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Structure of hyperiid amphipod assemblages on Isla Gorgona, eastern tropical Pacific off Colombia

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Temporal variation of hyperiid amphipod structure assemblages was studied on Isla Gorgona, eastern tropical Pacific (ETP) off Colombia between September 2005 and August 2006. Forty-six species were found during the entire sampling period: Hyperioides sibaginis, Lestrigonus bengalensis, Phronimopsis spinifera, Tetrathyrus forcipatus *and* Paralycaea gracilis *dominated the assemblage, representing 92%. The dendogram based on the Bray–Curtis similarity index showed that the hyperiid assemblages were separated into two groups, which did not coincide with the seasonality described for the ETP (wet versus dry season). Rather, groups comprised wet (May to November) and dry season months (December to April). The first group included November, December, February and March. During these months, significantly higher hyperiid richness, diversity and abundance were found, although colder subsurface water temperatures in Gorgona were registered only during February and March. The other group included May to October and January, and was characterized by lower hyperiid diversity and abundance values. Significant correlations were found between hyperiid abundance and the possible gelatinous zooplankton hosts (medusae, siphonophores and salps). This study contributes to increasing knowledge of the zooplankton community in the Panama Bight, as well as of a poorly studied group in the ETP.*

Keywords: Hyperiidea, zooplankton, Colombia, Panama Jet, eastern tropical Pacific

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INTRODUCTION

On an annual scale, the zooplankton community in the eastern tropical Pacific (ETP) is principally modulated by a mesoscale upwelling process in the Gulfs of Tehuantepec, Papagayo, and Panama (Fernández-Álamo & Färber-Lorda, 2006). This process is the result of the combined effect of wind jets and the seasonal movement of the Intertropical Convergence Zone (ITCZ) (Amador *et al.*, 2006). Geographically, the Pacific Ocean off Colombia is located within the Panama Bight, eastern portion of the ETP. In this region, the upwelling process generated by the Panama wind jet occurs during the southerly position of the ITCZ in March (about 3°N) (Forsbergh, 1969; Amador *et al.*, 2006), bringing colder and saltier waters to the entire zone (Rodríguez-Rubio *et al.*, 2003; Fiedler & Talley, 2006; Devis-Morales *et al.*, 2008). The intrusion of this cold subsurface water during the dry season (December to April) enhances a high biological productivity, which is reflected in high phytoplankton (Rodríguez-Rubio & Stuardo, 2002; Pennington *et al.*, 2006; D'Croz & O'Dea, 2007) and zooplankton biomass (Fernández-Álamo & Färber-Lorda, 2006). On the other hand, during the northerly position of the ITCZ (in September, about 10°N), the Panama jet completely disappears, and warm, fresh and less productive waters are observed in the region (Rodríguez-Rubio & Stuardo, 2002; Devis-Morales *et al.*, 2008). The low values of salinities (<34 psu) recorded in the Panama Bight are accentuated during this period (wet season, May to November), as a result of excess precipitation, a process that is enhanced in coastal waters due to the effect of river discharges (Fiedler & Talley, 2006).

In the ETP, most studies about the response of a specific group of the zooplankton community (e.g. copepods, polychaetes and euphausiids) to seasonal changes in hydrographic conditions have been conducted in the Gulf of Tehuantepec (Mexico) (Färber-Lorda *et al.*, 1994; Fernández-Álamo *et al.*, 2000; Fernández-Álamo & Sanvicente-Añorve, 2005). In other localities belonging to the ETP, such as the Panama Bight (Panama, Colombia and Ecuador), few zooplankton studies have been carried out (Fernández-Álamo & Färber-Lorda, 2006; Miglietta *et al.*, 2008). Furthermore, none of these studies has focused on hyperiid amphipods, although members of this group have been recognized as sensitive to slight variations in temperature directly or indirectly through their association with the gelatinous hosts (Laval, 1980; Lavaniegos & Ohman, 1999).

In temperate and polar regions, the ecological role of hyperiids is well documented (e.g. Bocher *et al.*, 2001; Yamada & Ikeda, 2006; Dalpadado *et al.*, 2008). However, when tropical environments of the eastern Pacific are considered, the panorama is quite different, because knowledge about the composition of the hyperiid assemblages is scarce, and information

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of their ecological role is limited (Répelin, 1978; Gasca & Franco-Gordo, 2008; Valencia & Giraldo, 2009; Gasca, 2009a, b; Gasca *et al.*, 2010). The only ecological study on hyperiids in the Panama Bight was carried out by Valencia & Giraldo (2009) in the northern portion of the Pacific coast of Colombia. In this study, an unexpectedly high abundance of hyperiids was reported. Nevertheless, the temporal and spatial resolution used did not allow obtaining significant conclusions about the local variation of the assemblage.

There are no previous studies of the temporal variation on an annual scale of a specific group of zooplankton in the Panama Bight, and due to the characteristic changes in water column temperature in this region between the dry and wet seasons, it is expected that the structure of the hyperiid amphipod assemblages responds to these changes. In this context, we expect: (1) that a change in species composition occurs between seasons in neritic waters of the Panama Bight (Isla Gorgona), due to the entrance of subsurface waters during the dry season (upwelling period); (2) that the abundance and diversity of the hyperiid amphipod assemblages will be higher during the upwelling period (cold, salty and productive); and (3) that the abundance of hyperiids may be associated with higher abundances of the possible gelatinous zooplankton hosts.

MATERIALS AND METHODS

Study area

Isla Gorgona is the most extensive insular territory (13.3 km^2) in the Colombian Pacific Ocean, located 30 km from the continent. This island was declared a National Natural Park in the 1980s, given its high marine biological diversity, being the most extensive marine protected area in the Colombian Pacific (UAESPNN, 1998). The local weather is characterized by a high precipitation level (4164–8176 mm.years^{-1}), high relative humidity (90%), and mean air temperature of 26°C (Díaz *et al.*, 2001; Blanco, 2009). An oceanographic study in this locality described two contrasting periods: the first one from May to December with a low surface salinity and a thermocline depth of 47 m, and a second one from January to April with a high surface salinity and a thermocline depth of 7.5 m (Giraldo *et al.*, 2008b).

Sampling design and analysis of the samples

Twelve oceanographic expeditions were carried out on a monthly schedule to Isla Gorgona (Figure 1) between September 2005 and August 2006. During each month, samples were collected following a grid of 24 stations around the island during daylight hours (8:00–18:00). Oblique zooplankton hauls using a bongo net of 30 cm mouth diameter and 250 μm mesh size provided with a General Oceanic flowmeter were carried out. Each haul had a mean duration of seven minutes and was made with a mean velocity of 1.1 $\text{m}\cdot\text{s}^{-1}$ to a maximum depth of 50 m, except for Stations 1, 22, 23 and 24, which were 10 m depth. Due to logistical problems, Stations 14, 23 and 24 were not sampled in December. Samples were fixed in 4% formaldehyde diluted in seawater. Additionally, a StowAway Tidbit data logger was deployed at 15 m on the eastern side of the island (Figure 1) to register water temperature at 30 minutes intervals between 1 September 2005 and 30 August 2006.

Hyperiids were sorted from each sample, identified, and counted. All counts were standardized to $\text{ind}\cdot 1000\ \text{m}^{-3}$. Taxonomic identification was made using the keys of Bowman (1973), Shih (1991), Vinogradov *et al.* (1996), Shih & Hendrycks (2003) and Zeidler (2004, 2009). Once identified, specimens were deposited in the Amphipod Collection at the Universidad del Valle, Cali, Colombia (CAN-UV).

Statistical analysis

The frequency of occurrence of each hyperiid species during a monthly schedule was estimated, establishing five categories: rare (R: 1 to 3 months), frequent (F: 4 to 6 months), common (C: 7 to 9 months) and abundant (A: 10 to 12 months). The structure of the hyperiid assemblages was described using the Shannon–Wiener diversity index (H′) (log e), while the differences in abundance among sampling months were tested by using a Kruskal–Wallis analysis, given that the assumptions of normality and homogeneity of variance were not supported (Statistica 7.0). The multiple

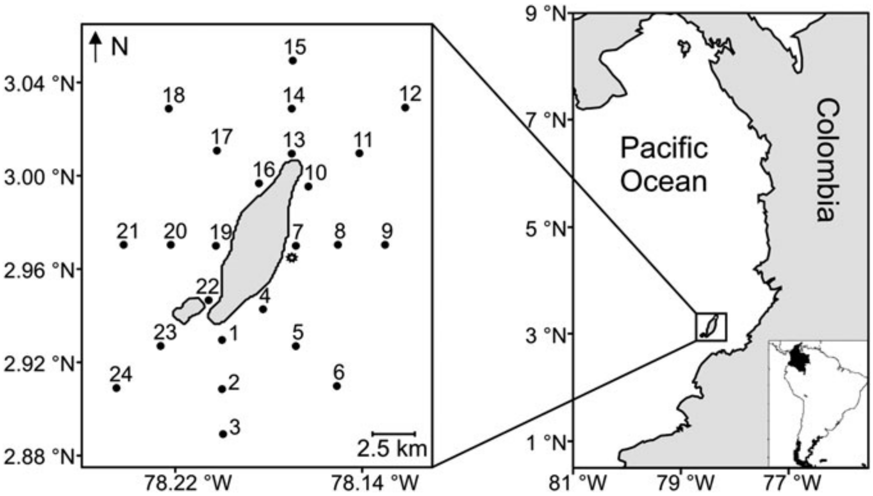

Fig. 1. Location of Isla Gorgona and zooplankton sampling stations on the Pacific coast off Colombia, eastern tropical Pacific. Asterisk indicates location of the temperature data logger.

comparison test of Nemenyi–Dunn for unequal samples was carried out to identify the source of variation. Because of the high variability in the abundance data, the geometric mean and the 95% confidence interval were used as descriptors. To establish the relation of the hyperiid structure assemblages between hydrographic periods, a hierarchical cluster analysis using group average linking was performed, after the exclusion of stations without amphipods. The similarity measure used was the Bray–Curtis similarity calculated on the transformed data (log x + 1) for all species, while the Simprof technique was used to identify the cluster significance (Primer 6.0) (Clarke & Warwick, 2001). To graphically represent the relations of the structure of the hyperiid assemblages, an ordination plot was constructed using the non-metric multidimensional scaling analysis, and the results obtained were compared with that of the cluster to evaluate the consistency of both methods. Based on the groups obtained, a similarity of percentages analysis was performed to examine which species contributed to the similarity within each group (Primer 6.0). Finally, a Spearman rank correlation was calculated to evaluate possible associations between hyperiid abundance (total and most abundant species) and the abundance of gelatinous zooplankton (Statistica 7.0). The Bonferroni criterion for significance level in multiple associations was used ($\alpha = \alpha/k$).

RESULTS

Temperature

A continuous register of temperature provided by the data logger placed at a 15 m depth on Isla Gorgona (Figure 1) showed that warm water prevailed most of the year (27.2 ± 0.6°C SD), while an abrupt decrease in temperature was observed in February and March (<17°C) (Figure 2). Mean minimum and maximum temperatures were recorded in February (16.6 ± 2.5°C SD) and August (28.3 ± 0.1°C SD), respectively.

The hyperiid assemblages

Forty-six species belonging to 14 families were found. November and March were the months with the highest number of species (31 and 29 species, respectively), while June and August presented the lowest (nine and seven species, respectively) (Table 1). Of the 46 species found, 19 were rare, 13 were frequent, seven were common and seven were abundant; of this last category, only *Hyperioides sibaginis*, *Lestrigonus bengalensis* and *Tetrathyrus forcipatus* were found during all 12 sampling months (Table 1).

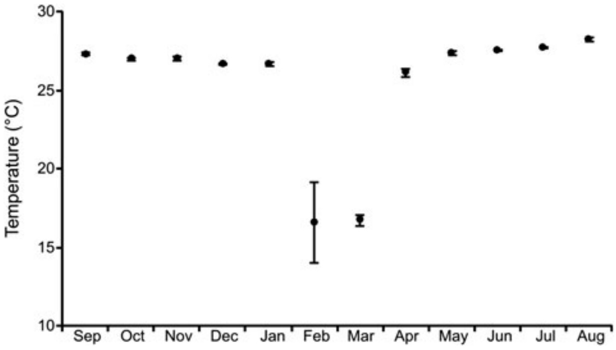

Fig. 2. Mean temperature (±SD) at 15 m depth on Isla Gorgona during an annual schedule (September 2005–August 2006).

Diversity (H′) presented a bimodal tendency, with peaks in November (1.42 ± 0.19) and March (1.80 ± 0.14). The lowest values were registered in January (0.72 ± 0.20) and June (0.31 ± 0.16) (Figure 3). The hyperiid assemblage was dominated by *Hyperioides sibaginis* (47.7%), *Lestrigonus bengalensis* (38.5%), *Phronimopsis spinifera* (2.1%), *Paralycaea gracilis* (1.7%) and *Tetrathyrus forcipatus* (1.5%). The relative abundance of these dominant species was variable. In general, *H. sibaginis* was highly dominant during June, representing 86% of the assemblage. The relative abundance of *L. bengalensis* was high during September, November and March. Likewise, *P. gracilis* was an important component of the assemblage during April and July, *P. spinifera* during September and October, and *T. forcipatus* during February, April, and July (Figure 4). Furthermore, in the months in which *H. sibaginis* presented the lowest relative abundance (September, October, November and March), *L. bengalensis* and *P. spinifera* presented the highest contribution to the assemblage.

Spatial distribution of abundance was highly variable, and a clear pattern was not found. In general, there were homogeneous distribution and low values (<2000 ind·1000 m^{-3}) during most of the study period (September, October, January, May, June, July and August). However, during November and December, abundance was highest on the eastern side of the island, while during February and March, abundance was highest on the western side. In April, highest abundance values were registered in the entire zone (>4000 ind·1000m^{-3}) (Figure 5).

Hyperiid abundance on Isla Gorgona was significantly variable during the study period ($H_{11,285} = 128.39$, $P < 0.0001$), with values ranging between zero and 9833 ind·1000 m^{-3} (672 ± 146 ind·1000 m^{-3}). Thus, abundance presented a bimodal form with peaks in November and April, with a remarkable decrease between April and May (Figure 6). Hyperiid abundance in November, December, March and April was significantly higher than during May, June and July ($P < 0.01$); likewise, abundance was significantly higher in April than in August, September and October ($P < 0.01$), higher in March than in September–October ($P < 0.07$), and higher in November than in September ($P < 0.02$). Although January belongs to the same thermal period as March and April, hyperiid abundance was significantly lower ($P < 0.02$) (Table 2).

The dendogram based on the Bray–Curtis similarity index indicated that two significant groups were formed. The first group encompassed the hyperiid assemblage of November, December, February, March and April, while the second group encompassed the hyperiid assemblage of September, October, January, May, June, July and August. Although it was expected that the January hyperiid assemblage would be grouped with the months belonging to the dry season, and the November assemblage with that of the wet season, they were grouped in contrary hydrographic periods (Figure 7A). A concordance aggregation pattern was observed in the multidimensional scaling plot, in which the low stress level obtained (0.08) indicates that an analysis considering higher dimensional solutions will not add relevant information to the structure of the hyperiid assemblage on Isla Gorgona (Figure 7B). When the percentage of contribution of the species that

Table 1. List of species, geometric mean (ind·1000 m^{-3}) and frequency of occurrence (FO) of hyperiid amphipods on Isla Gorgona between September 2005 and August 2006.

	September	October	November	December	January	February	March	April	May	June	July	August	FO
Infraorder Physosomata													
Family Scinidae													
Acanthoscina acanthodes (Stebbing, 1895)	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	R
Infraorder Physocephalata													
Family Vibiliidae													
Vibilia australis Stebbing, 1888	0.0	1.2	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.0	R
Vibilia chuni Behning & Woltereck, 1912	0.2	0.0	0.2	0.0	0.8	0.2	0.0	0.0	0.0	0.0	0.0	0.0	F
Vibilia propinqua Stebbing, 1888	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	R
Vibilia pyripes Bovallius, 1887	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	R
Vibilia stebbingi Behning & Woltereck, 1912	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	R
Family Paraphronimidae													
Paraphronima crassipes Claus, 1879	1.2	1.1	0.5	0.8	1.0	3.7	0.2	0.8	1.3	0.5	4.0	0.0	A
Family Hyperiidea													
Hyperoche medusarum? (Krøyer, 1838)	0.0	0.0	0.5	0.0	0.2	0.5	0.0	2.0	0.0	0.0	0.0	0.0	F
Family Lestrigonidae													
Hyperioides longipes Chevreux, 1900	0.0	0.2	0.2	0.6	0.2	1.1	5.2	0.0	0.0	0.0	0.0	0.0	F
Hyperioides sibaginis (Stebbing, 1888)	4.3	14.4	220.3	535.6	138.1	204.1	22.9	1161.3	111.2	51.7	13.4	176.9	A
Hyperietta stebbingi Bowman, 1973	0.4	0.4	0.6	1.9	0.0	0.0	12.2	1.0	0.5	0.0	0.0	0.0	C
Hyperietta vosseleri (Stebbing, 1904)	25.8	0.6	22.7	2.0	0.0	0.0	5.0	8.7	0.2	0.5	0.0	0.0	C
Lestrigonus bengalensis Giles, 1887	97.6	40.0	478.3	287.3	74.6	100.6	364.9	260.2	15.2	5.4	3.1	51.0	A
Lestrigonus macrophthalmus (Vosseler, 1901)	0.0	0.0	0.7	0.2	0.0	0.0	0.0	0.8	0.2	0.0	0.0	0.0	F
Lestrigonus schizogeneios (Stebbing, 1888)	0.0	0.2	0.0	0.8	0.0	0.0	1.5	0.8	0.0	0.0	0.0	0.0	F
Phronimopsis spinifera Claus, 1879	22.7	102.9	12.1	4.4	0.2	0.0	54.4	4.8	0.2	0.0	0.2	0.0	C
Themistella fusca (Dana, 1852)	0.0	0.0	0.9	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	R
Family Phronimidae													
Phronima atlantica Guérin-Méneville, 1836	0.2	0.2	0.0	0.0	0.0	0.0	0.2	0.2	0.2	0.0	0.0	0.0	F
Phronima bowmani Giles, 1887	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	R
Phronima dunbari Vosseler, 1901	0.0	0.0	0.2	0.2	0.0	1.1	9.1	4.8	0.0	0.0	0.0	0.0	F
Phronima sedentaria (Forskål, 1775)	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	R
Family Phrosinidae													
Anchylomera blossevillei Milne-Edwards, 1830	0.0	0.0	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	R
Phrosina semilunata Risso, 1822	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.8	0.0	0.0	0.0	R
Primno latreillei Stebbing, 1888	0.0	0.2	0.0	0.0	0.0	1.4	6.4	0.0	0.0	0.2	0.0	0.0	F
Family Lycaeopsidae													
Lycaeopsis themistoides Claus, 1879	0.2	0.5	1.8	2.6	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.2	C
Lycaeopsis zamboangae (Stebbing, 1888)	0.0	0.2	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	R
Family Pronoidae													
Eupronoe minuta Claus, 1879	0.0	0.0	0.5	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	R
Eupronoe laticarpa Stephensen, 1925	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	R
Paralycaea gracilis Claus, 1879	0.0	0.2	3.0	0.9	0.2	13.2	23.7	373.0	0.2	0.2	2.3	0.2	A
Parapronoe parva Claus, 1879	0.4	0.2	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	F
Family Lycaeidae													
Lycaea pulex Marion, 1874	0.0	0.0	0.0	1.2	0.2	5.8	48.1	0.8	0.0	0.0	0.0	0.0	F
Lycaea serrata Claus, 1879	0.0	0.0	0.0	0.0	0.2	0.0	0.5	0.0	0.0	0.0	0.0	0.0	R
Simorhynchotus antennarius (Claus, 1871)	0.0	0.4	0.5	1.4	0.4	1.1	13.6	3.6	0.2	0.0	1.1	0.2	A

Table 1. Continued

Family Brachyscelidae												
Brachyscelus rapax? (Claus, 1879)	0.2	0.2	0.7	0.3	0.2	1.5	4.8	31.1	0.2	0.0	0.0	0.0	C
Family Oxycephalidae													
Cranocephalus scleroticus (Streets, 1878)	0.0	0.0	0.0	0.0	0.0	0.0	0.2	1.0	0.0	0.0	0.0	0.0	R
Glossocephalus milneedwardsi Bovallius, 1887	0.0	0.0	3.5	0.0	0.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0	R
Oxycephalus clausi Bovallius, 1887	0.2	0.2	16.0	0.5	0.0	0.7	1.0	0.9	0.3	0.0	0.2	0.0	C
Rhabdosoma whitei Bate, 1862	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.0	R
Streetsia mindanaonis (Stebbing, 1888)	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	R
Family Platyscelidae													
Amphithyrus bispinosus Claus, 1879	0.8	0.2	0.4	0.0	0.0	0.4	0.0	0.0	0.2	0.0	0.0	0.0	F
Amphithyrus muratus Volkov, 1982	0.5	0.0	1.2	0.2	0.5	2.1	1.1	74.7	0.0	0.0	0.5	0.2	C
Amphithyrus sculpturatus Claus, 1879	0.2	0.0	0.2	0.0	0.2	1.7	1.1	161.0	0.0	0.0	0.0	0.0	F
Platyscelus serratulus Stebbing, 1888	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	R
Tetrathyrus forcipatus Claus, 1879	0.4	0.8	4.7	1.9	2.6	10.5	1.8	39.7	0.2	0.5	1.2	5.0	A
Family Parascelidae													
Parascelus edwardsi Claus, 1879	2.0	0.8	1.1	0.2	0.2	0.2	30.2	62.2	0.8	0.6	0.5	0.0	A
Schizoscelus ornatos Claus, 1879	0.0	0.2	0.0	0.5	0.2	3.0	0.0	0.5	0.0	0.0	0.0	0.0	F
Unidentified young	0.5	0.9	0.5	0.5	0.0	2.8	4.7	0.2	0.8	0.2	1.6	0.9	-
Species number	**18**	**22**	**31**	**21**	**18**	**23**	**29**	**22**	**16**	**9**	**12**	**7**	

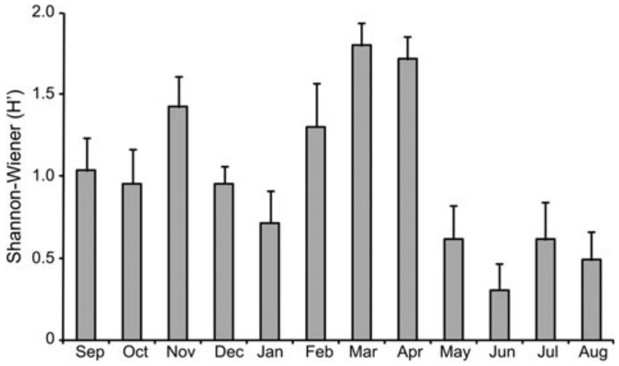

Fig. 3. Shannon–Wiener diversity index of hyperiids between September 2005 and August 2006 on Isla Gorgona.

identify each group was evaluated, it was found that *L. bengalensis* and *H. sibaginis* were the most important species for both assemblages, with their contribution higher in the second (b = 81%) than in the first group (a = 51%). Likewise, the contribution of these species changes between groups, with higher values for *L. bengalensis* in the first group, and for *H. sibaginis* in the second group. Additionally, of the five species that presented the highest percentages of contribution in each group, *Paralycaea gracilis*, *T. forcipatus* and *Phronimopsis spinifera* were important components in the first group, while *Paraphronima crassipes* and *Parascelus edwardsi* were important components for the second group (Figure 7C). The major diversity observed in the first group was also associated with higher abundances (559 ind·1000 m^{-3}) than that observed in the second group (73 ind·1000 m^{-3}) (Figure 7C).

The abundance of the gelatinous zooplankton (potential hosts of hyperiids) presented three peaks during the study period (December, March and July), which did not necessarily coincide with the hyperiid abundance peaks (Figures 6 & 8). Medusae presented higher abundances in December,

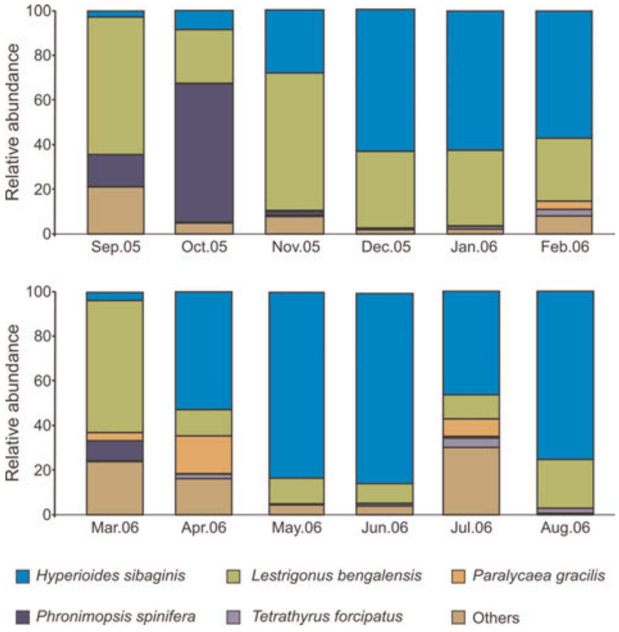

Fig. 4. Relative abundance of the five most abundant species of hyperiids between September 2005 and August 2006 on Isla Gorgona.

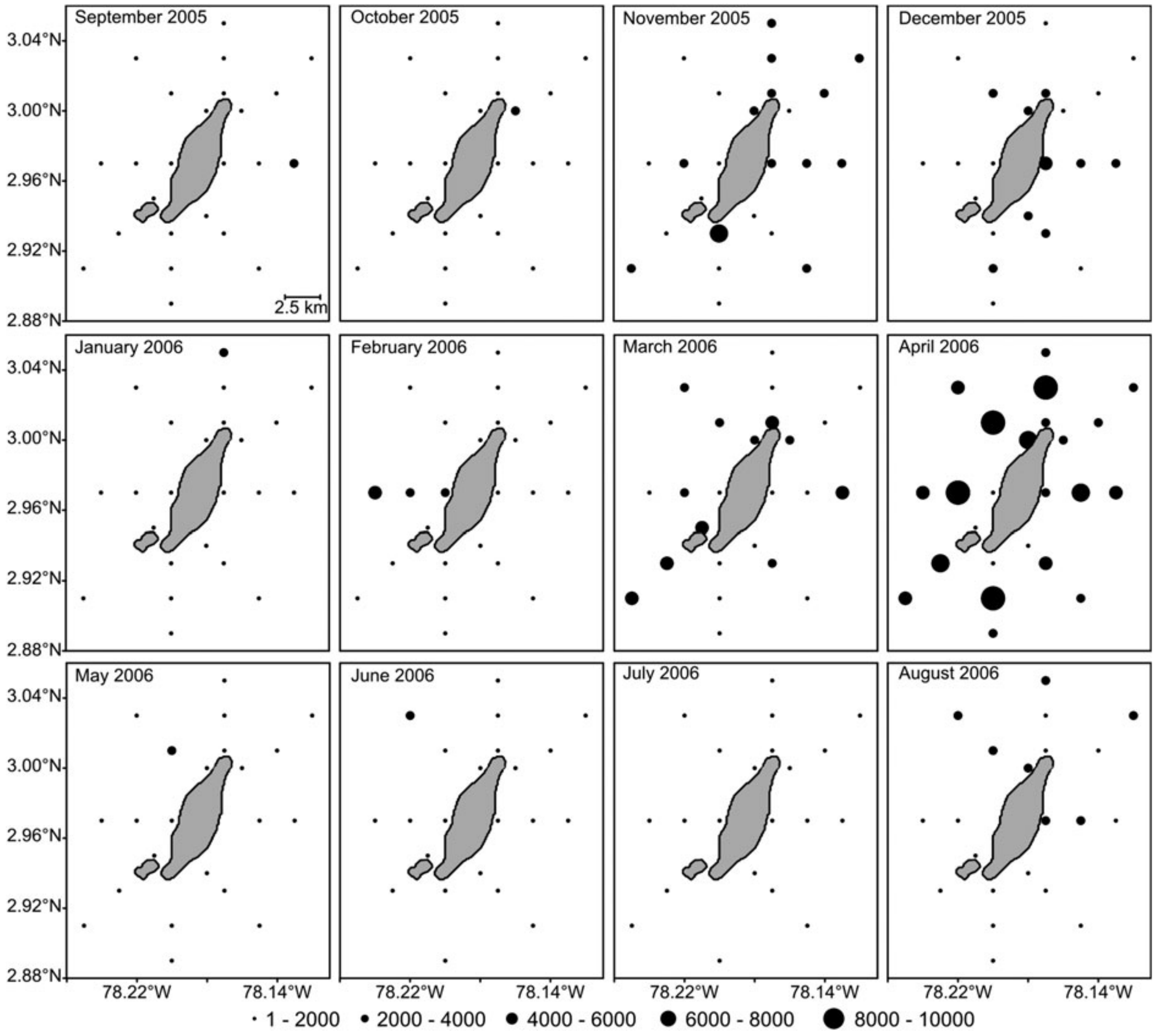

Fig. 5. Distribution of density of hyperiids (ind·1000 m^{-3}) between September 2005 and August 2006 on Isla Gorgona.

February and July (>10 ind·m^{-3}), siphonophores in December–January and April (>10 ind·m^{-3}), while salps presented a peak in abundance during March (>35 ind·m^{-3}). Significant associations were found between hyperiid abundance and the three gelatinous groups evaluated (medusae, siphonophores and salps) ($P < 0.01$) (Table 3). In a detailed analysis, three of the five most abundant hyperiid species were significantly associated with only one gelatinous group: *H. sibaginis* and *T. forcipatus* with siphonophores, and *P. spinifera* with medusae. *Lestrigonus bengalensis* abundance was significantly associated with medusae and siphonophores, while *P. gracilis* was significantly associated with the three gelatinous groups evaluated ($P < 0.01$) (Table 3).

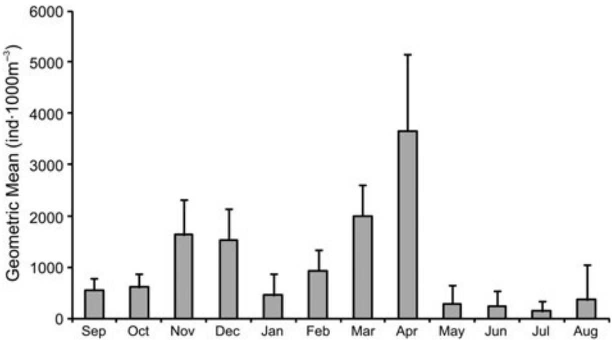

Fig. 6. Geometric mean (95% confidence interval) of hyperiids between September 2005 and August 2006 on Isla Gorgona.

DISCUSSION

Studies on hyperiid amphipods in the eastern tropical Pacific (ETP) have been temporally or spatially limited. For this

Table 2. *A posteriori* result of Nemenyi–Dunn analysis based on an annual variation of hyperiid abundance on Isla Gorgona. Only significant results are shown (α < 0.05).

Hyperiid abundance			***P***
February	>	July	<0.01
March, April, November	>	January, September	<0.02
March, April, November, December	>	May, June, July	<0.01
March, April	>	October	<0.01
April	>	February, August	<0.01

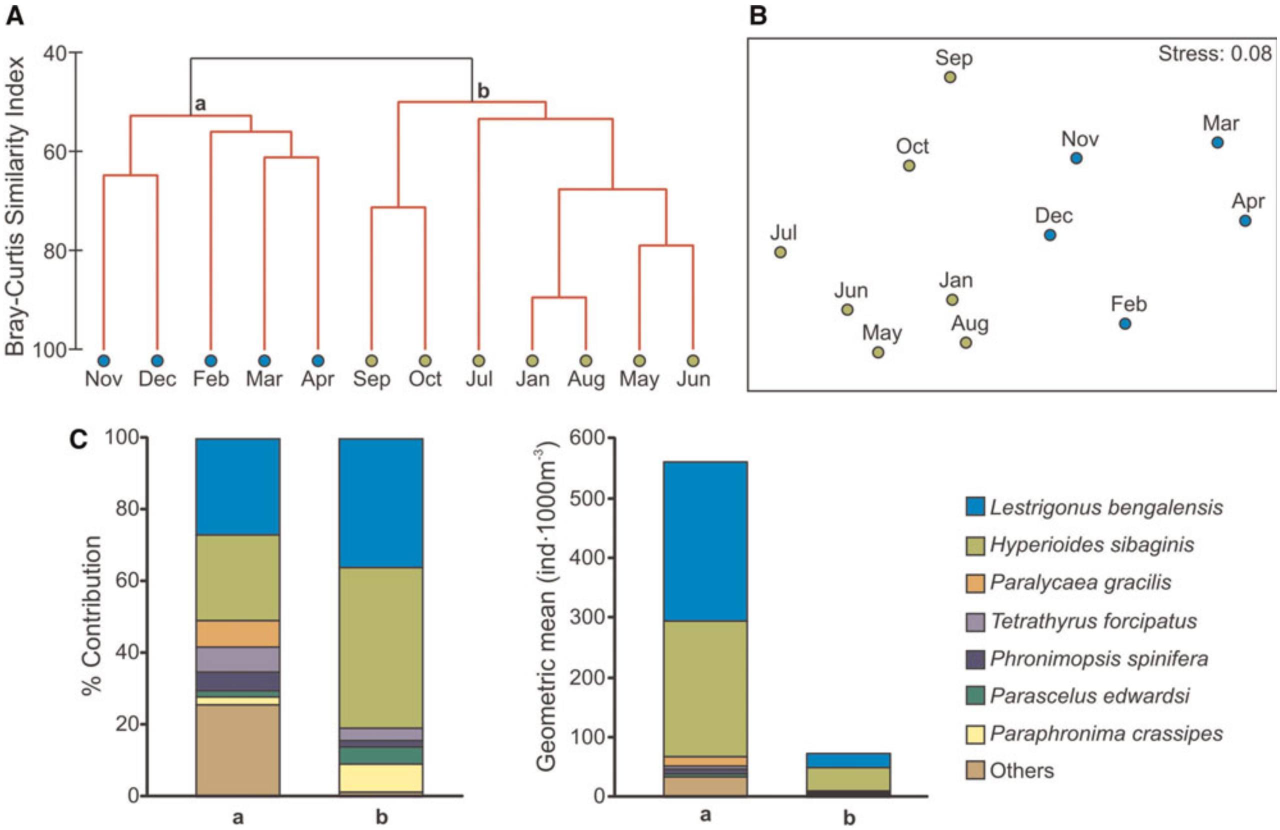

Fig. 7. Dendogram (A) and non-metric multidimensional scaling (B) analysis of hyperiid abundance using Bray–Curtis similarity index. Also based on similarity percentage analysis, the relative contribution and geometric mean (C) of the five most abundant species for each cluster are shown.

reason, the monthly sample carried out on Isla Gorgona between September 2005 and August 2006 had a high species richness ($S = 46$) compared with that reported in other localities of the ETP, like the northern Pacific coast of Colombia ($S = 20$; Valencia & Giraldo, 2009), the Pacific coast of Costa Rica ($S = 34$; Gasca, 2009a) and Banderas Bay in Mexico ($S = 20$; Gasca & Franco-Gordo, 2008). The species composition on Isla Gorgona was comprised mainly of tropical–subtropical species (Vinogradov *et al.*, 1996; Vinogradov, 1999), of which 18 were shared with Punta Cruces and Cabo Marzo (northern Pacific coast of Colombia) (Valencia & Giraldo, 2009), 17 with the Pacific coast of Costa Rica (Gasca, 2009a) and 16 with Banderas Bay (Gasca & Franco-Gordo, 2008). In relation to other tropical environments, the number of species found during this study was low (e.g. Gasca, 2004); this may be because Isla Gorgona is located near the coast (~30 km), whereas hyperiid amphipods are mostly oceanic (Bowman & Gruner, 1973; Vinogradov, 1999). Further studies that consider greater spatial scales, including oceanic waters and greater depths, will surely increase the species richness reported for this region.

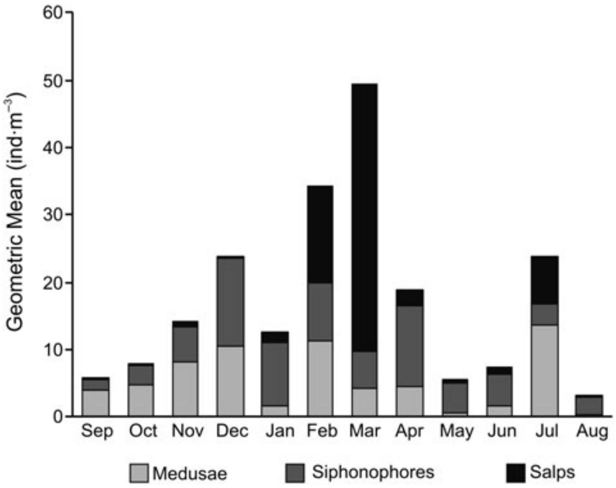

Fig. 8. Geometric mean of medusae, siphonophores and salps between September 2005 and August 2006 on Isla Gorgona.

In terms of composition, the only study of major groups of the zooplankton on Isla Gorgona identified only gammaridean amphipods of the families Colomastigidae and Ampeliscidae, and caprellids of the family Caprellidae (Soto *et al.*, 2001), all recognized as benthic forms. With this panorama, knowledge about hyperiids in particular and the zooplankton community in general on Isla Gorgona is meagre. For this reason, the study made by Valencia & Giraldo (2009), as well as the taxonomic study of the genus *Vibilia* in the ETP made by Shih & Hendrycks (2003), which took samples in waters of the Colombian Pacific (1°30′N to 6°30′N and 77°45′W to 84°00′W) are the only reliable antecedents. Thus, on Isla Gorgona as in Banderas Bay (Gasca & Franco-Gordo, 2008) and the northern Pacific coast of Colombia (Valencia & Giraldo, 2009), *Hyperioides sibaginis* and *Lestrigonus bengalensis* were the most abundant species, representing 86%, 94% and 93%, respectively, results that suggest the importance of these species in the neritic environments of the ETP.

Table 3. Spearman correlation rank between hyperiid amphipod abundance and the possible gelatinous zooplankton hosts on Isla Gogona ($\alpha = 0.02$; N = 285).

	Medusae		**Siphonophores**		**Salps**	
	r	***P***	**r**	***P***	**r**	***P***
Hyperiid total abundance	0.25	<0.01	0.42	<0.01	0.14	0.01
Hyperioides sibaginis	0.10	0.09	0.45	<0.01	−0.01	0.83
Lestrigonus bengalensis	0.18	<0.01	0.26	<0.01	0.08	0.18
Paralycaea gracilis	0.23	<0.01	0.34	<0.01	0.35	<0.01
Phronimopsis spinifera	0.23	<0.01	−0.03	0.66	−0.07	0.23
Tetrathyrus forcipatus	0.08	0.17	0.19	<0.01	0.14	0.02

On Isla Gorgona, the dominant species during most of the study period was *H. sibaginis*, while in Banderas Bay (Gasca & Franco-Gordo, 2008), as along the northern Pacific coast of Colombia (Valencia & Giraldo, 2009), *L. bengalensis* was the dominant species. Only during some months on Isla Gorgona did a switch in species abundance occur, as in September, November and March, where in proportion the contribution of *H. sibaginis* was at a minimum and that of *L. bengalensis* was at a maximum. It is possible that the importance of *L. bengalensis* in the hyperiid assemblage of the Colombian Pacific tends to decrease as we move offshore, and that this species is replaced in neritic and probably oceanic waters by *H. sibaginis*. Other species that formed important components of the hyperiid assemblages on Isla Gorgona, such as *Phronimopsis spinifera*, *Tetrathyrus forcipatus* and *Paralycaea gracilis*, were also important components on the northern Pacific coast of Colombia for the first two species, with *P. gracilis* absent (Valencia & Giraldo, 2009), while in Banderas Bay *T. forcipatus* and *P. gracilis* were an important and a minor component respectively, with *P. spinifera* absent.

Species composition found on Isla Gorgona was representative of neritic waters of the ETP, despite the small net size that was used (30 cm in diameter), and that zooplankton samples were collected during daylight hours up to 50 m depth. Even in other regions such as the North Pacific central gyre, where a larger bongo net was used (70 cm in diameter), small species like *H. sibaginis* represented important components of the hyperiid community (Shulenberger, 1977). In relation to the vertical distribution of hyperiids, Shulenberger (1977) reported that they are distributed mainly in the upper 100 m, day and night. A similar result was reported by Cornet & Gili (1993) in a study made on the northern edge of the Benguela System. These authors found that the vertical distribution of hyperiids was limited to the upper 40 m, a result that seems a consequence of a strong thermocline (Cornet & Gili, 1993). Waters on Isla Gorgona and in general in the ETP are also characterized by a strong and shallow thermocline (Fiedler & Talley, 2006; Giraldo *et al.*, 2008b). Then, it is possible that most of the hyperiids collected during this study on Isla Gorgona were restricted to the upper layers, day and night. It is important that future studies consider a sampling design that includes stratified tows.

Distribution of hyperiids on Isla Gorgona presented in general low abundances in most of the study area. During the wet season (May to November), this result possibly was due to the presence of homogeneous conditions in the water column around Gorgona, with higher temperatures and lower salinities in surface and subsurface waters (Giraldo, 2008). These conditions suggest that productivity in the area was also low and homogeneous. On the other hand, hyperiid abundance was higher on the western side of the island during February and March, a period in which significant subsurface lower temperatures and higher salinity values were registered on the eastern side (Giraldo, 2008). Likewise, higher abundances occurred on the eastern side during November and December; this result suggests that during this period the major contributions to the productivity are associated with local and continental sources, and not with regional processes.

The change in the structure of the hyperiid assemblages on Isla Gorgona seems to be associated with seasonal changes in hydrographic conditions (dry versus wet season). Nevertheless, these results should not be seen as a response to unique hydrological processes, because peaks in hyperiid diversity and abundance were registered both in colder waters and in warmer waters. Hence, the significantly higher values of hyperiid diversity and abundance registered during March and April seem to be a response to the colder-productivity waters registered during February and March (dry season). Likewise, significantly lower values of diversity and abundance observed from September to October and May to August, seem to be a response of the hyperiids to the warm and less productive waters characteristic of the wet season. These results agree with previous reports in the Panama Bight, in which highest zooplankton abundances are reported during the dry season, because of the entrance of oceanic subsurface productive waters during the effect of the Panama wind jet, while lowest zooplankton abundances are reported during the wet season given the presence of warm, less productive waters (Rodríguez-Rubio & Stuardo, 2002; D'Croz & O'Dea, 2007; Giraldo *et al.*, 2008a).

However, on Isla Gorgona higher values of hyperiid diversity and abundance were also registered during November and December, although during these months the water was warm. These results suggest that although the presence of the Panama wind jet and its colder waters was the most important process influencing hyperiid diversity and abundance in this zone, other local processes that produce a second peak in these variables seem to be involved. According to Blanco (2009), the maximum precipitation and river runoff in Gorgona occurs between May and October, a period coinciding with the lowest hyperiid abundance values. Nevertheless, it is possible that at the end of this period of maximum precipitation, the local and continental contribution of allochthonous nutrients associated with runoff enhance the water productivity around the island during November and December. Although data of nutrient and chlorophyll concentrations in Gorgona are lacking in this period to support or reject this hypothesis, a study of phytoplankton in the island during 1999 also found two abundance peaks: one between February and May dominated by diatoms and dinoflagellates, and a second one between October and December associated with an increase in the abundance of dinoflagellates and Cyanophyta (Soto *et al.*, 2001). Perhaps the sudden increase in Cyanophyta at the end of the year suggests a change in the source of nutrients in the island, possibly coming from river runoff, which in turn helps to explain the second abundance peak observed for hyperiids.

A consequent result was obtained in the cluster analysis because the two groups that defined the structure of the hyperiid assemblages on Isla Gorgona include November in the dry season while January was included in the wet season. These results suggest that environmental processes occurring in different time scales (e.g. Panama wind jet and local productivity) produce similar effects in the structure of the hyperiid assemblages, as in the 'dry season group', in which higher diversity and abundance values were registered. On the contrary, the warm, less productive waters registered on the island during most of the study period produce an assemblage with lower diversity and abundance values. In terms of species composition, *L. bengalensis* and *H. sibaginis* presented in proportion similar contributions to the structure of the assemblages during both seasons, with *P. gracilis*, *T. forcipatus* and *P. spinifera* as important components of the dry season assemblage, and *Paraphronima crassipes* and *Parascelus edwardsi* of the wet season assemblage. This result suggests that the change in hyperiid structure assemblages on Isla Gorgona were associated with a change in the contribution of the minor species, and with a minor change in the contribution of the dominant species.

Although the hyperiid structure assemblages on Isla Gorgona apparently respond to changes in hydrographic conditions, it is possible that their response is secondary, due to the characteristic life history of hyperiids. For this reason, some authors consider that changes in hyperiid species composition, abundance and distribution on a local scale must be viewed as a function of the dynamics of their gelatinous hosts (e.g. Harbison *et al.*, 1977; Madin & Harbison, 1977; Laval, 1980). During the study period, high abundances of salps occurred during the months with the lowest water temperatures (February and March), and apparently enhanced the presence of some species (e.g. *Lycaea pulex* and *Phronima dunbari*). Despite this clear tendency demonstrated by salps, a significant association was found only with *P. gracilis*. This species also presented significant associations with medusae and siphonophores, although in the literature it has been reported associated only with siphonopohores (Harbison *et al.*, 1977).

Gelatinous hosts used by *H. sibaginis* are unknown. However, in this study a significant association with siphonophores was found. This result is consistent with the report of Laval (1980), who found an association between a congener (*Hyperioides longipes*) and this gelatinous group. *Tetrathyrus forcipatus* presented a significant association with siphonophores only, coinciding with the reports of Harbison *et al.* (1977). For *P. spinifera* significant associations were found with medusae, nevertheless, the gelatinous host for this species is unknown. For *L. bengalensis* significant associations were found with medusae and siphonophores. Although apparently species of the genus *Lestrigonus* preferred medusae-like hosts (Harbison *et al.*, 1977), they have been reported also in association with siphonophores and salps (Lima & Valentin, 2001).

Despite the probable associations found with the correlation analysis, information obtained about associations between hyperiids and the gelatinous hosts from zooplankton samples gave only an overall idea of these relationships (Gasca *et al.*, 2009). Better results would be obtained if associations could be evaluated considering lower taxonomic levels for the gelatinous zooplankton, information that is lacking for the study area. Moreover, associations between gelatinous zooplankton and hyperiids are usually broken during sample tows (Madin & Harbison, 1977; Laval, 1980; Lima & Valentin, 2001), and because there is lack of knowledge about species composition of gelatinous zooplankton in the Colombian Pacific, it is more difficult to obtain an appropriate interpretation.

In conclusion, the hyperiid amphipod assemblages on Isla Gorgona presented a high similarity in species composition to other coastal localities of the ETP, assemblages characterized by the high dominance of *Hyperioides sibaginis* and *Lestrigonus bengalensis.* Highest values of hyperiid richness, abundance, and diversity were found during March and April, a period in which oceanic upwelling waters (cold, salty and productive) reach the neritic zone in the Colombian Pacific. Likewise, a second peak in hyperiid abundance was present during December, which may be influenced by local factors, like diminished precipitation levels and a possible increase in nutrient availability. Other factors, such as the abundance and composition of the gelatinous zooplankton that hyperiids use as hosts, also seem to be important. Finally, this study is the first effort in the Panama Bight to characterize a specific group of zooplankton on an annual schedule and to contribute significantly to the knowledge of a poorly studied group in the ETP.

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