

Mesoscale, cyclonic eddies as larval fish habitat along the southeast United States shelf: a Lagrangian description of the zooplankton community

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Govoni, J. J., Hare, J. A., Davenport, E. D., Chen, M. H., and Marancik, K. E. 2010. Mesoscale, cyclonic eddies as larval fish habitat along the southeast United States shelf: a Lagrangian description of the zooplankton community. – *ICES Journal of Marine Science*, 67: 403–411.

The Charleston Gyre region is characterized by continuous series of cyclonic eddies that propagate northeastwards before decaying or coalescing with the Gulf Stream south of Cape Hatteras, NC, USA. Over 5 d, chlorophyll-*a* concentration, zooplankton displacement volume, and zooplankton composition and abundance changed as the eddy moved to the northeast. Surface chlorophyll-*a* concentration decreased, and zooplankton displacement remained unchanged as the eddy propagated. Zooplankton taxa known to be important dietary constituents of larval fish increased in concentration as the eddy propagated. The concurrent decrease in chlorophyll-*a* concentration and static zooplankton displacement volume can be explained by initial stimulation of chlorophyll-*a* concentration by upwelling and nutrient enrichment near the eddy core and to possible grazing as zooplankton with short generation times and large clutch sizes increased in concentration. The zooplankton community did not change significantly within the 5 d that the eddy was tracked, and there was no indication of succession. Mesoscale eddies of the region are dynamic habitats as eddies propagate northeastwards at varying speeds within monthly periods. The abundance of zooplankton important to the diets of larval fish indicates that the region can provide important pelagic nursery habitat for larval fish off the southeast coast of the United States. A month of feeding and growth is more than half the larval duration of most fish spawned over the continental shelf of the southeastern United States in winter.

Keywords: larval fish food, mesoscale cyclonic eddies, zooplankton.

Received 30 March 2009; accepted 4 November 2009; advance access publication 16 December 2009.

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Introduction

Eddies and their attendant fronts may constitute important pelagic habitat for fish eggs and larvae in the ocean (Bakun, 2006). Cyclonic eddies, typically with upwelling within their cores, can provide water enriched with nutrients that enhances primary and secondary productivity (Yoder, 1985; Huntley *et al.*, 2000; Yoder *et al.*, 2001; Nixon and Buckley, 2002; Ressler and Jochens, 2003; Teira *et al.*, 2005). Zooplankton is the principal food of larval fish (Turner, 1984), so cyclonic eddies might provide improved feeding habitat (Yoder *et al.*, 1983; Govoni and Hare, 2001; Richardson, 2002). Eddies might also act to retain fish larvae near their spawning areas (Lobel and Robinson, 1986) and in favourable feeding environments, or provide mechanisms to transport them to suitable juvenile habitat (Sponaugle *et al.*, 2005). By increasing their survival through enhanced feeding, retention, and transport, eddies might contribute to the fishery production of ecosystems.

Off the southeastern United States, small, ephemeral, and large, more persistent, cyclonic eddies form in the trough of Gulf Stream meanders. Small frontal eddies form where the Gulf separates from

the shelf edge downstream of Cape Canaveral, FL (Lee *et al.*, 1991). Large, mesoscale (Haury *et al.*, 1978), cyclonic eddies form downstream of the Charleston Bump in association with a semi-permanent, offshore deflection of the Gulf Stream (Bane *et al.*, 2001). These mesoscale cyclonic eddies propagate northeastwards with meander troughs at speeds of 20–50 cm s⁻¹, and the core of the Gulf Stream flows northeastwards at speeds of 100–200 cm s⁻¹. The circulation of these eddies creates southwestward flow on the shoreward side of the eddy, which is typically at or on the shoreward side of the continental shelf break. This area of mesoscale cyclonic eddy genesis is termed the Charleston Gyre region (Govoni and Hare, 2001).

The importance of these mesoscale cyclonic eddies, known singularly as the Charleston Gyre, to the productivity of the southeast US continental shelf ecosystem is largely unexplored. Previous studies have demonstrated that their cyclonic circulation brings deep nutrient-rich water to near the surface, which can result in increased primary productivity (Atkinson, 1985). This increased primary productivity is an important contributor to overall primary production in the SE continental shelf ecosystem (Lee

et al., 1991). The influence of eddy-driven primary productivity on secondary productivity and on the food of larval fish is unknown. The survival of larval fish, a determinant of fisheries production, is dependent on adequate food for growth (Pepin *et al.*, 2003). The overall objective here was to gain a better understanding of the role of the Charleston Gyre in the production of larval fish food along the southeast continental shelf.

Material and methods

Specific objectives were: (i) to locate an eddy typical of the Charleston Gyre region with advanced very high-resolution radiometer (AVHRR) satellite images of sea surface temperature (SST); (ii) to intercept the northward propagation of an eddy and deploy satellite-tracked and global positioning system (GPS), radio-beaconed drifters within the eddy; (iii) to track and follow drifters through time as the eddy propagated northeastwards; (iv) to characterize the hydrography, surface chlorophyll-*a*, zooplankton displacement volume, and zooplankton community within the eddy; and (v) to relate zooplankton abundance to known diets of larval fish from the region.

Cruise and Lagrangian data to characterize the eddy

AVHRR satellite images showed a large cyclonic eddy forming north of the Charleston Bump in January 2003. On 2 January 2003, two transects were completed with conductivity (salinity), temperature, and density (CTD) profiles taken to verify its location (Figure 1).

Drifters with attached drogues were released on 30 January and 5 February 2003 (Figure 1). They were of standard design, as described by Sybrandt and Niiler (1990), with the drogue centred at 15 m. Initially, six drifters were released near the eddy core (Figure 1), one was tracked with a radio-beaconed GPS, and the other five were tracked by satellite (ARGOS). The drifters were released in a pentagonal pattern with the radio-beaconed GPS drifter in the centre. Three days after release, the radio-beaconed GPS drifter was retrieved before a strong low-pressure system moved through the area. The other five satellite-tracked drifters were not retrieved and continued to transmit data. Six days after release, one of the original satellite-tracked drifters was relocated and three additional satellite-tracked drifters were deployed in a rectangular pattern using the located drifter as one of the corners of the rectangle. The radio-beaconed GPS drifter was released in the middle of the rectangle. Hydrographic measurements and all biological collecting focused on the location of the radio-beaconed GPS drifter.

Hydrographic and biological oceanographic data to characterize the eddy

Eight CTD transects were completed in the cross-eddy dimension, i.e. perpendicular to the isobaths (Figure 1). Temperature, salinity, and density data from these transects were used to construct cross-eddy sections and to define the water masses in the area. Two water masses are typical off the southeastern US coast south of Cape Hatteras: Gulf Stream water and continental shelf water (Pietrafesa *et al.*, 1985; Xie and Pietrafesa, 1995). Eddy diffusion can result in their admixtures.

Chlorophyll-*a* was measured by taking varying volumes of surface water, depending on water mass, and filtering it through 25-mm GF/F Millipore filters. Filters were frozen in liquid nitrogen on board ship, and chlorophyll-*a* was extracted in acetone in

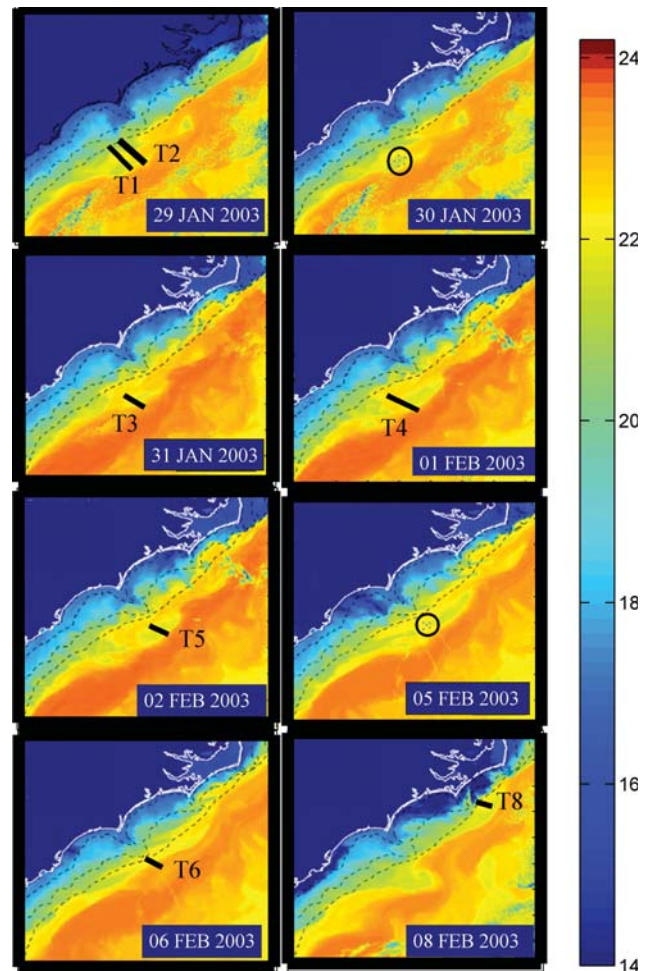


Figure 1. Composite, advanced very high-resolution radiometer (AVHRR) images of maximum SST for each day of collection on and off the continental shelf of the southeastern United States. Unbroken lines depict cross-shelf transects (T1–T6), and encircled dots indicate the location and configurations of satellite-tracked drifter releases (broken lines depict 20, 40, and 100 m isobaths).

the laboratory ashore, then measured fluorometrically, following Strickland and Parsons (1968).

Night-time collections of zooplankton and ichthyoplankton were made with a 1-m² Multiple Opening and Closing Nets and Environmental Sensing System (MOCNESS; Wiebe *et al.*, 1976). The MOCNESS was deployed on six nights nominally at 20:00, 00:00, and 04:00 h local time (Eastern Standard Time) or 01:00, 05:00, and 09:00 Coordinated Universal Time (near the radio-beaconed GPS drifter). Eight MOCNESS nets were opened and closed during each cast: five with 333- μ m mesh and three with 0.25 m², 64- μ m mesh nets embedded in the 333- μ m mesh 1 m² net frames. The three 64- μ m mesh nets were opened in the 150–200, 50–100, and 0–25 m depth intervals; only zooplankton from these nets was analysed. Operations were suspended in the middle of the time-series owing to the passage of the low-pressure cell and to consequent weather conditions.

Zooplankton displacement volumes, taken from each depth interval, were measured following Harris *et al.* (2000). The taxonomic composition and the concentration of the taxa of the zooplankton were assessed by splitting zooplankton collections. Three

aliquots of 10 ml of zooplankton were taken with a Stempel pipette from each collection for counting, with the goal of at least 1000 zooplankton individuals per aliquot. Counts from these three aliquots were pooled. The zooplankton was identified to the lowest taxon possible, counted and categorized as ecologically functional taxa (Reid *et al.*, 2000), taxa known to constitute the diets of larval fish (Govoni *et al.*, 1983, 2003), or taxa indicative of water mass (Paffenhöfer, 1985).

Changes in the eddy with northeastward propagation

Change in surface chlorophyll-*a* concentration was assessed with one-way analysis of variance (ANOVA). Zooplankton displacement volume and concentrations of zooplankton taxa were compared for differences among 6 d and three depths using two-way ANOVA. The application of Bartlett's tests determined whether data met the parametric assumptions of normality and homoscedasticity. Where parametric assumptions were not met, the data were transformed to common logarithms before ANOVA. Two-way ANOVAs determined significant effects on taxa concentrations among days, depths, and the interaction of effects. Where significant location and depth interactions were found, the significant effect from day or depth was ignored. Where the main effects of day and depth were both significant, one-way ANOVA with day as the main effect was applied for each depth interval. The application of Tukey's least-significant differences multiple-comparisons tests indicated significant effects for specific differences among groups. Correspondence analysis (CA) was used to determine whether the zooplankton communities of the Charleston Gyre region differed according to depth of collection and to determine whether zooplankton community composition and abundance changed over the period of collection (ter Braak, 1986). Ordinations were interpreted by the proximity of points and by the dimensionality of points. The distance between points on the ordination corresponds to the similarity between those points. Points along an axis (or dimension) fall along an environmental gradient.

Only zooplankton taxa that made up at least 1% of the abundance at a single station were identified. Cyphonautes larvae (phylum), Euphausiidae (family), Hyperiididae (family), Ostracoda (class), Siphonophora (order), and Sipuncula (phylum) were included because these higher taxa were present in abundances >1%, are important members of zooplankton assemblages, and comprise genera indicative of intrusions or eddies of the Charleston Gyre region (Paffenhöfer, 1985).

Results

Characterization of the eddy

There was fidelity between the GPS, radio-beaconed drifter and the eddy, as indicated by drifter tracks (Figures 1 and 2), and hydrographic profiles taken before and after zooplankton collections (Figure 3), which showed a structure characteristic of the eddy core. Temperature and salinity taken in and about the eddy core included Gulf Stream frontal zone and Gulf Stream water wrapped around the eddy core (Figure 3). For transects 1 through 4, which were north of and proximal to the Charleston Bump, warm surface water of Gulf Stream origin was evident inshore as part of the filament. Upwelling, indicated by domed isotherms of deep, cool water, was evident within the eddy core. The thermocline within Gulf Stream water was characteristically between 100 and 200 m deep (Schmitz *et al.*, 1993; Xie and

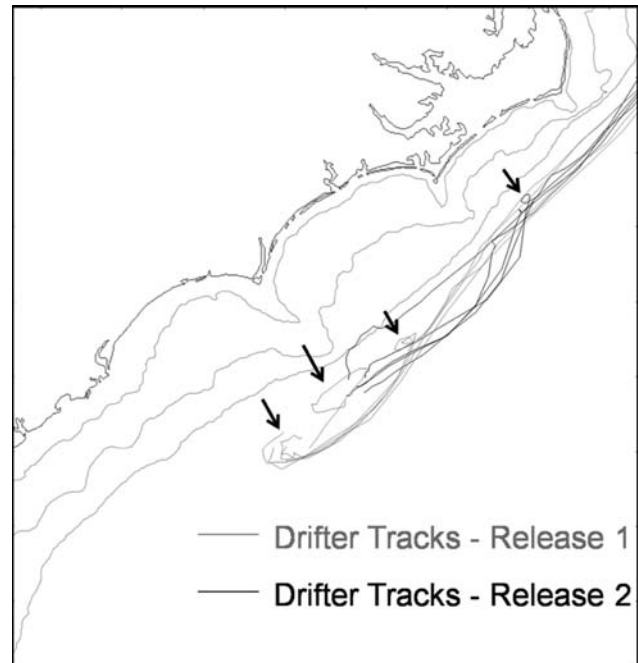


Figure 2. Tracks of drifters released within the eddy of the Charleston Gyre region. Grey and black lines trace the movements of the drifters released on 30 January 2003 and 5 February 2003. Arrows indicate the cyclonic circulation of the eddy.

Pietrafesa, 1995). The water column within the Gulf Stream frontal zone was isothermal below 30 m (Govoni and Pietrafesa, 1994; Hitchcock *et al.*, 1994). Upwelling was evident within the eddy core, with 12–16°C water elevated to 75–50 m. Temperature profiles taken attendant to zooplankton collections indicated the eddy core with a thermocline between 50 and 150 m. For transects 6 and 8, warm surface water characteristic of the Gulf Stream filament remained, but domed isotherms of the southwestern transects occupied during the first few days were no longer evident.

The taxonomic composition of zooplankton consisted of a broad phylogenetic spectrum that ranged from sarcomastigophorans to appendicularians. Taxa indicative of shelf water and water of Gulf Stream intrusions were present, e.g. doliolids and particular copepods (Grice and Hart, 1962; Owre and Foyo, 1967; Paffenhöfer, 1985). Taxa that are important in the diets of many larval fish in the northern Gulf of Mexico and the western North Atlantic (Govoni *et al.*, 1983, 2003; Turner, 1984) were consistently present in the collections. Of these, dinoflagellates, bivalve veligers, the pteropod *Limacina* spp., the tintinnid *Tintinnopsis* spp., copepod nauplii and copepodites, and the adult copepods *Eucalanus* spp. and *Temora* spp., *Oncaea* spp., *Oithona* spp., and *Euterpina acutifrons* were abundant, with mean concentrations in the highest 50% of all zooplankton and in concentrations <10 m⁻³. Ostracods and *Corycaeus* spp., also important dietary constituents of larval fish, were present, but not in consistently great abundance.

Changes in the eddy as it propagated northeastwards

Surface chlorophyll-*a* ranged from 0.409 to 1.283 µg l⁻¹ and decreased near the eddy core as the eddy moved northeastwards (Figure 4). Surface chlorophyll-*a* was significantly higher on the

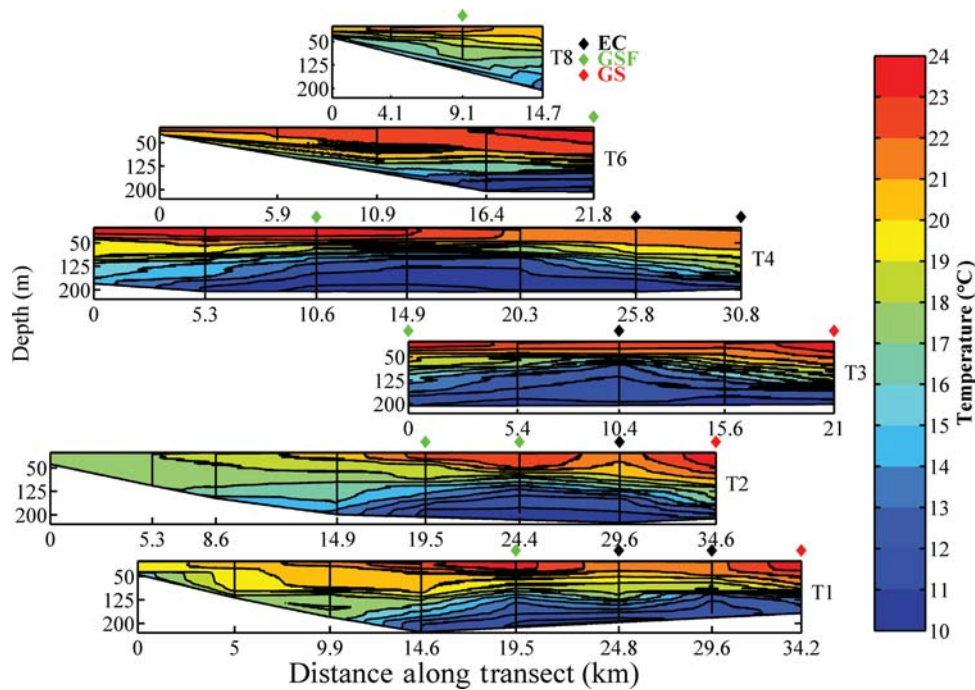


Figure 3. Cross-shelf temperature sections from CTD casts of the upper 250 m in the Charleston Gyre region. Black, green, and red diamonds indicate the approximate location of the eddy core (EC), Gulf Stream Filament (GSF), and Gulf Stream (GS) along each transect.

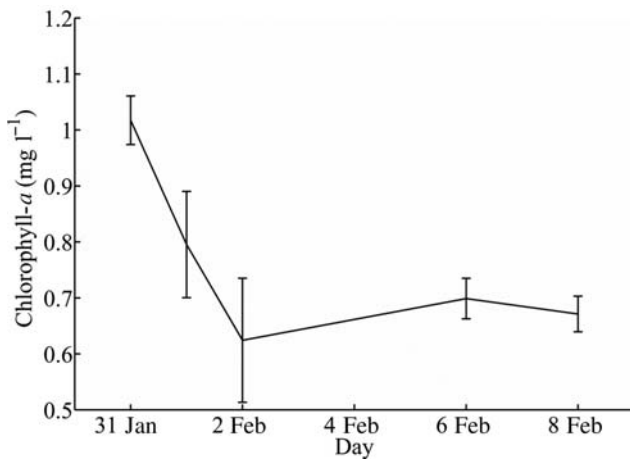


Figure 4. Mean chlorophyll *a* concentrations among days in the eddy of the Charleston Gyre region (error bars are the s.e. of the mean).

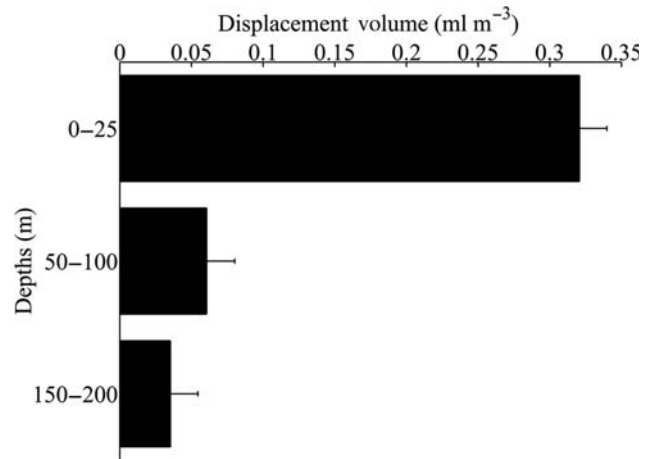


Figure 5. Mean displacement volume of zooplankton among depth intervals in the eddy of the Charleston Gyre region (error bars are the s.e. of the mean).

first day than on the third, fourth, and fifth days, when the eddy had propagated northeastwards.

Zooplankton displacement volume indicated higher biomass in the 0–25-m depth interval (one-way ANOVA; $SS = 1.042$; $d.f. = 2$; $MS = 0.52$; $F = 67.46$; $p < 0.001$). The 0–25-m depth interval ($\bar{X} = 0.32$; $s.e. = 0.02$) had a higher displacement volume than the 50–100 m ($\bar{X} = 0.06$; $s.e. = 0.02$) and 150–200 m ($\bar{X} = 0.04$; $s.e. = 0.02$) depth intervals, which were not different from each other (Figure 5). There were no significant differences among days (one-way ANOVA; $SS = 0.053$; $d.f. = 5$; $MS = 0.01$; $F = 0.412$; $p = 0.838$), or when partitioned by depth interval. The main effects of day and depth on mean concentrations were

observed for most zooplankton taxa, but only dinoflagellates displayed interactions among day and depth. The highest concentration of dinoflagellates ($\bar{X} = 1246$), at the 0–25 m interval on day 5, was different from all other day and depth combinations, except the concentrations on previous days at the surface and the concentrations at the 50–100 and 150–200 m depths on day 5.

The effect of day on concentrations of select zooplankton taxa varied among depths. The highest number of taxa (nine) with significant differences among days was at the 0–25 m depth interval (Table 1). At the 50–100 and 150–200 m depth intervals, the number of taxa was 1 and 8. *Euterpina acutifrons* was the only taxon with significant differences among days at each depth

Table 1. Results from one-way ANOVAs for the effect of day on displacement volume and selected taxa concentrations within the 0–25-m depth interval (an asterisk indicates a failure of the null hypothesis at $\alpha = 0.05$).

Taxa	SS	d.f.	MS	F-value	p-value
Displacement volume	0.130	5	0.026	1.381	0.286
<i>Centropages hamatus</i>	0.866	5	0.173	1.347	0.302
<i>Nannocalanus</i> spp.	0.560	5	0.112	0.758	0.594
Doliolida	2.061	5	0.412	4.095	0.010*
<i>Oncaea</i> spp.	1.613	5	0.323	2.810	0.055
<i>Temora turbinata</i>	6.602	5	1.320	4.440	0.006*
<i>Euchaeta</i> spp.	3.538	5	0.708	3.476	0.026*
<i>Limacina</i> spp.	3.226	5	0.645	3.666	0.021*
Ostracoda	1.565	5	0.313	3.393	0.030*
Bivalve veliger	4.064	5	0.813	3.655	0.019*
<i>Creseis</i> spp.	3.923	5	0.785	4.470	0.007*
<i>Paracalanus</i> spp.	1.940	5	0.388	0.837	0.539
<i>Temora</i> spp.	2.652	5	0.530	4.652	0.007*
<i>Microsetella</i> spp.	0.902	5	0.180	1.424	0.272
<i>Euterpina acutifrons</i>	2.156	5	0.431	3.714	0.019*
<i>Tintinnopsis</i> spp.	4.215	5	0.843	1.838	0.162
<i>Favella</i> spp.	1.965	5	0.393	2.375	0.089
<i>Oikopleura</i>	0.745	5	0.149	0.623	0.684

Table 2. Results from one-way ANOVAs for the effect of day on displacement volume and selected taxa concentrations within the 50–100-m depth interval (an asterisk indicates a failure of the null hypothesis at $\alpha = 0.05$).

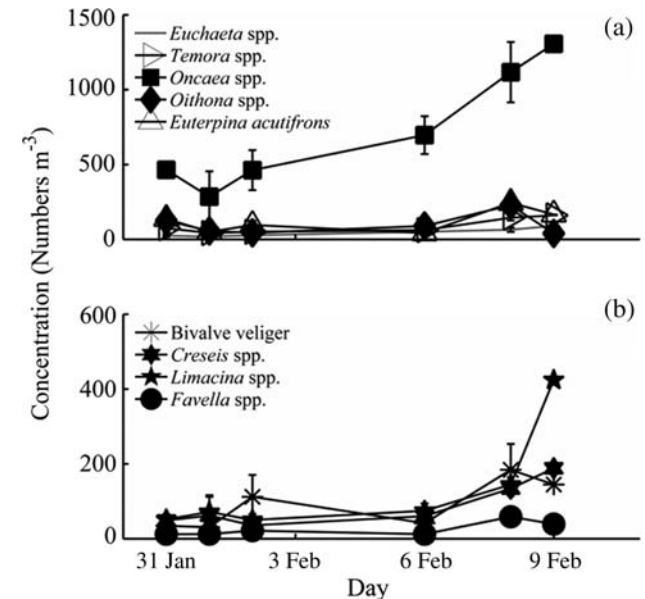
Taxa	SS	d.f.	MS	F-value	p-value
Displacement volume	0.015	5	0.003	2.507	0.080
<i>Centropages hamatus</i>	0.061	3	0.020	0.195	0.895
<i>Nannocalanus</i> spp.	0.366	4	0.091	0.885	0.515
<i>Eucalanus</i> spp.	1.129	5	0.226	1.671	0.206
Doliolida	1.308	5	0.262	1.663	0.208
Nauplii	0.412	5	0.082	0.381	0.853
Copepodites	0.904	5	0.181	1.549	0.238
<i>Oithona</i> spp.	0.686	5	0.137	1.315	0.317
<i>Oncaea</i> spp.	2.064	5	0.413	2.165	0.117
<i>Temora turbinata</i>	3.246	5	0.649	0.913	0.502
<i>Euchaeta</i> spp.	1.826	5	0.365	2.615	0.068
Dinoflagellate	4.678	5	0.936	6.738	0.002
<i>Limacina</i> spp.	0.859	5	0.172	0.516	0.760
Ostracoda	0.720	5	0.144	0.815	0.558
Bivalve veliger	1.087	4	0.272	1.309	0.311
<i>Creseis</i> spp.	1.137	5	0.227	1.813	0.185
<i>Paracalanus</i> spp.	0.655	5	0.131	0.927	0.493
<i>Temora</i> spp.	1.401	5	0.280	2.185	0.107
<i>Microsetella</i> spp.	0.523	5	0.105	0.865	0.528
<i>Euterpina acutifrons</i>	1.935	5	0.387	3.836	0.021*
<i>Tintinnopsis</i> spp.	0.328	4	0.082	0.553	0.700
<i>Favella</i> spp.	0.370	5	0.074	1.941	0.155
<i>Oikopleura</i>	1.055	5	0.211	1.924	0.146

(Tables 2 and 3). Doliolid and ostracod concentrations were different among days in the 0–25 and 150–200 m depth intervals.

Concentrations of some water-mass indicator taxa and concentrations of some taxa known to be important diet organisms for larval fish increased in abundance as the eddy propagated north-eastwards (Figure 6). In the 0–25 m depth interval, *Euchaeta* spp., *Oncaea* spp., *Oithona* spp., *Limacina* spp., bivalve veligers, *Creseis* spp., *Temora* spp., *E. acutifrons*, and *Favella* spp. were significantly different among days and increased in concentration as

Table 3. Results from one-way ANOVAs for the effect of day on displacement volume and selected taxa concentrations within the 100–200-m depth interval (an asterisk indicates a failure of the null hypothesis at $\alpha = 0.05$).

Taxa	SS	d.f.	MS	F-value	p-value
Displacement volume	0.005	5	0.001	2.265	0.101
<i>Centropages hamatus</i>	0.001	1	0.001	0.315	0.674
<i>Eucalanus</i> spp.	1.089	5	0.218	2.689	0.080
Doliolida	0.642	5	0.128	6.372	0.022*
Nauplii	1.621	5	0.324	3.194	0.037*
Copepodites	0.745	5	0.149	1.626	0.213
<i>Oncaea</i> spp.	4.260	5	0.852	5.452	0.005*
<i>Limacina</i> spp.	1.930	5	0.386	0.724	0.616
Ostracoda	1.106	5	0.221	3.032	0.044*
Bivalve veliger	1.092	5	0.218	0.822	0.557
<i>Creseis</i> spp.	1.031	5	0.206	0.766	0.590
<i>Paracalanus</i> spp.	0.777	5	0.155	0.486	0.780
<i>Temora</i> spp.	1.248	5	0.250	0.917	0.505
<i>Microsetella</i> spp.	4.058	5	0.812	8.702	<0.000*
<i>Euterpina acutifrons</i>	4.555	5	0.911	7.371	0.002*
<i>Tintinnopsis</i> spp.	3.679	5	0.736	3.775	0.019*
<i>Oikopleura</i>	1.303	4	0.326	0.884	0.511

**Figure 6.** Mean concentrations of zooplankton in the eddy of the Charleston Gyre region (error bars are standard error of the mean). (a) Selected copepod genera; (b) other zooplankton.

the eddy propagated northeastwards (Table 1). In the 50–100 m depth interval, there were no differences among days (Table 2), but in the 150–200 m depth interval, doliolids, dinoflagellates, and *Favella* spp. were significantly different among days and increased in concentration (Table 3). Doliolids, dinoflagellates, and *Favella* spp. had lower concentrations on day 1 and higher concentrations on day 5.

The zooplankton community at each depth interval differed (Figure 7). Two CA dimensions explained most of the variance (Table 4). Low eigenvalues among collections indicate no pattern, but eigenvalues indicated separation among depth

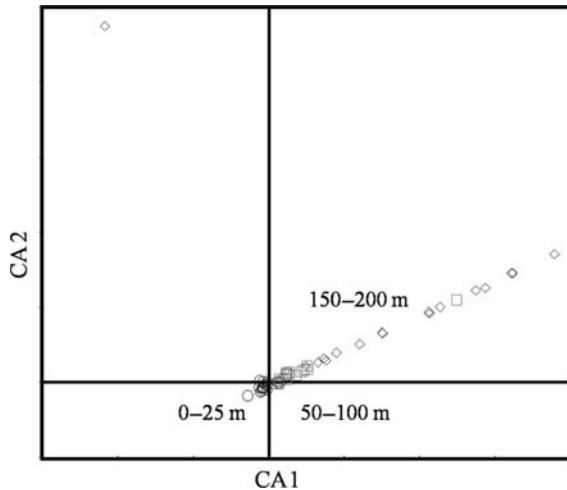


Figure 7. CA ordination of zooplankton assemblages among depths in the eddy of study in the Charleston Gyre region: ordination of collections labelled by depth interval (circles are 0–25 m, squares are 50–100 m, and diamonds are 150–200 m collections).

Table 4. Eigenvalues for CA axes for all sampling strata combined.

Axis	Eigenvalue
1	0.239
2	0.230
3	0.139
4	0.082

intervals. Collections from the 0–25 m interval formed a tight group near the origin of the ordination (Figure 7).

On average, there were fewer zooplankton taxa in the 50–100 m depth interval (21 taxa) than in the 0–25 m interval (24), and the fewest taxa were in the 150–200 m interval (19). The presence of *Favella* spp., *Petalotricha* spp., and *Codonellopsis* spp. separated the 50–100 and 150–200 m collections from the 0–25 m collections. Tintinnids (two unidentified species) were more frequent in collections from the 50–100 and 150–200 m intervals and separated those collections in the ordination (Figure 7). Collections from the 150–200 m interval were distinct from the 0–25 m collections and were spread primarily along a single dimension. One collection from the 150–200 m interval contained *Nannocalanus* spp., which separated that collection from all others in the ordination. Collections from the 50–100 m interval were intermediate between the 0–25 and 150–200 m collections. Collections from the 0–25 m interval grouped near the origin, indicating that all taxa were at that depth interval.

No pattern among days was evident in the zooplankton collected at 0–25 m and 50–100 m. Eigenvalues for both depth intervals were low, particularly for the 50–100 m depth interval (Table 5). Most of the 0–25 m collections and taxa grouped near the origin of the ordination (Figure 7), but two collections and three taxa separated from the group. One collection contained abundant sipunculids and larvaceans *Oikopleura* spp. The other collection included *Tintinnopsis* spp. in great abundance. The 50–100 m collections also grouped tightly around the origin of the ordination, but one collection differed owing to the abundance of *Tintinnopsis* spp. Another collection was set apart by the low abundance of zooplankton as a whole.

Table 5. Eigenvalues for four CA axes by depth interval.

Depth interval (m)	Axis 1	Axis 2	Axis 3	Axis 4
0–25	0.136	0.071	0.052	0.025
50–100	0.056	0.048	0.028	0.015
150–200	0.689	0.378	0.200	0.104

Temporal pattern was evident in the collections from the 150–200 m interval. Eigenvalues for that depth interval were higher than for the 0–25 and 50–100 m collections, and the first two dimensions described most of the variability (Table 5). Along the first dimension, the only sample in which *Nannocalanus* spp. was collected was separated from the rest. A gradient with time was evident along the second dimension (Figure 8). Collections from days 2 and 4 were dominated by tintinnids, *Creseis* spp. and *Limacina* spp., and *Centropages hamatus*. The abundance of these taxa decreased over time, whereas the abundance of *Oithona* spp., *Microsetella* spp., *E. acutifrons*, and *Temora* spp. increased. Collections from days 2 and 4 were represented by *Codonellopsis* spp., *Favella* spp., and *Petalotricha* spp. These three species were collected throughout the cruise in the 150–200 m depth interval. Collections from day 5 contained siphonophores, *Pleuromamma* spp., *Temora turbinata*, *Clio* spp., *Corycaeus* spp., euphausiids, *Rhincalanus* spp., *Euchaeta* spp., ostracods, *Eucalanus* spp., hyperiid amphipods, *Oikopleura* spp., and *Oncaea* spp. These taxa were collected inconsistently throughout the sampling period and were scarce. Collections from the final two nights contained *Oithona* spp., *Microsetella* spp., *E. acutifrons*, *Temora* spp., and *Nannocalanus* spp. in great abundance.

Discussion

Gulf Stream intrusions and the cyclonic circulation associated with these intrusions can bring nutrient-rich water from deep and off-the-shelf edge into the photic zone and onto the shelf. This enrichment can result in enhanced primary productivity (Yoder *et al.*, 1983; Verity *et al.*, 1993, 1998). The cyclonic circulation of these eddies entrains warm temperate zooplankton from the shelf and injects warm surface water with subtropical zooplankton onto the outer shelf (Paffenhöfer, 1985). As these eddies propagate northeastwards, succession of zooplankton communities (Margalef, 1967; Jamet *et al.*, 2005), driven by enhanced primary productivity (Mackas and Coyle, 2005), can also take place. Changes in zooplankton communities over time might serve fish production by providing an exceptional and more continuous food supply for fish larvae spawned in or entrained into eddies. In addition, fish larvae that risk entrainment into the Gulf Stream, and consequent loss from local populations, can be retained on, or near, the shelf edge when embedded within these eddies and not lost from the shelf. Although the region of the Charleston Gyre has potential as an important spawning and nursery habitat for fish, published evidence of habitat usage is limited (Govoni and Hare, 2001).

Surface concentrations of chlorophyll-*a* were within the same order of magnitude as concentrations over the outer continental shelf off the southeastern United States (Pomeroy *et al.*, 1993; Yoder *et al.*, 2001). It is not known if the high surface concentrations of chlorophyll-*a* resulted from Gulf Stream frontal water entrained into the eddy with the formation of the eddy or from nutrient enrichment within the eddy. Zooplankton displacement volume was roughly comparable with values observed across the

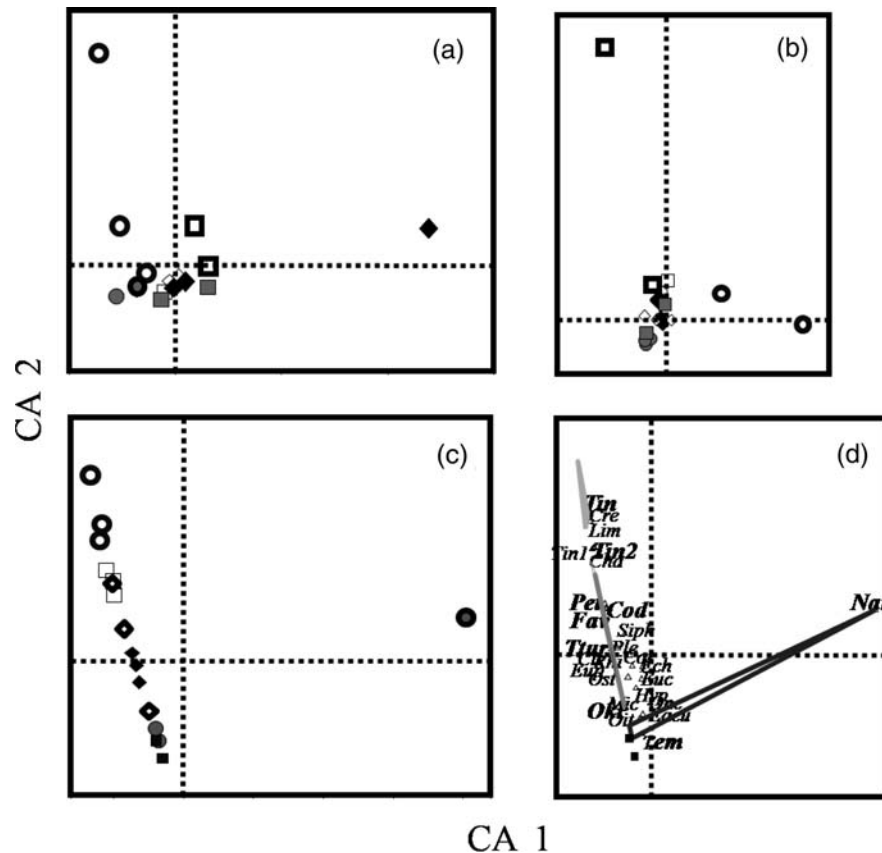


Figure 8. CA ordinations of (a), (b), and (c) the collections, and (d) the zooplankton taxa for each depth interval in the eddy of the Charleston Gyre Region. (a) 0–25 m collections; (b) 50–100 m collections; (c) and (d) 150–200 m collections. In panels (a), (b), and (c), open circles are collections on 30 and 31 January, open squares collections on 31 January and 1 February 2003, open diamonds collections on 1 and 2 February, filled circles collections on 7 and 8 February, and filled squares are collections on 8 and 9 February 2003. Open and half tone enclosures in (d) indicate clustering patterns among zooplankton taxa.

shelf and Gulf Stream to the north (Grice and Hart, 1962), and over the outer continental shelf in the northern reaches of the continental shelf south of Cape Hatteras (St John, 1958).

Surface chlorophyll-*a* concentrations decreased significantly over time as the eddy propagated northeastwards, and zooplankton displacement volume remained unchanged. Zooplankton displacement volume is a composite of taxa of various sizes and volumes. The concentration of many small copepods increased as the eddy propagated northeastwards, so the concomitant decrease in chlorophyll-*a* concentration and increase in small copepods might be attributable to grazing. A decline in chlorophyll-*a* as a consequence of zooplankton grazing and an increase in the developmental stages of copepods conforms with observations within Gulf Stream intrusions and associated upwelling zones that are common along the eastern edge of the continental shelf off the southeastern United States (Paffenhöfer, 1985).

Concentrations of many of the small copepods collected within the eddy were lower than average concentrations observed within Gulf Stream intrusions off the southeastern United States (Paffenhöfer, 1985), but the abundance of many zooplankton taxa known to be important in the diets of fish larvae (Govoni *et al.*, 1983, 2003; Turner, 1984) increased as the eddy propagated northeastwards. For instance, small calanoid (*Temora* spp.), cyclopoid (*Oithona* spp. and *Oncaea venusta*), and harpacticoid (*E. acutifrons*) copepods increased significantly at depth as the eddy

propagated northeastwards. Increases in the concentrations of these small copepods are congruent with their short generation times, multiple egg clutches (cyclopoids), and higher rates of egg production (Paffenhöfer, 1985; Turner, 2004). Other taxa that are also important dietary constituents of fish larvae, including the tintinnid *Favella* spp., ostracods, and the pteropod *Limacina* spp., were concentrated at depth, with significantly increasing abundance as the eddy propagated northwards. The increase in tintinnids is also compliant with their asexual mode of reproduction (Paffenhöfer, 1985).

At all depths taken together, there was no indication of a change in zooplankton community structure as the eddy propagated northeastwards. In the western North Atlantic, copepod communities across the continental slope and Gulf Stream are the characteristic of water mass and depth and are seasonal (Ashjian and Wishner, 1993). This overall lack of change indicates no succession of zooplankton assemblages, probably because of the short life of the eddies in the Charleston Gyre region, in the order of days or weeks (Govoni and Hare, 2001), much shorter than the lifespan of cyclonic eddies of the Mediterranean, where zooplankton succession does take place (Jamet *et al.*, 2005), and where eddies last of the order of months. The short life of eddies of the Charleston Gyre region may be inadequate for zooplankton succession to proceed beyond increases or decreases in the concentration of specific taxa. Mesozooplankton assemblages changed

within upwelling areas off the Iberian Peninsula in the eastern North Atlantic (Blanco-Bercial *et al.*, 2006), but the duration of upwelling and the duration of observation within such upwelling zones was longer than it was in the present study.

Differences in zooplankton concentration might be the result of differences in (i) the season of observation (winter for the present eddy vs. summer), (ii) the duration of observation (days vs. weeks), (iii) the aspect of observation (near the eddy core vs. across intrusions and accompanying frontal zones), (iv) the spatial scale and hydrodynamics of the features involved (an eddy vs. an intrusion that strands on the shelf), or (v) the methods of plankton collection. In the present study, a 1-m² MOCNESS frame was deployed with 505- μ m mesh netting in the main frame and 45- μ m mesh netting nested within the larger net (Govoni *et al.*, 1983). The 505- μ m mesh net collects fish larvae efficiently, and the 45- μ m mesh net collects a more diverse and small size fraction of zooplankton. The 45- μ m mesh net, however, clogs rapidly, which results in lesser concentrations being calculated as the number of zooplankton taxa per cubic metre. Other studies have employed 1-m ringnets or 60-cm bongo nets with 333- μ m mesh netting, a more efficient mesh for the collection of zooplankton, though of a larger-size fraction.

Fish larvae spawned on the continental shelf off the southeastern United States are particularly abundant on the outer shelf, within the troughs of Gulf Stream intrusions (Yoder *et al.*, 1983; Paffenhöfer, 1985) or Gulf Stream frontal zones (Govoni and Pietrafesa, 1994). Some fish larvae appear to be abundant within and immediately about the cyclonic eddies of the Charleston Gyre region (Govoni and Hare, 2001). Larvae of clupeids, mainly *Brevoortia tyrannus*, and sciaenids, mainly *Leiostomus xanthurus*, were among the most frequently collected and most abundant fish larvae within the eddy. Larval fish growth in particular, and survival in part, depends on feeding (Houde, 1997; Govoni, 2005). Concentrations of many of the zooplankton taxa selectively eaten by larvae of *B. patronus* and *L. xanthurus* in the northern Gulf of Mexico (Govoni *et al.*, 1986) increased as the study eddy propagated northeastwards. Concentrations of small copepods and many other zooplankton taxa that are important dietary constituents of fish larvae in the eddy were of the same order of magnitude that was responsible for driving accelerated growth of *L. xanthurus* larvae in the northern Gulf of Mexico (Govoni *et al.*, 1985).

The eddies of the Charleston Gyre strand on the outer continental shelf decay as the eddies of the Charleston Gyre region move north beyond Cape Fear, NC, as do the Gulf Stream intrusions described by Paffenhöfer (1985) south of Cape Fear. Nutrient-rich upwelled water along with the zooplankton assemblages embedded within the decaying eddies are not lost, but are retained on the outer shelf, where populations of zooplankton taxa can expand and succession of zooplankton assemblages can proceed.

The zooplanktonic food of fish larvae evident within eddies of the Charleston Gyre region might support an appreciable part of the fishery production over the outer continental shelf off the southeastern United States (Govoni and Hare, 2001). Survival of fish through their early life history is a crucial factor in determining fisheries production. Eddies might also offer the benefit of an enhanced feeding habitat. The short temporal span of single eddies and their propagation northeastwards, however, might limit their contribution to fish larvae that are entrained in the eddy proper. Larvae in the outer shelf region, where the cyclonic circulation of the eddies strands a mixture of warm subtropical water and upwelled water, might benefit from the continued passage of serial eddies.

Supplementary data

Supplementary data are available at www.icesjms.oxfordjournals.org.

Acknowledgements

The work was supported by an award from the Office of Ocean Exploration, NOAA. We thank M. Greene, B. Degan, F. Hernandez, R. Cheshire, and E. Jugovich for invaluable assistance in operations in the field, F. Hernandez for processing CTD data, A. Robertson for verifying copepod identifications in a voucher collection, and D. Vaughan and R. Waggett for valued reviews of the draft manuscript. The US government has the right to retain a non-exclusive, royalty-free license in and to any copyright covering this paper.

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