

Hyperiid amphipods (Crustacea: Peracarida) in relation to a cold-core ring in the Gulf of Mexico

R. Gasca

El Colegio de la Frontera Sur (ECOSUR)-Unidad Chetumal, Apdo. Postal 424, Chetumal 77000, Q.Roo, Mexico
E-mail: rgasca@ecosur-qroo.mx

Received 5 November 2002. in revised form 24 June 2003; accepted 30 July 2003

Key words: crustaceans, zooplankton, marine ecology, mesoscale eddy

Abstract

The species composition, distribution, and abundance of the hyperiid amphipods collected in March 1993 across a Gulf of Mexico cold-core ring (CCR) were analyzed. Day and night samples were collected by oblique tows (100 m to surface) with a plankton net. Hyperiids were represented by 56 species, 21 of which have not been recorded previously in gulf waters. The local oceanic community differs from that reported from adjacent neritic and neritic-oceanic areas of the Northwestern Tropical Atlantic. Overall, hyperiids were more abundant within (59% of total catch in org./1000 m³) than outside the CCR (41%). All inside CCR stations were sampled at night. Night outside vs. night inside CCR hyperiid faunas showed important differences in terms of species richness, composition and density. Cluster analysis indicated that day sta. 5 on the edge but outside the CCR was more similar to those stations inside the CCR (nighttime samples) than to the other daytime samples. Moreover, all the stations outside the CCR were clustered together independently of their day or night origin. It is suggested that the differences found were more related to differential conditions related to the CCR than to diel vertical migration. The analysis of three congeneric pairs with inverse CCR-related abundance and with known or inferred migratory patterns strengthened the idea that these pairs are probably separated by thermal preferences; also, their vertical migratory patterns seem to be abnormal inside the CCR. A relatively higher concentration of immature stages inside the CCR supports the idea that the enriched CCR waters constitute areas of increased production. Furthermore, this higher productivity enhances the chances of hyperiids to find their hosts, the gelatinous zooplankters, which are also more abundant inside the CCR.

Introduction

The influence of the Loop Current (LC) and its derived dynamic eddy field constitute a predominant feature of the mesoscale circulation in the Gulf of Mexico. The resulting meander formation processes yield continuous events of eddy separation (Lewis & Kirwan, 1985). These eddies, also called rings, can be warm-core (anticyclonic) or cold-core (cyclonic). The cold-core rings (CCRs) are local systems in which primary productivity in near-surface waters is relatively higher than in the oligotrophic areas outside. Conversely, the warm-core rings (WCRs) are regarded as nutrient-limited, low productivity areas

(Biggs, 1992; Wormuth et al., 2000). The zooplankton community related to these systems in the Gulf of Mexico has been studied following a general approach (i.e. biomass, general abundance and distribution) (see Biggs et al., 1988; Biggs, 1992; Wormuth et al., 2000). The available information about the behavior of selected taxa at the species level (Biggs et al., 1997; Suárez-Morales et al., 2003) is quite limited; these surveys are likely to provide new data with a relatively higher level of resolution.

Hyperiid amphipods are among the most abundant groups of crustacean zooplankton in the oceanic realm. Previous surveys have suggested that this group shows distributional patterns related to the influence

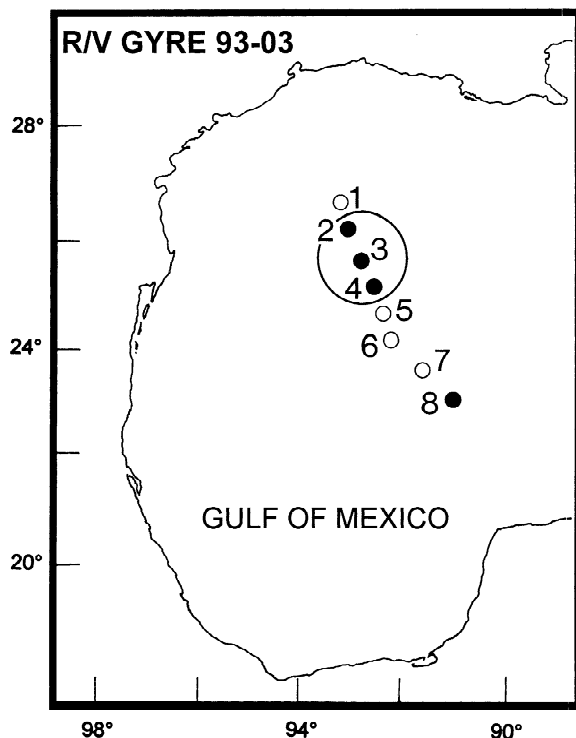


Figure 1. Surveyed area showing arrangement of day (open circles) and night (filled circles) zooplankton sampling stations during transit of a CCR in the central western Gulf of Mexico. The large circle indicates the approximate location of the CCR in relation to the position of the sampling sites.

of different water masses and to mesoscale features such as upwelling and eddies (Young, 1989). It is also noteworthy to mention that hyperiid amphipods have been advanced as a group sensitive to global thermic changes (Lavaniegos & Ohman, 1999). Therefore, it was expected that this group would show a measurable response to the thermal differences related to the mesoscale dynamics of a mesocyclonic gyre in the Gulf of Mexico.

The general composition and distributional patterns of these crustaceans in the oceanic waters of the Gulf of Mexico and adjacent areas remain poorly known. Among the works that deal with the hyperiid fauna of the Gulf of Mexico are those by Fage (1960), Yang (1960), and Stuck et al. (1980), who also cited the earliest surveys about the group in the gulf. Overall quantitative information on the oceanic zooplankton community as related to these eddies is still scarce (Gasca, 1999; Wormuth et al., 2000; Suárez-Morales et al., 2003). Therefore, in order to determine if the hydrographic conditions of a mesoscale cyclonic eddy are reflected in the hyperiid amphipod community, this

study describes changes in the numerical abundance, composition, and species diversity of these crustaceans as collected during the transit of the research vessel "Gyre" (Texas A&M University) across a CCR in March, 1993, in the Gulf of Mexico. The eddy surveyed was located in the western central Gulf of Mexico between the 26° 30' N, 93° 30' W and 25° 30' N, 92° 56' W (Fig. 1). The CCR was detected from space as a region of surface temperatures 1–2 °C cooler than the adjacent oceanic waters and as an elliptical local depression in sea surface height (SSH) (see Biggs et al., 1997; Wormuth et al., 2000).

Materials and methods

During transit from Texas to the Campeche Bank by R/V Gyre, operated by Texas A&M University, 33 expendable bathythermograph probes (XBTs) were dropped and 8 net tows were made as the ship crossed the CCR (Fig. 1; see also Biggs et al., 1997). Zooplankton samples were obtained by performing oblique hauls (0–100 m) with a standard plankton net (0.33 mm mesh-size, diameter of mouth 1 m). A mechanical flowmeter was attached to the net mouth to estimate the volume of water filtered (this ranged between 450–800 m³ per haul). This gear allowed collection of small and medium-sized zooplankters. Samples were fixed and preserved in a buffered 4% formalin solution (Smith & Richardson, 1979). Net tows were made at every third XBT site of the hydrographic transect beginning at 27° 00' N. Data from a 153 kHz acoustic Doppler current profiler (ADCP) were also logged allowing sampling of near-surface currents from 8–250 m below the surface. Zooplankton samples were collected in day and nighttime, upon arrival at the designed station. Four of the eight tows were made during daylight hours (sta. 1, 5–7) and the other 4 were made at night. The first tow was made in daylight outside and to the northwest of the CCR, and then tows 2–4 were at night within the CCR. Tows 5–7 were daylight tows outside the CCR and tow 8 was outside the CCR, at night (Fig. 1). Table 1 shows the geographic position, time and date of collection, and the volumes of water filtered by the net at each station.

Hyperiid amphipods were sorted from 1/4 aliquots and specimens were transferred to 70% ethanol for taxonomic examination. The material was identified to species level using the descriptions, keys, and illustrations by Harbison & Madin (1976), Shih & Chen (1995), Vinogradov et al. (1996), and Zeidler (1990,

Table 1. Data of zooplankton sampling during the R/V "Gyre" cruise in March, 1993

EST.	Date	Time	Filtered volume(m ³)	Salinity o/oo	Temp. °C	Biomass gr/1000 m ³
1	10-03-93	12:12	810	35.95	23.1	125.98
2	10-03-93	15:52	559	35.97	23.4	34.92
3	10-03-93	19:29	584	36.15	22.7	76.03
4	10-03-93	23:18	508	36.03	22.0	94.57
5	11-03-93	03:08	485	36.07	22.3	99.05
6	11-03-93	07:03	454	36.19	22.7	41.94
7	11-03-93	11:10	670	36.18	23.9	31.70
8	11-03-93	16:08	616	36.17	23.8	43.64

1992, 1998). Density data were calculated as number of organisms per 1000 m³ for all species. Analysis of the numerical abundance of hyperiids was made with these standardized data. Shannon–Wiener's Diversity was determined, and the Bray–Curtis Similarity Index was used to cluster stations with similar density and composition (Ludwig & Reynolds, 1988). These indices were calculated using the ANACOM software (De la Cruz, 1997). A Spearman rank order correlation analysis was used to determine the link between the hyperiids and the potential hosts in the same area.

Results

Hydrography

The ADCP-measured currents were anti-clockwise in direction around the CCR and were in close agreement in speed with those computed from the along-track horizontal geopotential gradient in relation to a reference level of 800 db. The CCR was detected as a 14 cm difference in sea surface height (SSH) from the surrounding water (a low 88 dyn cm in the interior of the CCR versus 102 dyn cm to the north and south). Both TOPEX Cycle 18 and TOPEX Cycle 17 linages from 10 days earlier confirmed the location of this cold-core ring (Biggs et al., 1997). The CCR measured about 150 km in diameter and in its interior the 8 °C isotherm domed to <500 m and the 15 °C isotherm to <150 m.

Composition and density

The local hyperiid community was represented by 56 species belonging to 14 families and 28 genera (Table 2). On average, 51% of the hyperiids were repres-

ented by a group of five dominant species or forms: *Primno abyssalis* (13.7% of total hyperiid numbers; mean density: 95 org./1000 m³), *Phronimella elongata* (10.2%; 70 org./1000 m³), unidentifiable juveniles of *Primno* sp. (9.7%; 67 org./1000 m³), *Hyperioides longipes* (9%; 62 org./1000 m³), and *Anchylomera blossevillei* (7.7%; 53 org./1000 m³). Only three species: *H. longipes*, *P. abyssalis*, and *Eupronoe intermedia* occurred at all the eight sampling stations where net tows were performed.

The highest total density of the hyperiids was recorded during tow 4 (1674 org./1000 m³), followed by tows 3 (843 org./1000 m³) and 2 (712 org./1000 m³), all of them inside the CCR. The average density during daylight samples (sta. 1, 5–7) (471 org./1000 m³) was nearly two-fold lower than the nighttime average (905 org./1000 m³). Up to 58.7% (1076 org./1000 m³ in average) of the hyperiid numbers were captured at three stations within the CCR and the remaining 41.3% (455 org./1000 m³ in average) was collected at the five stations outside (Table 3).

Of the daytime stations, 565 org./1000 m³ was the average at station 1 (daylight: NW of CCR), and 440 org./1000 m³ at stations 5, 6, and 7 (daylight: SE of CCR). The average density at daytime samples was 471 org./1000 m³; an average of 391 org./1000 m³ occurred in the nighttime station outside the CCR (sta. 8).

However, the two most abundant species in the CCR (*Primno abyssalis* and *Phronimella elongata*) reached an abundance 2–4 times higher within the CCR than outside it (*Primno abyssalis*: 178 org./1000 m³ ± 67 (*n* = 3) inside vs. 44 org./1000 m³ ± 12 (*n* = 5) outside the CCR; *Phronimella elongata*: 103 org./1000 m³ ± 32 (*n* = 3) inside vs. 49 org./1000 m³ ± 107 (*n* = 5) outside the CCR). Differences in the

Table 2. Hyperiid amphipods collected in the surveyed area indicating their occurrence inside (*) or outside (+) the cold core ring

Class CRUSTACEA	Family PHROSINIDAE
Subclass MALACOSTRACA	<i>Phrosina semilunata</i> Risso, 1822 * +
Superorder PERACARIDA	<i>Anchylomera blossevillei</i> Milne-Edwards, 1830* +
Order AMPHIPODA	<i>Primno abyssalis</i> (Bowman, 1968) * +
	<i>P. brevidens</i> Bowman, 1978 * +
Suborder HYPERIIDEA	<i>P. latreillei</i> Stebbing, 1888 * +
Infraorder PHYSOSOMATA	<i>Primno</i> (juveniles) * +
Family LANCEOLIDAE	Superfamily LYCAEPSOIDEA
<i>Lanceola</i> sp. +	Family LYCAEPSOIDAE
	<i>Lycaeopsis themistoides</i> Claus, 1879 * +
Family SCINIDAE	<i>L. zamboangae</i> (Stebbing, 1888) * +
<i>Scina curvidactyla</i> Chevreux, 1914 *	
<i>S. indica</i> Vinogradov, 1964 *	Family PRONOIDAE
<i>S. submarginata</i> Tattersall, 1906 *	<i>Eupronoe maculata</i> Claus, 1879 +
<i>S. similis</i> Stebbing, 1895 *	<i>E. minuta</i> Claus, 1879 * +
<i>Scina</i> sp. * +	<i>E. laticarpa</i> Stephensen, 1925 * +
	<i>E. intermedia</i> Stebbing, 1888 * +
Infraorder PHYSOCEPHALATA	
Family VIBILIIDAE	Family LYCAEIDAE
<i>Vibilia propinqua</i> Stebbing, 1888 *	<i>Lycaea pachypoda</i> (Claus, 1879) *
<i>V. stebbingi</i> Behning & Woltereck, 1912 * +	<i>L. bajensis</i> Shoemaker, 1925 *
<i>V. chuni</i> Behning & Woltereck, 1912 *	<i>L. bovalloides?</i> Stephensen, 1925 *
<i>Vibilia</i> sp. *	
Family PARAPHRONIMIDAE	Family BRACHYSCCELIDAE
<i>Paraphronima gracilis</i> Claus, 1879*	<i>Brachyscelus cruscum</i> Bate, 1861 *
<i>P. crassipes</i> Claus, 1879 +	<i>B. globiceps</i> (Claus, 1879) * +
Family HYPERIIDAE	Family OXYCEPHALIDAE
<i>Hyperioides longipes</i> Chevreux, 1900 * +	<i>Oxycephalus piscator</i> Milne-Edwards, 1830 * +
<i>Lestrigonus schizogeneios</i> (Stebbing, 1888) * +	<i>Streetsia challengerii</i> Stebbing, 1888 +
<i>L. macrophthalmus</i> (Vosseler, 1901) +	<i>S. steenstrupi</i> (Bovallius, 1887) +
<i>L. latissimus</i> (Bovallius, 1889) * +	<i>S. porcella</i> (Claus, 1879) *
<i>L. bengalensis</i> Giles, 1887 * +	<i>Leptocotis tenuirostris</i> (Claus, 1871) * +
<i>Hyperietta luzoni</i> (Stebbing, 1888) *	
<i>H. vosseleri</i> (Stebbing, 1904) * +	Family PLATYSCCELIDAE
<i>H. stephenseni</i> Bowman, 1973 * +	<i>Platyscelus ovoides</i> (Risso, 1816) +
<i>Themistella fusca</i> (Dana, 1852) +	<i>P. crustulatus</i> (Claus, 1879) +
<i>Phronimopsis spinifera</i> Claus, 1879 * +	<i>Paratyphis maculatus</i> Claus, 1879 * +
Family PHRONIMIDAE	<i>P. parvus</i> Claus, 1887 * +
<i>Phronima sedentaria</i> (Forskål, 1775) * +	<i>Tetrathyrus forcipatus</i> Claus, 1879 *
<i>Ph. atlantica</i> Guérin-Ménéville, 1836 * +	<i>Amphithyrus bispinosus</i> Claus, 1879 +
<i>Ph. stebbingi</i> Vosseler, 1901 *	
<i>Ph. colletti</i> Bovallius, 1887 +	Family PARASCELIDAE
<i>Ph. pacifica</i> Streets, 1877 * +	<i>Schizoscelus ornatus</i> Claus, 1879 +
<i>Phronimella elongata</i> (Claus, 1862) * +	<i>Thyropus sphaeroma</i> (Claus, 1879) +
	<i>Parascelus edwardsi</i> Claus, 1879 * +
	<i>Hemiscelus diplochelatus</i> Stewart, 1913 +

Table 3. Total, inside cold core ring (CCR), outside CCR (out), overall day and night abundances (org./1000 m³), averages and percentages of the hyperiid amphipods with more than 0.39% of total numbers collected in the surveyed area

Species /	Total	Avg	%	CCR avg	CCR%	Out avg	out%	Day avg	Day%	Night avg	Night%
<i>Primno abyssalis</i>	757	95	13.7	178	9.7	44	4.0	42	3.1	147	10.7
<i>Phronimella elongata</i>	562	70	10.2	103	5.6	51	4.6	63	4.6	77	5.6
<i>Primno spp. juveniles</i>	536	67	9.7	140	7.6	23	2.1	23	1.7	111	8.1
<i>Hyperioides longipes</i>	495	62	9.0	105	5.7	36	3.3	43	3.2	80	5.8
<i>Anchylomera blossevillei</i>	425	53	7.7	118	6.4	14	1.3	2	0.1	105	7.6
<i>Hyperietta stephensi</i>	290	36	5.3	14	0.7	50	4.5	52	3.8	20	1.5
<i>Lestrignus bengalensis</i>	286	36	5.2	29	1.6	40	3.6	38	2.7	34	2.4
<i>Primno letreillei</i>	285	36	5.2	49	2.62	8	2.5	32	2.3	39	2.9
<i>Eupronoe intermedia</i>	229	29	4.2	32	1.7	27	2.4	27	2.0	30	2.2
<i>Lestrignus schizogeneios</i>	207	26	3.8	52	2.9	10	0.9	11	0.8	41	3.0
<i>Hyperietta vosseleri</i>	140	17	2.5	33	1.8	8	0.7	8	0.6	27	1.9
<i>Brachyscelus globiceps</i>	135	17	2.5	5	0.2	24	2.2	26	1.9	8	0.6
<i>Phrosina semilunata</i>	132	16	2.4	24	1.3	12	1.1	14	1.0	19	1.4
<i>Phronima atlantica</i>	76	10	1.4	8	0.4	11	1.0	13	1.0	6	0.4
<i>Phronima pacifica</i>	70	9	1.3	13	0.7	6	0.6	6	0.5	11	0.8
<i>Vibilia stebbingi</i>	69	9	1.2	19	1.0	2	0.2	0	0.0	17	1.2
<i>Primno brevidens</i>	68	9	1.2	11	0.6	7	0.6	9	0.6	8	0.6
<i>Lycaeopsis zamboangae</i>	66	8	1.2	10	0.5	7	0.7	8	0.6	9	0.6
<i>Eupronoe minuta</i>	47	6	0.9	11	0.6	3	0.3	4	0.3	8	0.6
<i>Brachyscelus cruscum</i>	47	6	0.9	16	0.9	0	0.0	0	0.0	12	0.9
<i>Scina sp.</i>	44	6	0.8	11	0.6	2	0.2	0	0.0	11	0.8
<i>Thyropus edwardsi</i>	43	5	0.8	9	0.5	3	0.3	4	0.3	7	0.5
<i>Vibilia chuni</i>	40	5	0.7	13	0.7	0	0.0	0	0.0	10	0.7
<i>Lestrignus latissimus</i>	33	4	0.6	3	0.1	5	0.4	2	0.1	6	0.5
<i>Paraphronima gracilis</i>	32	4	0.6	11	0.6	0	0.0	0	0.0	8	0.6
<i>Phronimopsis spinifera</i>	28	4	0.5	2	0.1	4	0.4	5	0.4	2	0.1
<i>Lycaeopsis themistoides</i>	28	3	0.5	5	0.3	3	0.2	3	0.2	4	0.3
<i>Phronima sedentaria</i>	22	3	0.4	5	0.3	1	0.1	2	0.1	4	0.3

latter species are not significant. The juvenile *Primno* were the third most abundant group of hyperiids in the area; they were 6 times more abundant inside (average: 140 org./1000 m³ ± 144, $n = 3$) than outside (23 org./1000 m³ ± 24, $n = 5$) the CCR. Overall, 78% of *Primno* juveniles occurred within the CCR.

Species richness and distribution

Although the number of species within and outside the CCR is almost the same (47 inside vs. 44 outside), several species (13) were not recorded within the CCR and 17 species were not collected outside. Nearly half of the species recorded (29 species) was present both inside and outside the CCR (Table 2). Table 3 shows that the two most abundant species (*Primno abyssalis*

and *Phronimella elongata*) together comprised only 26% of all hyperiids inside the CCR and were slightly less relevant outside the CCR (21%). None of the species occurring only outside the CCR were common in the surrounding zone, only five species were found in two of the non-CCR stations (*Streetsia challengerii*, *S. steenstrupi*, *Platyscelus cruscum*, *Schyzoscelus ornatus*, and *Thyropus sphaeroma*).

In order to determine if part of the inside-outside CCR differences can be attributed to night vertical migration patterns, rather than being a product of differential CCR conditions, night sta. 8 (outside CCR) was compared with the CCR night sta. 2–4. The night station outside the CCR differs mainly in terms of species richness (22 vs. ≥ 45, respectively), composition (28 species recorded in CCR stations did not occur

at sta. 8), and a significantly lower abundance ($391 \text{ org./1000 m}^3$ ($n = 1$) vs. $1076 \pm 522 \text{ org./1000 m}^3$ ($n = 3$), respectively). This was confirmed by the cluster analysis as shown later.

Most of the hyperiid species recorded are epipelagic forms, but those of the genus *Scina* have been described as deeper water dwellers. The five species of *Scina* recorded in the survey and up to 84% of the individuals of this genus were present inside the CCR only; the remaining 16% occurred at night sta. 8.

Two species of *Lestrignos* showed a contrasting distribution in relation to the CCR. *Lestrignos bengalensis* averaged 29 org./1000 m^3 inside the CCR vs. 40 outside. Only 31% of the total numbers of this species were found inside the CCR. *Lestrignos schizogenios* showed an inverse tendency (52 org./1000 m^3 inside vs. 10 outside, up to 76% of the individuals occurred at stations inside the CCR). Two additional cases of opposite CCR-related abundance patterns in congeneric pairs were observed: *Hyperietta vosseleri* and *H. stephensi*, the former had 71.4% of its numbers within the CCR and the latter species figure was 14%; the other couple is *Brachyscelus cruscum* and *B. globiceps* (100% and 10% within the CCR, respectively). The abundance of both species of *Brachyscelus* was significantly different inside from outside (*B. cruscum* $16 \pm 9 \text{ org./1000 m}^3$ ($n = 3$) inside vs. 0 ($n = 5$) outside; *B. globiceps* 24 ± 5 ($n = 5$) outside vs. 5 ± 5 ($n = 3$) inside the CCR).

Unidentifiable immature specimens of *Primno* were also very common, they were the third most abundant hyperiids overall (see Table 3). The distribution of their abundance is also different inside and outside the CCR, up to 73% of their numbers occurred within the CCR.

The Shannon–Wiener diversity was high overall, averaging 3.74 bits/ind; values ranged between 3.47 and 3.98. Diversity values averaged slightly higher (3.89 bits/ind.) at the three stations within the CCR than at the five outside it (3.65 bits/ind.).

Cluster analysis

The Bray–Curtis clustering analysis revealed two large station groups; one group contained all the CCR stations plus sta. 5, the second group included the daytime stations 1, 6 and 7, and night station 8 (Fig. 2). Cluster analysis sorts sta. 8 from the 2–4 group despite the fact that both sta. 3 and 8 were sampled at nearly the same night hour. Station 5, on the perimetral zone south from the gyre was clustered with stations

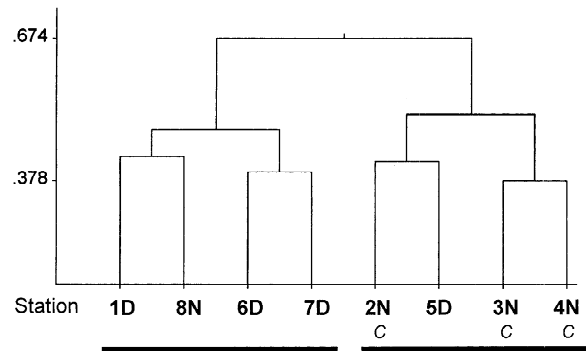


Figure 2. Dendrogram showing clusters of stations from the Bray–Curtis Index for hyperiid amphipods during the surveyed period. Each branch indicates the station number and distinguishes day (D), night (N), and within cold-core ring at night (C) samples.

within the CCR despite the fact that it was sampled at daytime.

Discussion

All the species recorded in this survey are within their known general distributional range (Shih & Chen, 1995; Vinogradov et al., 1996); only three species (i.e. *Eupronoe laticarpa*, *Primno lattareillei*, and *Scina indica*) have not been recorded in the Northwestern Tropical Atlantic region. These three species are considered new regional records. Two decades ago Stuck et al. (1980) presented a list of 54 hyperiid species that were considered new records at that time; results of this survey adds 21 other species not previously recorded in the Gulf of Mexico. Therefore, the current number of species of hyperiid amphipods recorded in the Gulf of Mexico is around 78 (see taxonomic remarks).

There is no published information on the abundance of the hyperiid species in the Gulf of Mexico. However, Stuck et al. (1980) did mention that the commonest species in their survey of coastal waters of the northern Gulf of Mexico was *Lestrignos bengalensis* followed by *Simorhynchotus antennarius* and *Tetrathyrus forcipatus*. *L. bengalensis* is also known to be the most abundant species in the western Caribbean, followed by *Eupronoe intermedia* (Gasca & Shih, 2001). *L. bengalensis* has been regarded as a circumtropical species, which, although an oceanic form, tends to move into coastal areas (Vinogradov et al., 1996). None of these species was dominant in this survey, probably because the CCR was surveyed while moving in a fully oceanic area. It is known that

hyperiid amphipods tend to form well-defined groups with similar distributional patterns (see Schulenberger, 1979); hence, neritic and oceanic hyperiid communities are expected to be widely different. The hyperiid fauna of the western central Gulf of Mexico represents an oceanic community with a strong tropical affinity, dominated by typically tropical forms such as species of *Primno*, *Hyperioides*, *Anchylomera*, and *Lestrignonus*.

Overall, the abundance and composition of this group within and outside the CCR suggest differential conditions and community structure. Results from the Bray–Curtis clustering suggest that differences of the hyperiid night community between inside (sta. 2–4) and outside (sta. 8) the CCR can be attributed to the conditions related to the gyre, thus suggesting a low exchange between these two distinct water masses. It is probable that the large group of species (28) that are absent from the night station outside and occurred within the CCR have better conditions (nutrient-richer, relatively lower temperatures) within the cyclonic system. Although we were not able to compare directly outside day vs. inside day samples, the cluster arrangement showed that day sta. 5 is more similar to the inside CCR night stations 2–4 than it is to the other day samples (Fig. 2). Hence, it is speculated that the inside CCR daytime and nighttime hyperiid community had essentially the same structure; this would support the general concept that the differences observed in the local hyperiid community are related to the CCR. The progressive mixing processes and the environmental changes related to the development of these features seem to affect zooplankters in different ways; Wiebe & Boyd (1978) and Boyd et al. (1978) reported both physiological and morphological changes in the euphausiid *Nematoscelis megalops* in relation to the cold-core rings associated to the Gulf Stream.

There are at least three pairs of species (*Lestrignonus bengalensis*–*L. schizogeneios*; *Hyperietta vosseleri*–*H. stephenseni*; *Brachyscelus cruscum*–*B. globiceps*) with a contrasting distributional and abundance patterns in reference to the CCR (Fig. 3). This is considered to be evidence of the different conditions prevailing inside the CCR more than a plain day/night effect. Schulenberger (1979) described the migratory patterns for *Hyperietta vosseleri* and *H. stephenseni* as opposite, the former up and the latter down at night. If this holds true for the other congeners, and except for *L. bengalensis*, these sets of opposite migrational patterns seems to explain the day/night differences in the other two pairs consistent with the observations by

Schulenberger (1979). Therefore, these species appear to follow the expected migrational patterns (see Fig. 3) described by Schulenberger (1979) outside the CCR both at day and night. However, this pattern changes drastically inside the CCR (see Fig. 3). The thermal difference (1–2 °C) inside and outside the CCR (Biggs et al., 1997) seems to be one parameter to be considered, as hyperiids have been known to be sensitive to slight temperature variations (Young, 1989; Lavaniegos & Ohman, 1999). Hence, those species preferring relatively colder conditions are more abundant inside the CCR (*H. vosseleri*, *L. schizogeneios*), whereas the warmer water forms (*H. stephenseni*, *L. bengalensis*, *B. globiceps*) are more abundant outside the CCR independent of day and night changes. This seem to confirm, for these species, that day–night variations were less important than differences within and outside the CCR. Some other groups such as medusae and siphonophorae seem to avoid cooler waters (Gasca & Suárez-Morales, 1991; Segura-Puertas & Ordóñez-López, 1994); this was noted also by Suárez-Morales et al. (2003) as related to the same CCR.

The occurrence of species of *Scina* was exclusive to the inside of the CCR. Only one species of this genus was reported by Stuck et al. (1980) in the Gulf of Mexico. Known vertical ranges for the species recorded in this survey are highly variable (0–300, 100–500 or 0–1500 m) (see Vinogradov et al., 1996), and all of them have been recorded in the surface layers. However, it is suggested that the shallower part of the migratory pattern of these species could be enhanced by an upward transport from subsurface waters into the upper 100 m as a consequence of the doming of isotherms within the ring (Biggs et al., 1997).

Results of the cluster analysis provide further evidence about the differences between the hyperiid fauna inside and outside the CCR. As mentioned above, day sta. 5 was clustered with the inside night CCR stations. Given the dynamics and influence of these cyclones (Biggs et al., 1997; Wormuth et al., 2000), it seems that sta. 5, the closest to the CCR hydrographic influence behaves as a transitional stage between the full CCR conditions and the surrounding oligotrophic waters.

The noticeably higher density of *Primno* immature specimens (assignable at least in part to *P. abyssalis*, the most abundant species) inside the CCR surveyed area appears to be indicative of a relatively increased reproductive activity within the CCR. Biggs et al. (1997) described this CCR as a system with higher primary and secondary productivity than that of the

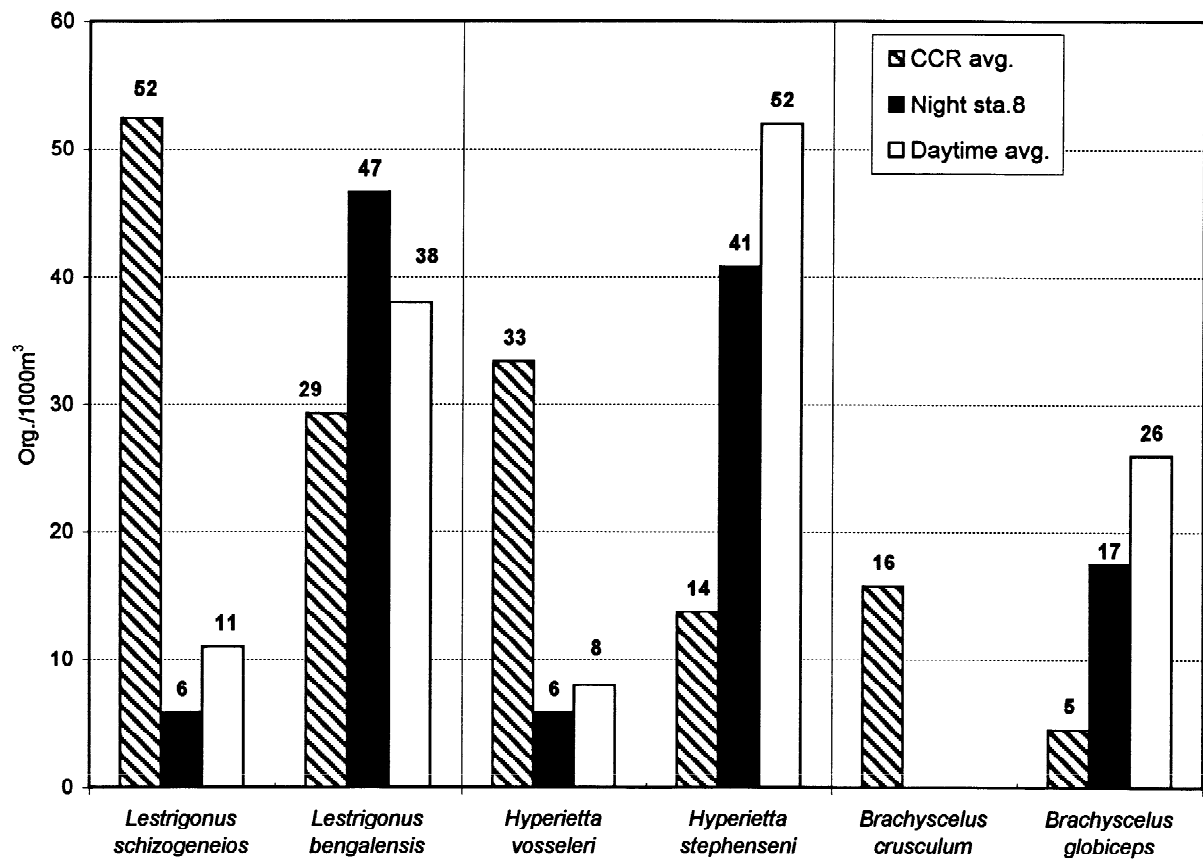


Figure 3. Average abundance (org./1000 m³) of selected pairs of species belonging to three hyperiid genera in different conditions related to the CCR in the surveyed area.

surrounding gulf waters; it is probable that this species finds better conditions for reproduction inside because of the more productive conditions and consequent increased host (pelagic cnidarians) availability related to the inside of the CCR (Suárez-Morales et al., 2003).

These results on the CCR-related hyperiid community generally support the hypothesis that these cyclonic systems are areas with near-surface faunal assemblages different from those dwelling in the oligotrophic oceanic waters outside them (Biggs et al., 1997; Wormuth et al., 2000). Thus, differences at the species level indicate that hyperiid amphipods can be sensitive to the changes of conditions set by the mesoscale cold core rings and even modify their vertical migration patterns. Tranter et al. (1983) described mesoscale eddies as “faunistic islands in a foreign biotope”, but Young (1989) added data from a warm-core eddy stating that the ‘island’ has in fact exchange with the surrounding waters. Results agree with both views; as shown in this survey, the studied CCR has

a transitional band; therefore, the inside CCR fauna is distinct, but not tightly isolated from that of the surrounding waters. Eventually, the eddy will end up becoming progressively mixed with the surrounding waters. The observed differences are probably related to the effect of frontal boundaries of different water masses marking local regions of physical and biological interaction at the mesoscale level in the gulf (Lamkin, 1997).

Anticyclones are particularly oligotrophic systems, with low zooplankton concentrations (Hattori, 1991; Wormuth et al., 2000). In a warm core eddy studied in the Tasman Sea, zooplankton crustaceans (McWilliam & Phillips, 1983) and hyperiid amphipods (Young, 1989) have been found to be less abundant inside than outside these systems, as opposed to the cold core eddies. Gelatinous zooplankton have been found to behave the same opposite way when CCR and WCR were compared (Gasca, 1999; Suárez-Morales et al., 2003). It is a well-known fact that the distribution of

hyperiid is closely linked to that of their hosts (Laval, 1980); although the data presented herein did not emphasize this factor, it was considered that the species occur in the patterns observed independently of the identity of their hosts.

The concentration of potential host species is probably enhanced by the hydrographic conditions and a relatively higher secondary productivity within the CCR (Biggs et al., 1997; Wormuth et al., 2000); hence, the numerical abundance of hyperiids was expected to follow the same pattern as medusae and siphonophores as reported by Laval (1980) and Harbison et al. (1977) and at a larger scale by Lavaniegos & Ohman (1999). This is supported by the slightly higher overall average numerical abundance of medusae but not by the lower numerical abundance of siphonophores within the CCR (Suárez-Morales et al., 2003).

Taxonomic note

The specimens recorded here as *Hemiscelus diploche-latus* could be juvenile forms of *Hemityphis tenu-imanus* (Pirlot, 1939; Zeidler, 1998), its presence in the Gulf of Mexico must be confirmed by examination of more material with fully developed individuals. *Lanceola* sp. is a juvenile, the species is unrecognizable at this stage, and it is the only specimen of the genus found in this survey. *Scina* sp. are either juvenile or damaged specimens. Many unidentifiable juveniles of *Primno* were found, they were included in our analysis because of their abundance.

Acknowledgements

John Wormuth (Texas A&M University) kindly shared with me and with colleagues of El Colegio de la Frontera Sur (ECOSUR) the samples of zooplankton that were collected jointly during the March 1993 cruise of the R/V "Gyre". Chang-tai Shih (National Taiwan University) confirmed the identity of some species and identified the species of *Phronima*. Douglas C. Biggs (Texas A&M University) provided valuable information about the hydrographic features of the eddies; he also transmitted me his interest to study these intriguing systems. Rosa Ma. Hernández Flores and I. Castellanos were a valuable help in the advancement of this project. This work was developed during a sabbatical year spent at the National Museum of Natural History, Smithsonian Institution, Washington, D.C; I received support from CONACYT

(Mexico) through a sabbatical award for a research leave in foreign institutions (ref. 010379/2002).

References

- Biggs, D. C., 1992. Nutrients, plankton, and productivity in a warm-core ring in the western Gulf of Mexico. *Journal of Geophysical Research* 97: 2143–2154.
- Biggs, D. C., A. C. Vastano, R. A. Ossinger, A. Gil-Zurita & A. Pérez-Franco, 1988. Multidisciplinary study of warm and cold-core rings in the Gulf of Mexico. *Memorias de la Sociedad de Ciencias Naturales de Venezuela* 48: 11–31.
- Biggs, D. C., R. A. Zimmerman, R. Gasca, E. Suárez-Morales & I. Castellanos, 1997. Note on plankton and cold-core rings in the Gulf of Mexico. *Fishery Bulletin* 95: 369–375.
- Boys, S. H., P. H. Wiebe & J. L. Cox, 1978. Limits of *Nematoscelis megalops* in the Northwestern Atlantic in relation to Gulf Stream cold-core rings. 2. Physiological and biochemical effects of expatriation. *Journal of Marine Research* 36: 143–159.
- De la Cruz, A., 1997. Análisis de Comunidades ANACOM. Software. Mérida, México.
- Fage, L., 1960. Oxycephalidae. Amphipodes pélagiques. *Dana Reports* 52: 1–145.
- Gasca, R., 1999. Siphonophores (Cnidaria) and summer mesoscale features in the Gulf of Mexico. *Bulletin of Marine Science* 65: 75–89.
- Gasca, R. & C.-T. Shih., 2001. Hyperiid amphipods of surface waters of the western Caribbean Sea (1991). *Crustaceana* 74: 489–499.
- Gasca, R. & E. Suárez-Morales, 1991. Siphonophores of upwelling areas in the Campeche Bank and Mexican Caribbean Sea. *Hydrobiologia* 216/217: 497–502.
- Harbison, G. R. & L. P. Madin, 1976. Description of the female *Lycaea nasuta* Claus, 1879 with an illustrated key to the species of *Lycaea* Dana, 1852 (Amphipoda, Hyperiidea). *Bulletin of Marine Science*. 26: 165–171.
- Harbison, G. R., D. C. Biggs & L. P. Madin, 1977. The associations of Amphipoda Hyperiidea with gelatinous zooplankton – II. Associations with Cnidaria, Ctenophora and Radiolaria. *Deep-Sea Research* 24: 465–468.
- Hattori, H., 1991. Vertical distribution of zooplankton in the warm core off Sanriku (86B) and adjacent Oyashio water, with special reference to copepods record. *Bulletin of the Hokkaido National Fisheries Research Institute* 55: 59–65.
- Lamkin, J., 1997. The Loop Current and the abundance of larval *C. pauciradiatus* in the Gulf of Mexico: evidence for physical-biological interaction. *Fishery Bulletin* 95: 251–267.
- Laval, P., 1980. Hyperiid amphipods as crustacean parasitoids associated with gelatinous zooplankton. *Oceanography and Marine Biology Annual Review* 18: 11–56.
- Lavaniegos, B. E. & M. D. Ohman, 1999. Hyperiid amphipods as indicators of climate change in the California Current. In Schram, F. R. & J. C. von Vaupel Klein (eds), *Crustaceans and the Biodiversity Crisis. Proceedings of the Fourth International Crustacean Congress*, Amsterdam, The Netherlands, July, 1998. Vol. I. E.J. Brill, Leiden 489–509.
- Lewis, J. K. & A. D. Kirwan, 1985. Some observations of ring topography and ring–ring interactions in the Gulf of Mexico. *Journal of Geophysical Research* 90: 9017–9028.
- Ludwig, J. A. & J. F. Reynolds, 1988. *Statistical Ecology. A Primer on Methods and Computing*. John Wiley & Sons. 337 pp.

- McWilliam, P. S. & B. F. Phillips, 1983. Phyllosoma larvae and other crustacean macrozooplankton associated with eddy J, a warm-core eddy off south-eastern Australia. *Australian Journal of Marine and Freshwater Research* 34: 653–663.
- Pirlot, J.-M., 1939. Sur des Amphipodes Hypérides provenant des Croisières du Prince Albert 1er de Monaco. *Résultats des Campagnes Scientifiques Monaco* 102: 1–63, pl. 1–2.
- Segura-Puertas, L. & U. Ordóñez-López, 1994. Análisis de la comunidad de medusas (Cnidaria) de la región oriental del Banco de Campeche y el Caribe Mexicano. *Caribbean Journal of Science* 30: 104–115.
- Shih, C.-T. & Chen, Q.-C., 1995. Zooplankton of China Seas (2). The Hyperiidea (Crustacea: Amphipoda). China Ocean Press. Beijing: 295 pp.
- Shulenberger, E., 1979. Distributional pattern and niche separation among North Pacific hyperiid amphipods. *Deep-Sea Research* 26A: 293–315.
- Smith, P. E. & S. L. Richardson, 1979. Técnicas modelo para prospecciones de huevos y larvas de peces pelágicos. *FAO Fisheries Technical Paper* 175: 1–107.
- Stuck, K. C., H. M. Perry & A. G. Fish, 1980. New records of Hyperiidea (Crustacea: Amphipoda) from the North Central Gulf of Mexico. *Gulf Research Reports* 6: 359–370.
- Suárez-Morales, E., R. Gasca, L. Segura-Puertas & D. C. Biggs, 2003. Planktonic cnidarians in a cold-core ring in the Gulf of Mexico. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México. Series Zoología* 73: 19–36.
- Tranter, D. F., D. J. Tafe & R. L. Sandland, 1983. Some zooplankton characteristics of warm core eddies shed by the East Australian Current, with particular reference to copepods. *Australian Journal of Marine and Freshwater Research* 34: 625–652.
- Vinogradov, M. E., A. F. Volkov & T. N. Semenova, 1996. Hyperiid amphipods (Amphipoda, Hyperiidea) of the world oceans. Science Publ. Inc. Lebanon, U.S.A.: 632 pp.
- Wiebe, P. H. & S. H. Boyd, 1978. Limits of *Nematoscelis megalops* in the Northwestern Atlantic in relation to Gulf Stream cold-core rings. 1. Horizontal and vertical distribution. *Journal of Marine Research* 36: 119–142.
- Wormuth, J. H., P. H. Ressler, R. B. Cady & E. J. Harris, 2000. Zooplankton and micronekton in cyclones and anticyclones in the Northeast Gulf of Mexico. *Gulf of Mexico Science* 18: 23–34.
- Yang, W. T., 1960. A study of the subgenus *Parahyperia* from the Florida Current (genus *Hyperia*; Amphipoda: Hyperiidea). *Bulletin of Marine Science of the Gulf and Caribbean* 10: 11–39.
- Young, J. W., 1989. The distribution of hyperiid amphipods (Crustacea: Peracarida) in relation to warm-core eddy J in the Tasman Sea. *Journal of Plankton Research* 11: 711–728.
- Zeidler, W., 1990. Pelagic amphipods, infraorder Physosomata (Crustacea: Amphipoda: Hyperiidea) from the CSK International Zooplankton Collection (western North Pacific) with the description of four new species of *Scina*. *Publications of the Seto Marine Biological Laboratory* 34: 167–200.
- Zeidler, W., 1992. Hyperiid amphipods (Crustacea: Amphipoda: Hyperiidea) collected recently from eastern Australian waters. *Records of the Australian Museum* 44: 85–133.
- Zeidler, W., 1998. Pelagic Amphipods (Crustacea: Amphipoda: Hyperiidea) collected from eastern and southeastern Australian waters by the CSIRO research vessel “Warreen” during the years 1938–1941. *Records of the Australian Museum. Monograph Series No. 4*: 1–143.