the change from a unimodal to a bimodal seasonal distribution

Table 1. Pearson correlations and their significance levels between the annual explanatory variables. NAO: North Atlantic Oscillation Index; *T*: temperature; *S*: salinity; *chla*: chl *a* concentration; *C*: central tendency; *zpl*: zooplankton biomass. Subscripts W and S indicate a winter mean from January to March and summer mean from July to September, respectively. Residuals from a linear regression against time are used for the variables marked superscript *R*. ***p ≤ 0.001, **p ≤ 0.01, *p ≤ 0.05, •p ≤ 0.1

	NAO^R	T_W	T_S	S_W	S_S	$chla_S$	$chla_W$	C^R	zpl_S	zpl_W
T_W	0.59**									
T_S	0.01	−0.04								
S_W	0.46*	0.72***	−0.12							
S_S	0.24	−0.13	−0.1	−0.18						
$chla_S$	0.08	0.23	−0.21	0.03	0					
$chla_W$	−0.42•	−0.81***	0.22	−0.54*	0.33	−0.34				
C^R	0.51*	0.75***	−0.2	0.25	0.07	0.59**	−0.81***			
zpl_S	−0.11	−0.39	−0.05	−0.26	0.14	−0.22	0.25	−0.28		
zpl_W	−0.23	−0.36	0.13	−0.1	0.35	−0.56*	0.59*	−0.51*	0.18	
C_{zpl}^R	0.15	−0.14	−0.13	−0.15	0.16	−0.06	−0.09	0.01	0.56*	−0.22

due to the change from a unimodal to a bimodal seasonal distribution. The timing of the other phenological variables — dates of first and last observation and the span between these — showed no significant linear trends for either species.

Several of the annual phenological variables were correlated within species (Table 2). For both species, the annual percentage and mean value of positive observations were positively correlated. This implies that the calculated expected number of annual observations (E) reflects true interannual differences rather than single peaks in abundance. The span of the jellyfish season correlated negatively with date of first observation for *Cyanea* spp. and positively with the last observation for *Aurelia aurita.* The date of first occurrence of *Cyanea* spp. also had a significant negative correlation with the percentage of positive *Cyanea* spp. observations during the year and a marginally significant negative correlation with their mean value. There were fewer significant correlations between the phenological variables for *A. aurita* than for *Cyanea* spp. Despite known intraguild predation and competition between the species (Titelman et al. 2007), significant between-species correlations were scarce (Table 2).

Monthly abundance

The best fit model for monthly *Cyanea* spp. abundance was found to include the *Year × Month* interaction, the *Cyanea* spp. abundance during the previous month and the zooplankton biomass 6 mo ago (Tables 3 & 4). The model seems to be relatively good at predicting the level of the annual *Cyanea* spp. peak, although it sometimes misses its exact timing (Fig. 5).

We were unable to get a satisfactory model for the monthly *Aurelia aurita* abundance to converge. The problems may have been partly due to the change in the *A. aurita* seasonality from a unimodal to a bimodal distribution during the time series, which made modeling the seasonality challenging. The

Table 3. Backwards selection of the model for monthly *Cyanea* spp. abundance. Initial model $J \sim Year × Month + S + T + chla + zpl + S_{lag6} + T_{lag6} + chla_{lag6} + zpl_{lag6} + J_{lag1} + offset(logMonthdays)$, where J = number of jellyfish, S = salinity, T = temperature, $chla$ = chl a concentration and zpl = zooplankton biomass; lag6 and lag1 indicate variables lagged with 6 and 1 mo, respectively. Final model $F \sim Year × Month + zpl_{lag6} + J_{lag1} + offset(logMonthdays)$. In step 8, $chla$ was removed and the simpler model chosen since there was a less than one unit difference in AIC and comparison of the models indicated no significant differences between them (ANOVA, p_{Chi} = 0.09)

Step	Deleted variable	df resid.	AIC
1		177	2075.9
2	zpl	178	2073.2
3	T	179	2071.5
4	T_{lag6}	180	2069.8
5	S	181	2068.5
6	S_{lag6}	182	2067.6
7	$chla_{lag6}$	183	2067.3
8	$chla$	184	2068.3

Table 2. Spearman correlations and their significance levels between the annual phenological variables (from left: date of first occurrence, date of last occurrence, span between these, percentage of positive observations $PO_\%$, mean positive observation PO_{mean}, and the centre of gravity for the monthly mean observations C). ***p ≤ 0.001, **p ≤ 0.01, *p ≤ 0.05, •p ≤ 0.1

		Cyanea spp.					Aurelia aurita				
	First	Last	Span	$PO_\%$	PO_{mean}	C	First	Last	Span	$PO_\%$	PO_{mean}
Cyanea spp.											
First											
Last	0.17										
Span	−0.86***	0.26									
$PO_\%$	−0.49*	0.23	0.57*								
PO_{mean}	−0.44•	0.46*	0.55*	0.58**							
C	0.50*	0.02	−0.47*	−0.39	−0.42•						
Aurelia aurita											
First	0.45•	0.11	−0.36	−0.49*	−0.01	0.44•					
Last	0.00	−0.21	−0.11	−0.15	−0.11	0.56*	0.38				
Span	−0.39	−0.26	0.22	0.23	−0.03	0.19	−0.35	0.69**			
$PO_\%$	−0.19	−0.21	0.14	0.33	0.06	−0.33	−0.35	−0.01	0.32		
PO_{mean}	0.29	−0.1	−0.29	0.12	−0.24	−0.07	−0.35	−0.2	0.01	0.65**	
C	−0.01	0.03	0.03	0.25	0.01	0.12	−0.03	0.50*	0.54*	0.43•	0.1

Table 4. Numerical output of the best fit model for the monthly abundance of *Cyanea* spp. Only significant levels for the nominal variable *Month* and the *Year × Month* interaction shown. *Month2, Month11* and *Month12* refer to February, November and December, respectively. J_{lag1} is the response variable J (number of jellyfish) lagged by 1 mo and zpl_{lag6} the zooplankton biomass lagged by 6 mo

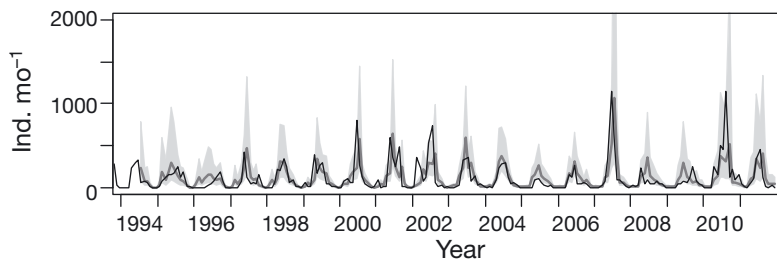| Variable	Estimate	SE	Z	Pr(>|Z|)
(Intercept)	78.52	133.90	0.587	0.558
J_{lag1}	2.01×10^{-3}	6.74×10^{-4}	2.976	0.003
zpl_{lag6}	2.07	1.00	2.08	0.038
Month2	451.70	191.10	2.364	0.018
Month11	−475.60	185.30	−2.566	0.010
Month12	−683.30	209.70	−3.259	0.001
Year:Month2	−0.23	0.10	−2.36	0.018
Year:Month11	0.24	0.09	2.566	0.010
Year:Month12	0.34	0.10	3.252	0.001
AIC	2068.3			
Deviance explained	44 %			
Theta (k)	0.58			
SE	0.06			

Fig. 5. Observed vs. modeled monthly abundances of *Cyanea* spp. Black line shows the aggregated monthly jellyfish observations. Grey line and shading show model predictions and their 95 % CI, respectively. The model starts at a later date than jellyfish observations due to the availability of zooplankton data

A. aurita data also contained more zeros and a larger overall variance than the data on *Cyanea* spp. Some of these issues may be resolved as more data are accumulated in the years to come.

Annual abundance

There is a significant diminishing trend in the expected number of annual observations for *Aurelia aurita*, while no significant trend was observed for *Cyanea* spp. (Fig. 6). In addition to a decreasing trend, *A. aurita* abundances seemed to vary with a 5-yr cycle (Fig. 6).

The best fit model for annual expected number of *Cyanea* spp. contained the explanatory variables T_W and zpl_S, both of which had a positive effect on the expected number of *Cyanea* spp. observations

(Fig. 6, Tables 5 & 6). The model correctly predicted only some of the peak years, suggesting that significant explanatory variables are missing from the model. For *Aurelia aurita*, none of the explanatory variables except for year were significant, so the model only shows the general negative trend in the expected number of annual *A. aurita* observations (Fig. 6, Tables 7 & 8). There are also obvious patterns in the residuals of the *A. aurita* model, with statistically significant autocorrelation at lag 5 (Fig. 6), indicating that significant, unidentified explanatory variables are missing from the model.

DISCUSSION

Local trends in jellyfish abundance

In contrast to common expectations of globally increasing jellyfish abundances, our results show a decrease or no trend in the abundance of the common Skagerrak scyhophozoans *Aurelia aurita* and *Cyanea* spp. On the contrary, there is a significant decline in the amount of *A. aurita* observed during the past 20 yr, with the expected number of annual observations falling from thousands at the beginning of the study period to just a few dozen in 2006 and 2007. This decrease is not unique; a recent analysis of jellyfish time series exceeding 10 yr duration also found that although 27 % of the examined sites showed an increase in jellyfish numbers over time, 16 % showed a decline of similar magnitude (Condon et al. 2013).

Even though *Cyanea* spp. abundances showed no sustained trend, their year-to-year fluctuation seems to have increased. Large summer swarms of *C. capillata* have been frequently featured in Norwegian newspapers in recent years, especially in 2010, often presented together with the hypothesis of a global increase in jellyfish numbers (ATEKST 2004–2012). However, our data suggest that these 'jellyfish summers' may be a result of large annual variation in *Cyanea* spp. numbers rather than a symptom of a persistent increase in abundance. Interestingly, for *Cyanea* spp., the date of first observation has a signif-
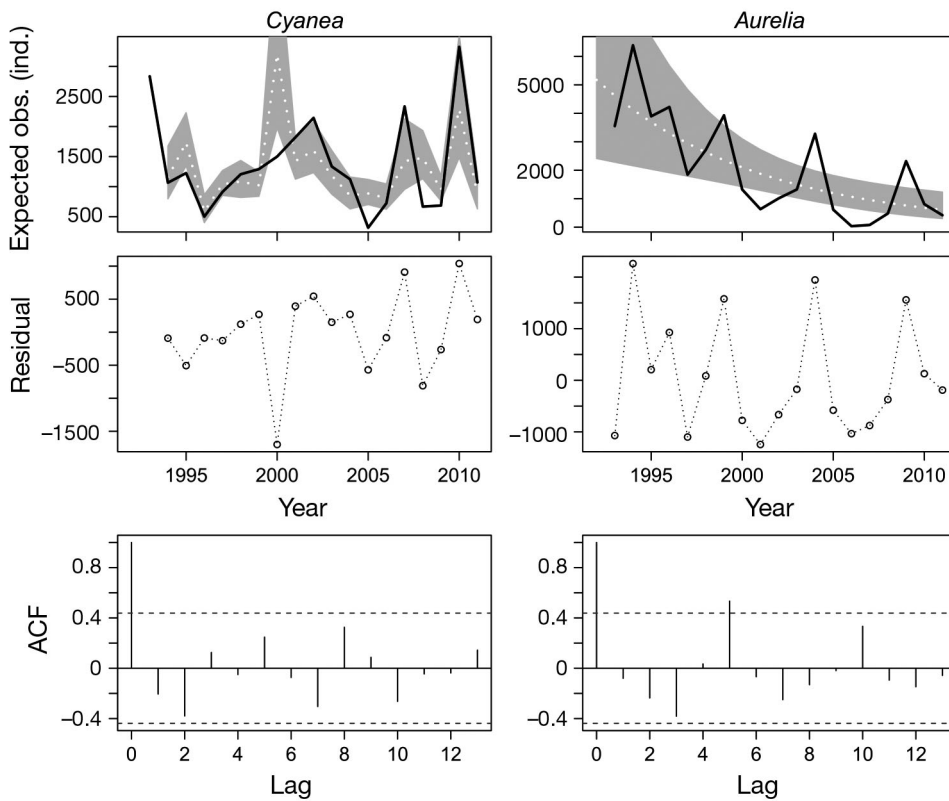
Fig. 6. Modeling of annual observations of *Cyanea* spp. and *Aurelia aurita.* Black lines in upper panels show the expected annual observations (*E*) calculated from actual observations, while the dotted white lines show the predicted means and the shading the 95% CIs for the best fit models (see text for details). Note that none of the explanatory variables apart from *Year* were significant for *A. aurita*, resulting in a model that only describes the general decreasing trend in *A. aurita* abundance. Middle panels show response residuals from the models, and the lowest panels are the autocorrelation function (ACF) of these residuals

Table 5. Backwards selection of the model for expected annual *Cyanea* spp. abundance. Initial model $E \sim Year + T_W + T_S + S_S + chla_S + zpl_S + zpl_W$, where E = expected annual number of jellyfish observations, T = temperature, S = salinity, $chla$ = chl *a* concentration, zpl = zooplankton biomass. Subscripts W and S indicate a winter mean from January to March and summer mean from July to September, respectively. Final model $E \sim T_W + zpl_S$. In step 6, zpl_W was removed and the simpler model chosen since there was a less than one unit difference in AIC and comparison of the models indicated no significant differences between them (ANOVA, $p_{Chi} = 0.1$)

Step	Deleted variable	df resid.	AIC
1		10	282.09
2	*Year*	11	280.11
3	S_S	12	278.18
4	T_S	13	276.34
5	$chla_S$	14	275.99
6	zpl_W	15	276.86

Table 6. Numerical output of the best fit model for the expected annual observations of *Cyanea* spp. T_W is winter (January to March) mean temperature and zpl_S summer (July to September) mean zooplankton biomass

Variable	Estimate	SE	Z	Pr(>|Z|)
(Intercept)	4.82	0.54	8.89	$<2 \times 10^{-16}$
T_W	0.27	0.08	3.21	0.0013
zpl_S	0.88	0.23	3.85	0.0001
AIC	276.86			
Deviance explained	47%			
Theta (k)	6.63			
SE	2.17			

icant negative correlation (rho = −0.48, p < 0.05) with the expected number of annual observations, as well as the span of the season, percentage of positive observations and, at a borderline significant level, average positive observation. Years with early observations of *Cyanea* spp. may thus be more likely to develop into years with high abundances.

For *Cyanea* spp., it should be noted that we are dealing with 2 species with differing geographic and seasonal distributions. *C. lamarckii* is endemic to the northern European seas and is here the more southern of the 2 species, while the more widespread, boreal *C. capillata* dominates the northern parts of the area, including the Skagerrak coast (Gröndahl 1988). *C. capitata* also consistently dominates in Flødevigen Bay, and is responsible for the large peaks observed in some years (T. Falkenhaug pers. obs.). Nevertheless, these species may react differently to environmental changes, such as increasing tempera-

Table 7. Backwards selection of the model for expected annual *Aurelia aurita* abundance. Initial model $E \sim Year + T_W + T_S + S_S + chla_S + zpl_S + zpl_W$ (see Table 5 for abbreviations)

Step	Deleted variable	df resid.	AIC
1		10	314.52
2	$chla_S$	11	312.53
3	T_S	12	310.65
4	S_S	13	308.95
5	zpl_W	14	307.32
6	zpl_S	15	306.01
7	T_W	16	304.41

Table 8. Numerical output of the best fit model for the expected annual observations of *Aurelia aurita*

Variable	Estimate	SE	Z	$Pr(>|Z|)$
(Intercept)	233.00	68.40	3.41	0.0007
Year	−0.113	0.03	−3.30	0.0010
AIC	324.22			
Deviance explained	35%			
Theta (k)	1.51			
SE	0.45			

tures, and their relative contributions may have changed during the study.

Our results of decline or no change in jellyfish abundances seem to conflict with reported increases in the frequency of cnidarian nematocysts in continuous plankton recorder (CPR) samples from the North Sea (Attrill et al. 2007, Kirby et al. 2009). However, it has been suggested that the nematocysts in CPR samples largely stem from the more oceanic scyphomedusa *Pelagia noctiluca* (Baxter et al. 2010), rarely advected to Skagerrak in numbers of consequence, or from smaller hydrozoan medusae or siphonophores (Gibbons & Richardson 2009, Lynam et al. 2010). Thus, the CPR data may not reflect changes in the numbers of the larger, more neritic scyphozoans like *Aurelia aurita* and *Cyanea* spp.

Role of life history

Changes in the abundance of *Cyanea* spp. and *Aurelia aurita* should be seen in the context of their metagenic lifecycles, which comprise a perennial, benthic polyp stage as well as a shorter-lived, pelagic medusa stage (Arai 1997, Boero et al. 2008, Lucas et al. 2012). In temperate waters, this life cycle is usually seasonal and follows the temperature and productivity cycles (Gröndahl 1988, Lucas et al. 2012).

Sexual reproduction by the jellyfish results in planktonic planula larvae, which settle down and metamorphose into polyps. The polyps can encyst and excyst in response to prevailing conditions, as well as reproduce asexually to form new polyps (reviewed by Arai 1997, Arai 2009, Lucas et al. 2012). Seasonal changes in environmental conditions trigger them to strobilate and produce ephyrae. The survival and reproductive success of the polyp stage thus has a direct impact on the size of the observed medusa populations (reviewed by Lucas et al. 2012). Unfortunately, the polyp stages are inconspicuous and scantily studied. Their geographic distribution along the Norwegian coast is poorly mapped, and nothing is known regarding local changes in their numbers.

Temperature and nutrition

The annual *Cyanea* spp. abundance in Flødevigen Bay was positively related to temperature during the preceding winter months. This could be due to temperature effects on reproduction and strobilation of polyps, or on survival and growth of the ephyrae and young medusae. In nearby Gullmarsfjorden, *C. capillata* strobilate in the spring (Gröndahl 1988), suggesting it is the polyp stage that is affected. Temperature is known to impact polyp strobilation (Holst 2012, reviewed by Lucas et al. 2012) as well as encystment and excystment processes (reviewed by Arai 2009). Holst (2012) found a rise in winter temperatures from 5 to 10 and 15°C to be deleterious for *C. capillata* strobilation, but beneficial for *C. lamarckii.* While Gröndahl (1988) observed no strobilation by *C. lamarckii* polyps in Gullmarsfjorden adjacent to Skagerrak, presumably due to the northern location, climate warming may allow *C. lamarckii* to expand its range and presence in the northern North Sea (Holst 2012). However, our *in situ* winter temperature range (January to March mean 3.9°C, max. 6.1°C) is still much below the increases simulated by Holst (2012). For *Aurelia aurita*, temperature is known to have a positive effect on ephyra feeding and growth rates (Båmstedt et al. 1999), likely enhancing survival of the young jellyfish.

Changing temperatures can also affect the phenology, and thus the degree of match/mismatch in the timing of prey and predator species (e.g. Edwards & Richardson 2004). Our time series indicate potentially diverging trends for the central tendencies (C) of *Cyanea* spp. and its zooplankton prey, with the bulk of both chl *a* and zooplankton biomass occurring earlier during the study period and *Cyanea* spp.

showing a borderline significant change towards a later timing. Changes in *Cyanea* spp. phenology could also result from changes in relative abundances of *C. capillata* and *C. lamarckii*, which differ in their seasonal timing (Gröndahl 1988)

We also found zooplankton prey availability to have a significant effect on the expected number of *Cyanea* spp. observations. On the monthly scale, it was food availability 6 mo earlier that had an impact. Food availability and nutritional status are known to influence strobilation and ephyra production in many scyphozoans (reviewed by Purcell 2007, Lucas et al. 2012). Naturally, food availability is also important for growth and survival of ephyrae and young medusae. At the annual level, the positive influence of summer zooplankton biomass on *Cyanea* spp. abundances could reflect good conditions for the growth and survival of the jellyfish. Plentiful zooplankton late in the summer may also allow the *Cyanea* spp. populations to persist later in the year, thus increasing the number of observations in these years. Either way, the result suggests that the *Cyanea* spp. are not decimating their zooplankton prey populations.

Similar results have been reported by Gibbons & Richardson (2009), who found interannual changes in the abundance of oceanic jellyfish in the North Atlantic to vary with zooplankton abundance and temperature changes, but not with the NAO index or chl *a* concentrations. As for jellyfish abundance in the North Atlantic shelf areas in general, they found that none of the investigated environmental variables — sea surface temperature, NAO, zooplankton and phytoplankton abundance — explained the interannual variation. However, they did observe a significant correlation with NAO in western central and western northern areas of the North Sea. Earlier studies by Lynam et al. (e.g. 2010), on the other hand, have indicated that abundances of *Aurelia aurita* and *Cyanea lamarckii* in the North Sea west of Denmark are negatively correlated with the NAO index. Our results seem contrary to this, as winter temperature, which we found to have a positive impact on *Cyanea* spp. numbers the following summer, is positively correlated with the NAO along the Skagerrak coast (Fromentin et al. 1998).

Biological interactions

None of the examined environmental or biological variables explained the decrease or the cyclicity in the expected number of *Aurelia aurita* observations at the annual scale. This suggests abundances are controlled by other factors not included in the current analyses, possibly biological interactions. The 5-yr cyclical trend in the expected annual observations of *A. aurita* was not explained by the region's dominant climatic oscillation, NAO, and is shorter than the frequently indicated decadal or multi-decadal fluctuations (Gibbons & Richardson 2009, Condon et al. 2013). Population cycles like this could result from predator–prey cycles or density-dependent factors (Begon et al. 1990), possibly affecting the polyp generation. Post settlement, polyp and planulocyst numbers can be significantly reduced by predation (Hernroth & Gröndahl 1985, Östman 1997, Lucas et al. 2012) as well as inter- and intraspecific competition for substrate (reviewed by Lucas et al. 2012). Interannual differences in this stage specific mortality may be expected to have a strong impact on the annual abundances of jellyfish.

Our observation period coincided with a possible regime shift in the coastal waters of the Norwegian Skagerrak around the turn of the millennia. Major changes in the plankton community have taken place and are possibly to blame for concurrent collapses in gadoid recruitment (Alvarez-Fernandez et al. 2012, Johannessen et al. 2012). Abrupt increases in particulate organic carbon and nitrogen as well as dissolved organic nitrogen and non-autotrophic material have been attributed to increased freshwater runoff (Frigstad et al. 2013). Simultaneously, sugar kelp *Laminaria saccharina* has been increasingly replaced by ephemeral filamentous macroalgae, possibly as a result of the increased nutrient and particle loading (Moy & Christie 2012). These changes could also impact jellyfish. While reductions in available zooplankton prey are likely to impact their abundances negatively, both eutrophication and reduced optical conditions are potentially favorable for jellyfish (reviewed in Purcell et al. 2007). Sugar kelp is a preferred habitat for *Aurelia aurita* polyps (Östman 1997), and its demise, together with increased substrate competition from ephemeral algae, could partly explain the reduction in jellyfish observations. However, verifying any of these potential links requires further study.

Even though *Cyanea capillata* is a known intraguild predator of *Aurelia aurita* (Titelman et al. 2007), our present data revealed no connection between the monthly or annual occurrence of the 2 species. Although it has been suggested that *C. capillata* is dependent on gelatinous prey in its early development (Båmstedt et al. 1997), the decline in *A. aurita* numbers seems to not have had a deleterious effect on *Cyanea* populations. It is interesting that the

change in the seasonal distribution of *A. aurita* coincides with first observations of the invasive ctenophore *Mnemiopsis leidyi* in the area (Oliveira 2007). A generalist zooplanktivore, *M. leidyi* could also contribute to changes in the scyphozoan numbers through competition as well as predation on their planula larvae (Javidpour et al. 2009).

Advection and aggregation

We have no data on whether the jellyfish in Flødevigen Bay are produced locally or advected to the area. The westward flowing NCC includes water of both Baltic and Atlantic origin as well as freshwater run-off (Aure et al. 1998). Interannual differences in the relative contributions of these water masses could affect the species composition of scyphomedusae in the study area. Gröndahl (1988) proposed that in Gullmarsfjorden, the *Cyanea capillata* population is more influenced by immigration from the North Sea than *Aurelia aurita*, while *C. lamarckii* does not reproduce in the area and is entirely dependent on transport from the southern North Sea.

For Flødevigen Bay, wind direction and speed may also affect the distribution of planktonic organisms. Westerly winds retard the current and force it off the coast, causing upwelling of water and associated plankton from deeper layers, whereas wind from the east and onshore wind stress will create onshore transport of water, causing jellyfish to aggregate in coastal areas of Skagerrak. Preliminary analyses of wind direction, upwelling and jellyfish abundance in Flødevigen Bay did not show a clear relationship, with both onshore and offshore wind increasing the number of jellyfish in the bay (J. Albretsen & L.-J. Naustvoll unpubl. data). We assume effects of wind on the observed abundances are in the current analyses dampened by the pooling of the data to monthly and annual observations.

Concluding remarks

Our results reflect the importance of considering differences between localities, regions and species when discussing trends in jellyfish abundances. In contrast to popular expectations regarding a global increase in jellyfish numbers, *Aurelia aurita* at Flødevigen Bay has declined in abundance during the last 2 decades, while *Cyanea* spp. showed no temporal trends in abundance. While the daily counts used in our analyses cannot be considered strictly quantita-

tive and are certainly affected by the weather, winds and tides, we believe that averaging such frequent counts over months and years gives a reliable indication of the long term trends in the abundances and seasonality of the observed species. Even though it is possible that the observed changes in *A. aurita* abundances are simply part of an unidentified multi-decadal oscillation typical for jellyfish (Condon et al. 2013), it seems unlikely given the dramatic nature of the decrease. Also, no simultaneous decrease was observed for *Cyanea* spp. While there is a plethora of studies discussing anthropogenic influences that may positively affect jellyfish numbers, those discussing reductions in numbers are scarce. Due to the complex metagenic life cycles of the scyphozoans in question, as well as the multitude of environmental and biological interactions potentially involved, pinpointing the causes behind interannual variation is challenging. Temperature and prey availability explained part of the variation in *Cyanea* spp. abundances. The decline and cyclical patterns in *A. aurita* abundances, however, remain unexplained. So far, unidentified factors involved may include biological interactions such as competition, predation or density dependent processes, possibly involving the benthic stages. Changes may also be attributable to a possible concurrent regime shift along the Norwegian Skagerrak coast, which has caused changes both in prevailing optical conditions (Frigstad et al. 2013) as well as available prey (Johannessen et al. 2012) and substrate for polyps (Moy & Christie 2012). In addition to meager availability of long term monitoring data on jellyfish abundances, there is an evident lack of information regarding both the *in situ* distribution and abundance of their benthic stages. Environmental and biological interactions impacting the polyp generation are also poorly known. A better understanding of polyp ecology is, thus, crucial for adequately explaining the observed fluctuation in jellyfish numbers.

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