Impact of climate change on long-term zooplankton biomass in the upwelling region of the Gulf of Guinea

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We investigated long-term changes in coastal zooplankton in the upwelling region in the Gulf of Guinea, 1969–1992, in relation to climatic and biotic factors. We considered the role of hydrographic and climatic factors, i.e. sea surface temperature (SST), salinity, sea level pressure, windfield, and Southern Oscillation Index (SOI), in the long-term variation of zooplankton in a multiple regression analysis, along with the abundance of *Sardinella*. Annual variation in zooplankton biomass was cyclical, with the annual peak occurring during the major upwelling season, July–September. Over the 24-year period, there was a downward trend in zooplankton biomass (equivalent to 6.33 ml per 1000 m^3 per year). The decomposed trend in SST during the major upwelling revealed gradual warming of surface waters. This trend was believed to be the main influence on the abundance of the large copepod *Calanoides carinatus* (sensitive to temperatures above 23°C), which appears in the coastal waters only during the major upwelling season. The warming trend associated with global climate change could affect zooplankton community structure, especially during the major upwelling season. Global warming coupled with "top–down" (predation) control by *Sardinella* might be responsible for the long-term decline in zooplankton biomass in the upwelling region of the Gulf of Guinea.

Keywords: *Calanoides carinatus*, climate change, global warming, Gulf of Guinea, *Sardinella*, upwelling, zooplankton.

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Introduction

The upwelling region of the Gulf of Guinea extends from the coast of Côte d'Ivoire around to Benin. The region is also referred to as the Central West African Upwelling (Frost *et al*., 2005), and the coastal oceanography has been described by several authors (Howat, 1945; Longhurst, 1962; Bakun, 1978; Houghton, 1983; Mensah and Koranteng, 1988; Binet and Marchal, 1993). Four distinct and predictable hydrographic seasons have been described: the minor (December–March) and major upwelling (July–September) interspersed with periods of stratification, typically with a thermocline 30–40 m below the surface.

Changes in local hydrography and climatic effects are not the only physical factors that influence zooplankton production in the Gulf of Guinea. It has been demonstrated that the entire Gulf of Guinea is influenced to a large extent by the meteorological and oceanographic processes of the South and North Atlantic Ocean (Merle and Arnault, 1985; Fontaine *et al*., 1999), principally their oceanic gyral currents, which in turn reveal relationships with global atmospheric changes, such as the *El Niño* Southern Oscillation (ENSO).

Zooplankton studies in the Gulf of Guinea date back to the late 19th century, when several expeditions visited the region and assessed the species composition and diversity. The Danish Atlantide expedition of 1945/1946 provides extensive coverage of the copepods of the region (Vervoort, 1963, 1965). By the mid-1960s, Ghana, Côte d'Ivoire, Sierra Leone, and Nigeria had set up fishery laboratories which, in addition to stock assessments, also carried out monitoring of the zooplankton biomass in relation to the fishery.

During the upwelling, zooplankton are more abundant, though with less species diversity, than during the thermally stratified periods (Bainbridge, 1972). This applies mainly to outer-shelf stations because, in the inshore waters, meroplanktonic larvae (e.g. polychaete, echinoderm, and caridean larvae), mask the effect. During periods of thermal stability formation, the zooplankton is relatively sparse, with high species diversity and a considerable proportion of carnivorous species.

In addition to the annual cycle of abundance, which is clearly related to the annual hydrographic cycle, zooplankton abundance is variable over a longer period. Given the importance of hydrography in shaping the annual cycle, it is logical to relate these variations quantitatively to changes in the physical environment or, more specifically, to climate change, which drives most of the physical factors in the oceans. Studies in the Atlantic (Taylor and Stephens, 1980; Colebrook, 1986; Fransz *et al*., 1991; Verheye, 1991) and the Pacific oceans (Brodeur and Ware, 1992; Francis and Hare, 1994; Mackas, 1995), for example, relate zooplankton distribution to oceanographic condition.

Variations in zooplankton abundance have also been examined at various temporal scales; diurnal (Lampert, 1989), seasonal (Colebrook, 1982), and long-term (Jossi and Goulet, 1993; Mollmann *et al*., 2000). Among the abiotic factors, temperature

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is considered to be one of the important factors influencing the distribution of planktonic communities (Parsons *et al*., 1984). Global warming has become a topic of concern (IPCC, 2007), and the commensurate rise in sea surface temperature (SST), therefore, might be expected to play an important role in the plankton dynamics of upwelling regions such as the Gulf of Guinea. Climatic trends in the Gulf of Guinea have been consistent with global changes (Koranteng and McGlade, 2000).

This study examines the time-series of zooplankton biomass from the Gulf of Guinea, the longest time-series of zooplankton in the region, to understand changes in the pelagic ecosystem. Mensah (1995) reported on the declining trend in the zooplankton without attributing any causal agent. In this study, patterns of long-term trend in zooplankton biomass are described and examined in relation to parallel changes in the environmental variables, including climatic drivers and biota.

Methodology

Zooplankton biomasses from 1969 to 1992 were obtained from the Marine Fisheries Research Division (MFRD) in Ghana, which carried out monitoring, monthly or fortnightly, along a transect off the coast of Ghana, within the Gulf of Guinea (Figure 1). Five stations (A0, A1, A2, B, and C) along this transect were sampled with an International Cooperative Investigations of the Tropical Atlantic (ICITA) net, with a mesh size of 330 μm, ring diameter of 1 m, and filtering section 2.4 m long. However, data obtained from Station A0 (the harbour jetty) were excluded from statistical analysis because the station was a late addition to the programme, and therefore data were incomplete.

At each station, the net was towed in a step-oblique fashion at five steps for 10 min at a towing speed of 2 knots. A 10-m length of wire was released at each step, totalling 50 m of wire. The samples collected were fixed with buffered formaldehyde to a final strength of 4%. Later in the laboratory, zooplankton and *Sardinella* larvae were sorted out separately, and the displacement volume of each was measured and standardized as millilitres per 1000 m^3 of seawater (Harris *et al*., 2000). Monthly data were calculated as averages over the pooled data for all stations, except Station A0.

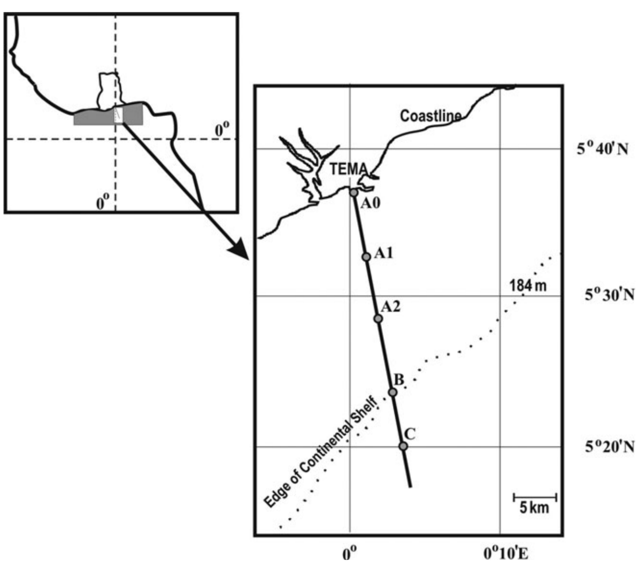

Figure 1. Map of the central eastern Atlantic Ocean showing the upwelling region of the Gulf of Guinea (shaded), and the sampling locations along the hydrographic transect (A0, A1, A2, B, C) off the coast of Ghana.

Climatic and oceanographic data on SST, sea level pressure, and zonal and meridional windstress were obtained from the International Comprehensive Oceanic and Atmospheric Data Sets (I-COADS) of the National Oceanic and Atmospheric Administration (NOAA), USA. These were monthly data of 1° × 1° resolution from 1°W to 1°E and 5°N to 6°N. In addition, monthly data on the Southern Oscillation Index (SOI) of similar resolution and coverage were obtained from the Climate Diagnostic Centre of NOAA. The SOI was included among the environmental factors because of its significant influence on local hydro-climatic processes (Binet, 1996).

Variations added by seasonal or other cycles, in time-series analyses, make it more difficult to detect long-term trends. To overcome this problem, the data were decomposed into the four hydrographic seasons. Mensah (1991) and Wiafe (2002) have identified periods for the four hydrographic seasons in the Gulf of Guinea as minor upwelling (December–March), thermocline formation (April–June), major upwelling (July–September), and thermocline formation (October–November). In this study, the two thermally stratified periods will be referred to as hydrographic thermocline 1 (April–June) and hydrographic thermocline 2 (October–November).

A Mann–Kendall trend test was performed on the data, an improvement upon using regression as a trend test (Gilbert, 1987). The Mann–Kendall test statistic (Z) is calculated as follows:

$$Z = \frac{S-1}{\sqrt{S_y}},$$

where

$$S = \sum_{k=1}^{n=1} \sum_{i=k-1}^{n} \operatorname{sign}(X_j - X_k) \text{ and } S_y = 1/18[n(n-1)(2n-5)],$$

the sign $(X_j - X_k)$ is the sign of all $n(n-1)/2$ possible differences, n is the number of points in the distribution. The Z-statistic was referred to a standard cumulative normal distribution table (Pearson and Hartley, 1966) at null hypothesis acceptance level of $p < 0.05$. Significant correlations between time-series can be criticized because, if there is autocorrelation in the series, the true number of independent points could be overestimated. This problem was detected using the method of Quenouille (1952) to calculate the effective number of independent observations.

The effect of physical and/or biological factors on zooplankton biomass was determined from multiple regression analysis. The biomass of zooplankton and *Sardinella* larvae used in the analysis were log-transformed to improve homogeneity of variance for statistical analysis. The multiple regression analysis was performed in stepwise fashion, where independent variables were included one at a time to assess their contribution to the variation in the dependent variable.

Results

The anomalies in zooplankton biomass revealed cyclical variation, with peaks during the major upwelling season (Figure 2a). Periods in which peak abundance was above or below the long-term mean were considered as "high productive" and "low productive" years, respectively. Similarly, there was a cyclical variation in the

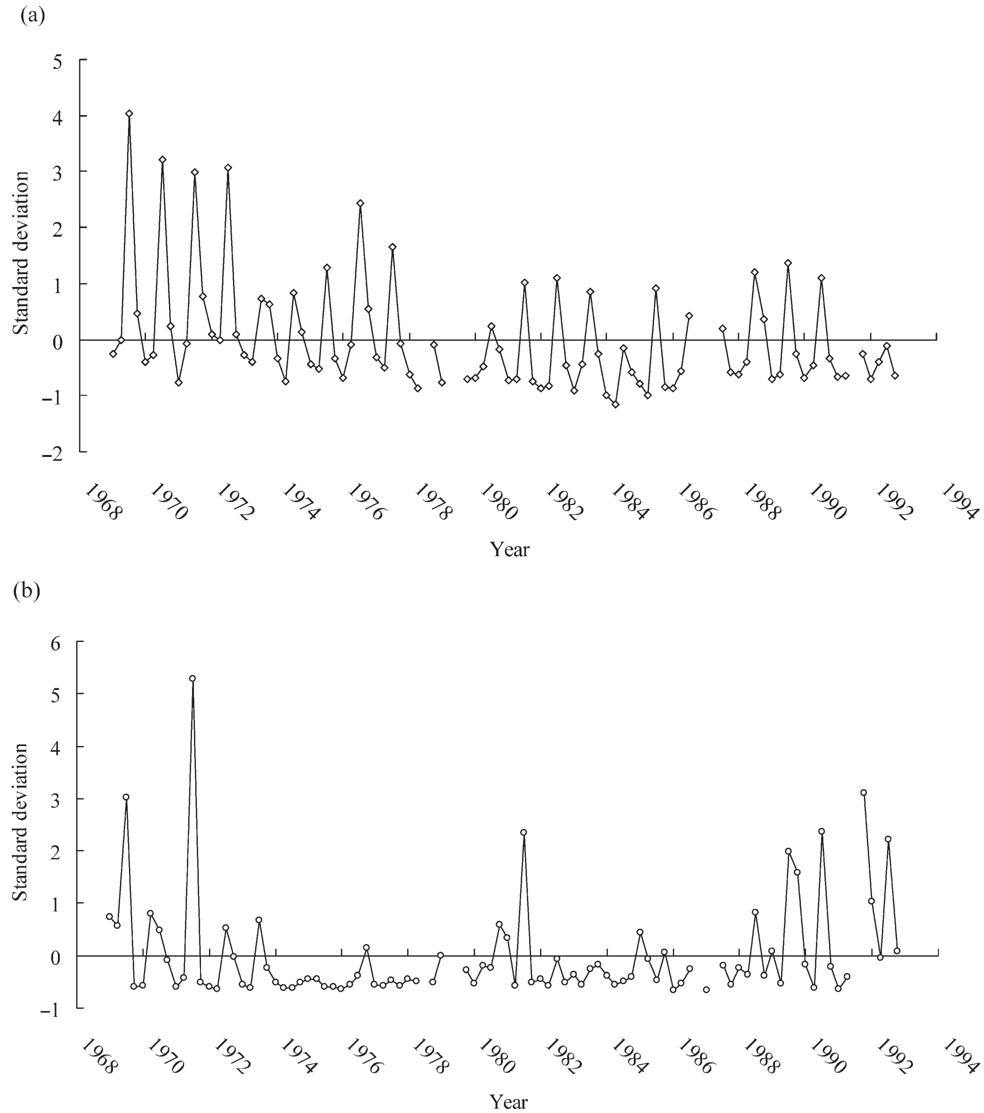

Figure 2. Anomalies of biomass of zooplankton and *Sardinella* larvae, 1969 – 1992, in the upwelling region of the Gulf of Guinea. Data points refer to averages for each hydrographic season; for each year it follows the minor upwelling, hydrographic thermocline 1, major upwelling, hydrographic thermocline 2 (see text).

Sardinella larvae, with peaks during the major upwelling but no discernible trend in their long-term biomass (Figure 2b).

Mann–Kendall trend analysis confirmed the negative trend in zooplankton biomass and the lack of any trend in *Sardinella* larval abundance. Linear trend, estimated by the least-squares method, revealed that the rate of decrease in zooplankton biomass was 6.33 ml per 1000 m^3 of seawater per year ($r^2 = 0.320$; Figure 3).

SST during the major upwelling and hydrographic thermocline 2 periods of the annual cycle have risen gradually (Table 1; see Figure 4). From the data shown in Figure 2a, we noted high production of zooplankton during the major upwelling season. A plot of SST vs. zooplankton biomass demonstrated a significant negative relationship (Figure 5), and that low zooplankton production coincided with high SST.

Zooplankton temporal variation in each of the hydrographic seasons revealed that the rate of decline during the major upwelling was higher than the other seasons (Figure 6). From multiple regression analysis, *Sardinella* larvae biomass, SST, local sea level pressure, zonal windstress, SOI, and salinity were identified as significant predictors of zooplankton biomass during the various hydrographic seasons (Table 2). During the hydrographically stratified period from October to November, zooplankton production was strongly influenced by regional atmosphere–ocean dynamics, as indicated by the SOI.

During the remainder of the year, the SST (in both upwelling periods) and/or the abundance of *Sardinella* larvae (April–September) were the principal factors influencing variation in zooplankton biomass. Comparison of seasonal variation in biomass between zooplankton and *Sardinella* larvae revealed a month's lag between their peaks (Figure 7). Multiple regression analysis based on seasonal biomass, averaged over the study period, revealed that SST alone accounted for 82.2% ($p < 0.001$) of the total variance in zooplankton biomass.

Figure 3. Interannual variation in zooplankton biomass in the upwelling region of the Gulf of Guinea.

Table 1. Results of Mann–Kendall trend tests on biotic and abiotic time-series data.

Hydrographic season	Mann–Kendall statistic (Z)						
	Zooplankton biomass	*Sardinella* larvae biomass	SST	Sea level pressure	Zonal wind intensity	Salinity	SOI
Minor upwelling	−82	87	–	–	–	–	–
Hydrographic thermocline 1	–	–	–	–	82	–	–
Major upwelling	−70	–	64	–	89	–	−67
Hydrographic thermocline 2	−100	69	78	70	116	–	−2.45
Overall Trend	−5.14	1.99	–	–	3.88	–	–

Positive and negative signs indicate upward and downward trends, respectively. Only significant ($p < 0.05$) trends are reported in the table.

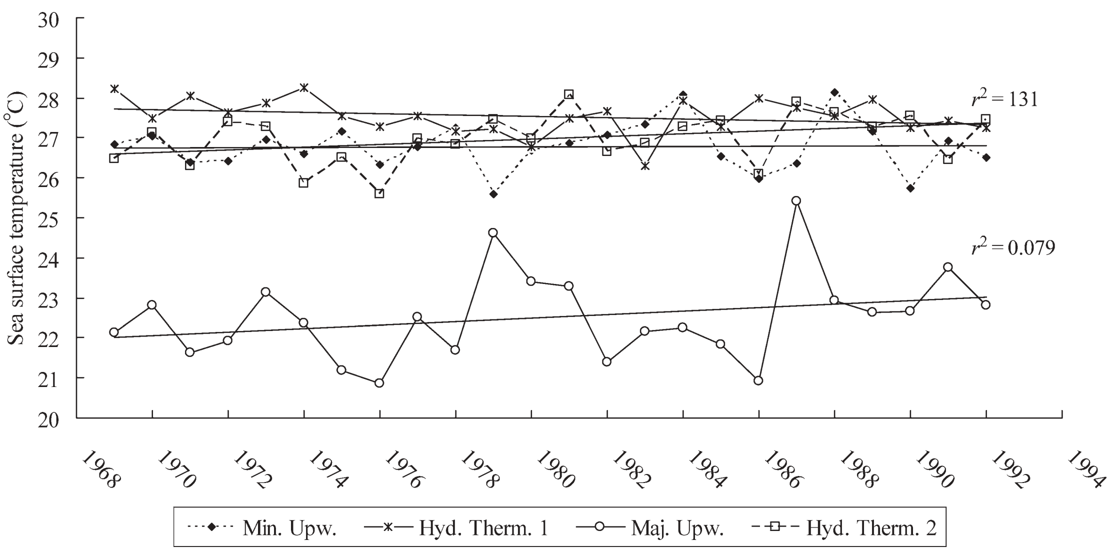

Figure 4. Distribution of SST with respect to the hydrographic seasons. Values of r^2 have been reported for positive trend lines only [i.e. major upwelling and thermocline 2].

Discussion

On a global scale, anthropogenic emissions of greenhouse gases have contributed to the radiative balance of the Earth, thereby increasing global temperature and altering the hydrological cycle and atmospheric and oceanic circulation, weather patterns, and precipitation (IPCC, 2007). Bakun (1990) has identified the trend towards increasing windstress over the world's major upwelling areas during the period from 1950 to the late 1980s as an effect that can be attributed to long-term global

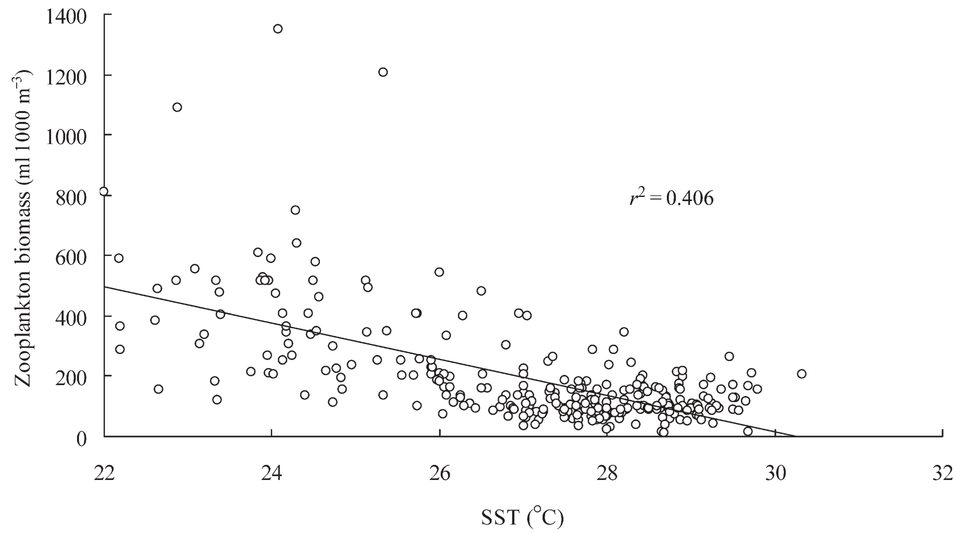

Figure 5. Relationship between zooplankton biomass and SST over a 24-year period, 1969 – 1992. Data points refer to monthly values.

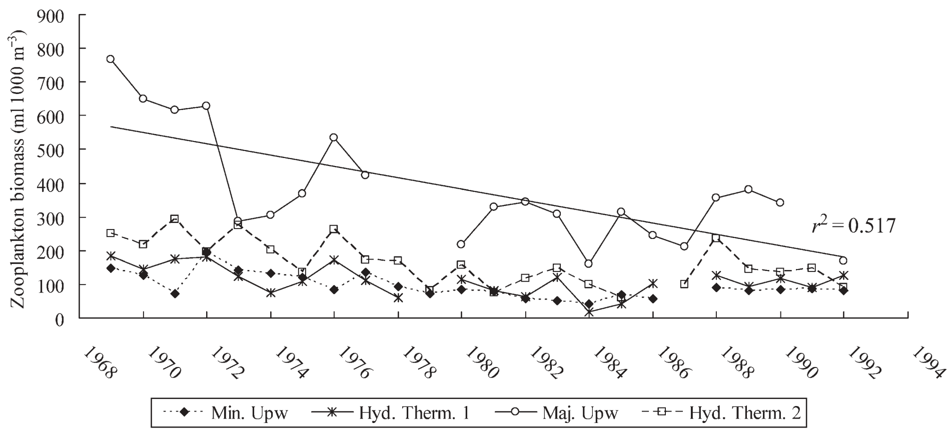

Figure 6. Seasonal variation in zooplankton biomass in the upwelling region of the Gulf of Guinea. Four hydrographic seasons are identified in the Gulf of Guinea (see text).

Table 2. Percentage variance in the seasonal biomass of zooplankton accounted for by biotic and abiotic factors based on data, 1969 – 1992.

Hydrographic season	Significant factors in model	% variation explained by model ($p < 0.05$)
Minor upwelling	SST	30.2
	Sea level pressure	14.8
	Zonal wind stress	9.0
Hydrographic thermocline 1	*Sardinella* larvae	20.1
Major upwelling	*Sardinella* larvae	29.1
	SST	18.6
	Zonal wind stress	10.8
Hydrographic thermocline 2	SOI	52.0
	Salinity	10.2

warming. For upwelling regions, this phenomenon could influence the biological dynamics, as noted for the zooplankton community in several ICES regions (ICES, 2006). In most regions, increasing windstress will increase upwelling; however, in the Gulf of Guinea, the upwelling is not locally forced but results from complex changes in the pressure field within the tropical Atlantic.

During this study, we noted that zooplankton biomass in the Gulf of Guinea, which experiences a seasonal upwelling, has declined significantly over a 24-year period. The gradually increasing trend in SST, especially during the upwelling season, accounted for >50% of the variability in the long-term biomass of zooplankton, suggesting that global warming could be an important factor in the declining trend in zooplankton of the region.

It has been reported that a significant proportion of total zooplankton biomass during the major upwelling is caused by the copepod *Calanoides carinatus* (Bainbridge, 1972; Mensah, 1974a). The species is advected into the coastal waters from South Atlantic Central Water as a result of the upwelling (Mensah, 1974a). This species is temperature-sensitive. It migrates down to 500 m as diapause Stage V copepodites when water temperatures exceed 23°C, reappearing the next upwelling season (Mensah, 1974a). In this study, we attempt to demonstrate that the changing conditions during the major upwelling, as a result of global

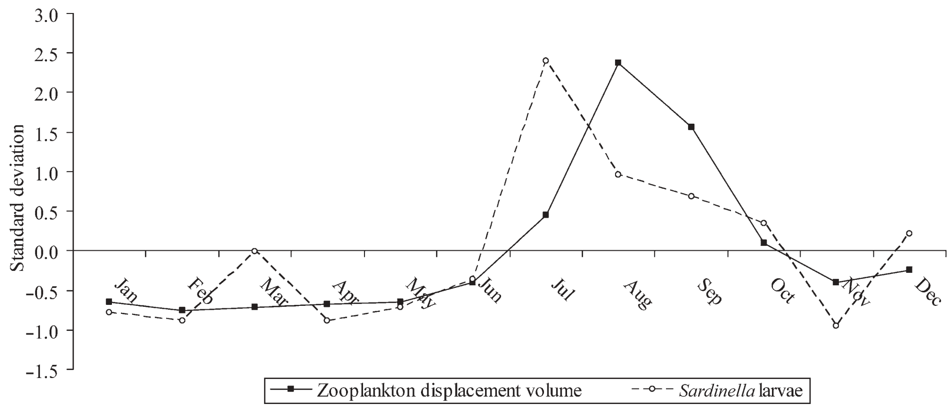

Figure 7. Standardized monthly distribution of zooplankton and *Sardinella* larvae averaged over a 24-year period, 1969–1992.

warming, may be ecologically significant. The abundance of *C. carinatus* might be reduced by the observed surface warming, leading to a possible shift in zooplankton community structure. This will have direct consequences on the pelagic fisheries in the region.

The most abundant pelagic species in the upwelling region of the Gulf of Guinea are *Sardinella aurita*, *S. maderensis*, *Engraulis encrasicolus*, and, in certain years, *Scomber japonicus* (Mensah and Koranteng, 1988; Koranteng, 1995). Spawning of *S. aurita* commences in response to the start of the coastal upwelling (Quaatey and Maravelias, 1999). However, Binet (1995) suggested that plankton abundance, providing forage for juvenile or adult fish, is more important for sustaining the biomass of the stock than spawning success and larval survival. Of the large number of relationships between fish and zooplankton, the most important is that linking the latter with the recruitment of fish, for which information has been gathered for the past three or four decades (Cushing, 1995). Among other foods, fish larvae eat nauplii and copepodite stages, and part of the recruitment mechanism may depend on this process.

Mensah (1995) investigated the potential effect of zooplankton on the *Sardinella* fishery by considering whether the declining trend in zooplankton was affecting the fishery. He concluded that the zooplankton production would be adequate for survival of the fish stock. Thus, the fishery might not be resource-limited (i.e. bottom–up process). A month's lag exists between the peaks of *Sardinella* larval abundance and total zooplankton biomass, suggesting a "match" between the predators and larval food and, hence, the potential for a climate-change induced "mismatch" to compromise recruitment in *S. aurita* stocks (Cushing, 1974, 1975, 1982, 1990). This study has reported a significant decline in zooplankton biomass from the late 1960s to the early 1990s, and attributes the trend to global warming. Although biological (top–down) control was also important, there was no long-term trend in the abundance of the predatory fish larvae. Although the zooplankton time-series analysis was at the biomass level rather than species level, knowledge of the biology and distribution of the dominant species during the major upwelling (i.e. *Calanoides carinatus*; Mensah, 1974b) gives credence to the assertion that the current trend in warming of the ocean, especially during the major upwelling, might result in a shift in zooplankton community structure and impacts on fishery resources.

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