Composition of the Epifaunal Community Associated with the Seagrass *Zostera marina* in San Quintin Bay, Baja California

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Abstract.—The epifaunal community associated with eelgrass beds in San Quintin Bay, Baja California, Mexico, was studied from April to November 1993. Taxonomic identification, univariate community descriptors, and biomass data were obtained for each sample. Multivariate analyses of community composition were also performed, and plant–animal relationships were analyzed. The epifaunal community was characterized by the high abundance of a few dominant species, with the mollusk *Assiminea dubiosa* representing 70% of the total abundance. Summer samples had the highest similarity, as indicated by the Analysis of Similarity (ANOSIM) test. Polychaetes and amphipod abundances seemed to follow the variations in eelgrass aboveground biomass.

Seagrasses are aquatic angiosperms with a high degree of uniformity in their vegetative appearance. Almost all genera have well-developed subterranean rhizomes and strap-shaped leaves. There is however, a considerable degree of diversity in the mode of growth, the branching system, and in the anatomical structure (Den Hartog 1967). Seagrasses grow in suitable shallow marine waters worldwide, and are represented by 7 tropical and 5 temperate genera (Den Hartog 1970). Although present across only 0.15% of the ocean surface, they account for about 1% of the net primary production and 12% of the net ecosystem production of the global ocean (Duarte and Cebrián 1996).

Seagrasses are among the most productive autotrophic communities on the planet (Hillman et al. 1989; Duarte and Chiscano 1999). Their high biomass and production is directly linked with their important role in the ecosystem. For this reason, seagrasses have been considered among the most valuable ecosystems in the world in terms of the value-added services they provide (Costanza et al. 1997).

Ecological functions associated with seagrasses include nutrient recycling, detritus production and export, sediment stabilization, and provision of optimal habitat for growth, survival and reproduction of a diverse array of vertebrate and invertebrate taxa (Heck et al. 1997, 2003). Further, biodiversity generally appears to be higher in seagrass relative to adjacent habitats (Orth et al. 1984; Bell and

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Pollard 1989; Orth 1992), although the magnitude of this difference depends on seagrass species composition and biomass (Heck et al. 2003). For this reason, seagrasses are viewed as extraordinarily rich habitats (Kikuchi 1980; Heck et al. 2003).

Recent theories on mechanisms controlling energy flow in seagrass beds emphasize the importance of intermediate trophic levels, with large invertebrates acting as effective predators on the smaller invertebrate fauna (Klumpp et al. 1989) and small invertebrate grazers controlling epiphytic algal abundance (van Montfrans et al. 1982; Hootsman and Vermaat 1985). Experimental research has shown important top-down effects in determining the composition and abundance of seagrass-associated plants and animals in natural conditions, thus supporting the hypothesis that small grazers can often control the abundance of epiphytes, and emphasizing the need to know how grazer populations are regulated in order to fully understand the consequences of human perturbations (e.g. nutrient enrichment) on seagrass ecosystems (Heck et al. 2000).

With this functional perspective in mind, and recognizing the urgent need to have detailed information on the composition of the mobile fauna in San Quintin Bay, we collected data on the epifaunal and mobile species assemblages. We here present the epifauna data, for which we first characterized the species composition, performed univariate community analysis, and calculated biomass. We then performed multivariate analysis of community composition, and analyzed plant–animal relationships using correlation analysis. Our data on species composition, changes in community composition over time, and plant–animal relationships were compared with those reported for other locations, and other seagrass species.

Materials and Methods

Study Site

San Quintin Bay is a Y-Shaped coastal lagoon located on the Pacific coast of Baja California. The east arm is known as Bahia San Quintin, and the west arm as Bahia Falsa (Fig. 1). The bay covers an area of about 42 km^2 and has a mean depth of about 2 m. Tides are semidiurnal with a mean amplitude of 1.6 m (C. Nava, Sea Level Laboratory, CICESE, personal communication). Water exchange with the coastal ocean is intense, with about 11 days water residence time for San Quintin Bay, and 4 days for Bahia Falsa (Camacho-Ibar et al. 2003). Water temperature ranges from 13 to 27°C inside the bay and from 11 to 22°C at the mouth (Alvarez-Borrego and Alvarez-Borrego 1982).

Total evaporation in summer (164 $\times$ 10^3 m^3 day^{-1}) and winter (91 $\times$ 10^3 m^3 day^{-1}) exceed total rainfall (4 $\times$ 10^3 m^3 day^{-1}), and there is ordinarily no significant runoff or groundwater inflow. Consequently, San Quintin Bay is a net evaporative system (Ibarra-Obando et al. 2001), with summer and winter salinities in the interior (38.7–33.8‰) always higher than in the adjacent ocean (33.8–33.6‰) (Millán-Núñez et al. 1982).

San Quintin Bay is characterized by extensive eelgrass (*Zostera marina*) beds, best developed in the middle bay on soft sediment bottom plains that are covered with between 0.3 m and 0.9 m of water at the lowest tide. Present eelgrass coverage is about 40% (Ward et al. 2003). The benthic invertebrates of vegetated and unvegetated areas have been studied, both at the taxon level (Keen 1962;
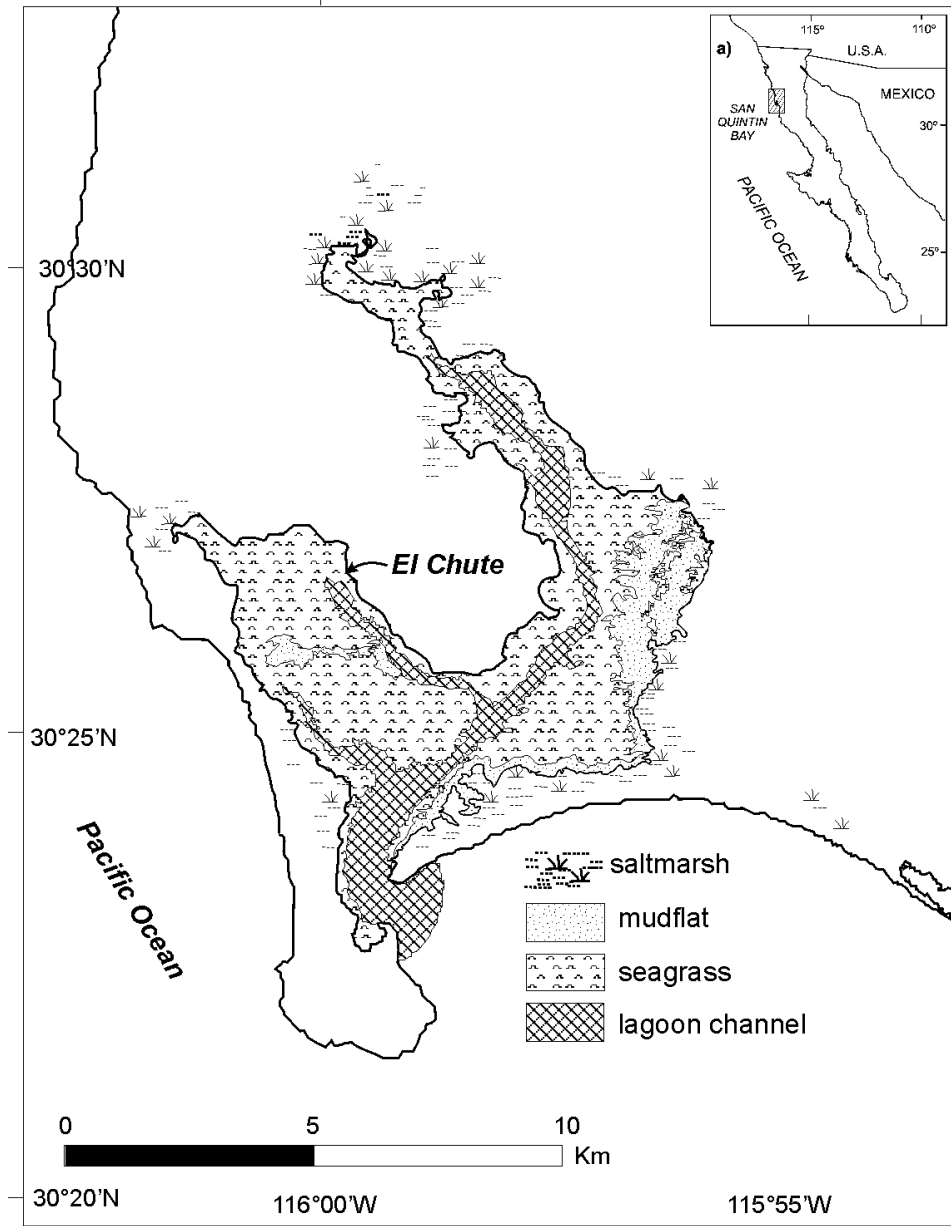
Fig. 1. Location of the sampled area inside San Quintin Bay, Baja California, Mexico (modified from Ibarra-Obando et al. 2004).

Reish 1963; Barnard 1964; Cook 1974; Calderón-Aguilera and Jorajuira-Corbo 1986; Bretado-Aguirre 1987; Cantú-Martínez 1987; Griffis and Chavez 1988; Díaz-Castañeda and Rodríguez-Villanueva 1998), and at the community level (Barnard 1970; Calderon-Aguilera 1992; Sinicrope-Talley et al. 2000). Environmental conditions that play a role with the macro-infaunal (animals ≥ 0.3 mm)

distribution inside San Quintin Bay include: distance from the mouth, gradients of tidal amplitude, changing hydrodynamics, seasonal runoff, and a breakdown of the typical inverse-estuary currents by overriding unidirectional winds (Sinicrope-Talley et al. 2000).

Oyster aquaculture, low-density tourism and fisheries are the main economic activities, none of which has significantly negatively impacted the bay up to this point. Doubling of aquaculture and construction of tourist mega-resorts are potential threats for the next decade (Aguirre-Muñoz et al. 2001).

Field Work

Samples were collected from the west arm, Bahia Falsa, in front of the fish camp known as ''El Chute'' (Fig. 1). Sampling took place in April, May, July, August, October, and November, 1993. Fauna associated with eelgrass were collected at high tide with a trawl net with metal frame of 0.4×0.5 m (2.54 cm mesh size) with a cod end of 1 mm mesh size. Each trawl lasted one minute at a constant speed of one knot, and covered about 15 m^2. A total of six trawls were done during the study period (one each sampled month). In the field, samples were fixed in 10% formaldehyde, and transported to the laboratory in buckets.

In the laboratory, samples were rinsed several times with fresh water, and plant material was separated from animal material. Seagrass leaves, roots, and macroalgae were washed in sieves of 2 and 1 mm. Once the organisms were separated, they were placed in glass jars, preserved in 70% isopropyl alcohol, counted under the microscope, and identified with taxonomic keys for each group. Biomass, as dry weight (DW), was obtained by drying organisms in an oven at 105°C for 12–24 hrs. Large organisms were cut into small pieces and once dried, the material was homogenized in a blender, and 4 or 5 sub samples were used for AFDW determination. The ash free dry weight biomass (AFDW) was determined after burning the dry organisms in a muffle furnace at 550°C for 4–6 hrs (Brower and Zar 1977). Biomass per trawl and per m^2 was determined.

Eelgrass samples were collected from a 4.8 ha mudflat in front of ''El Chute'', along a 300 m long transect in the intertidal (-0.10 m with respect to Mean Lower Low Water, MLLW). Sampling took place at every spring tide. To assess eelgrass biomass, 7 random samples were collected using a 0.04 m^2 quadrat on each sampling date. Only aboveground material was collected. Samples were washed with seawater, using a 1 mm mesh sieve. All material was placed in labeled plastic bags and kept cool until transported to the laboratory. Rinsed samples were sorted to calculate shoot density. Aboveground material was processes as described in Poumian-Tapia and Ibarra-Obando (1999).

Data Analysis

For each sample, univariate community measures were determined: abundance (number of individuals, N), richness (number of species, N0), diversity (N1), evenness (Pielou's J′), and dominance (Krebs 1985). Relative abundances and densities for each species in each sample were also obtained. Diversity was measured by Hill indices (Hill 1972), as they take into account the Shannon-Weaver diversity index, and the Simpson diversity index:

$$N0 = S; \qquad N1 = e^{H'}; \qquad N2 = 1/\lambda; \quad \text{where}$$

$$S = \text{number of species}; \qquad H' = \text{Shannon Index}; \qquad \lambda = \text{Simpson Index}$$

As the Shannon-Weaver index and the Simpson index are affected by sample size, and number of organisms per sample, their joint use can reduce the bias in diversity assessment (Hill 1972). Dominance of the different species was estimated using the Importance Value Index (I.V.I.) that combines three determinant characteristics of the importance of any given species in the community: abundance, frequency and biomass (Krebs 1985):

$$\text{I.V.I} = \%N + \%F + \%B, \quad \text{where}$$

$$\%N = \text{relative abundance}; \qquad \%F = \text{relative frequency};$$

$$\%B = \text{relative biomass}$$

In order to identify differences and similarities in epifaunal community composition between samples, we performed a Non-metric Multidimensional Scaling (MDS) (Ludwig and Reynolds 1988). For this purpose, data were organized into abundance, and presence-absence matrices that were simplified by eliminating those species present in only one sample (F<16%), and in relatively low abundances (<0.001% of sample total abundance) (Stephenson and Cook 1980). Total abundance data were transformed to the 4th root of n to reduce the variability between values (Clarke and Green 1988). Seasonal variations were analyzed with a two-way nested Analysis of Similarity and (ANOSIM) test (Clarke and Warwick 1994), in which months were nested in seasons. For all tests, confidence level was set at 0.05.

The relationships between epifauna richness, and abundance, and eelgrass density and aboveground biomass were analyzed with a Rank Correlation Analysis (Zar 1966).

Results

Univariate Measures of Community Composition

The average number of organisms per trawl was 52,836±16,703 (±1 S.E.), representing 74 taxa belonging to four major groups: polychaetes, crustaceans, mollusks, and fishes. At the group level, species richness was highest for polychaetes and crustaceans, with 24 species each, representing 32% of the total species richness. Amphipods were the most frequent crustacean taxa, accounting for 15 of the 24 identified taxa. Fishes represented only 11% of the total, with 8 species. Of the 317,015 organisms collected, mollusks contributed 71% of the total abundance, followed by crustaceans, with 28%. Crustaceans and fish had the highest biomass, about 37% each (Table 1).

Of the 74 taxa collected, the 6 most abundant species were the mollusk, *Assiminea dubiosa*; the caridean, *Hippolyte californiensis*; the amphipods, *Amphitoe plumosa, Corophium baconi, Hyale nigra* and *Erichtonius brasiliensis.* The mollusk *A. dubiosa* represented 70% of the total abundance, and was the only species present in all samples. The next numerically important species was *H. californiensis* making up 5% of the total number of individuals. The four most abundant and common polychaete species and their total abundance per trawl were as follows: *Platynereis bicanaliculata* (2,280); *Polydora cirrosa* (207); *Exogone lourei*

Table 1. Richness, abundance, and biomass values and percentages for each epifaunal group found in San Quintin Bay between April and November 1993. Values represent the total of 6 trawls. NO = number of species; N = number of individuals. Biomass is expressed as g of Ash Free Dry Weight (AFDW).

Group	Richness		Abundance		Biomass	
	NO	%	N	%	g (AFDW)	%
Polychaetes	24	32.4	2,855	0.9	0.44	0.2
Crustaceans	24	32.4	88,981	28.06	87.5	36.5
Mollusks	18	24.3	224,672	70.8	63.6	26.6
Fishes	8	10.8	507	0.16	87.9	36.7
Total	74	99.9	317,015	99.9	239.4	100

(142), and *Eulalia bileneata* (105). The dominating abundance of the first species is evident.

The species with highest biomass was *H. californiensis,* comprising 32% of the total biomass, followed by *A. dubiosa* with 15%. Two fish species, *Syngnathus leptorhynchus,* and *Embiotoca jacksoni* had a similar contribution to total biomass (12%). The remaining 70 species had biomass values that represented between 7 and <1% of the total.

According to the I.V.I., the community was dominated by the following species: *A. dubiosa,* 88.5; *H. californiensis,* 40.1; *S. leptorhynchus,* 15.2; *E. jacksoni,* 13.8; and *H. nigra,* 10.0.

Values for the different community descriptors for each sampling time are presented in Table 2. No clear trends could be identified, given the limited number of trawls performed during this study.

Multivariate Measures of Community Composition

Ordination analysis using total abundances showed three well defined groups, which correspond to spring (April–May), summer (July–August), and autumn (October–November). The highest similarity was for the summer samples (80%) (Fig. 2). Spring and autumn groups were defined by *A. dubiosa* and *H. californiensis.* During summer, besides *A. dubiosa,* amphipods of the order Gammaridea (e.g. *Corophium baconi, Erichtonius brasilensis, H. nigra*) made a significant contribution (Table 3).

Plant–animal Relationships

A significant positive correlation between epifaunal diversity and eelgrass aboveground biomass was observed (r = 1, p<0.05), but no other significant

Table 2. Values obtained for the different community descriptors on each sampling date.

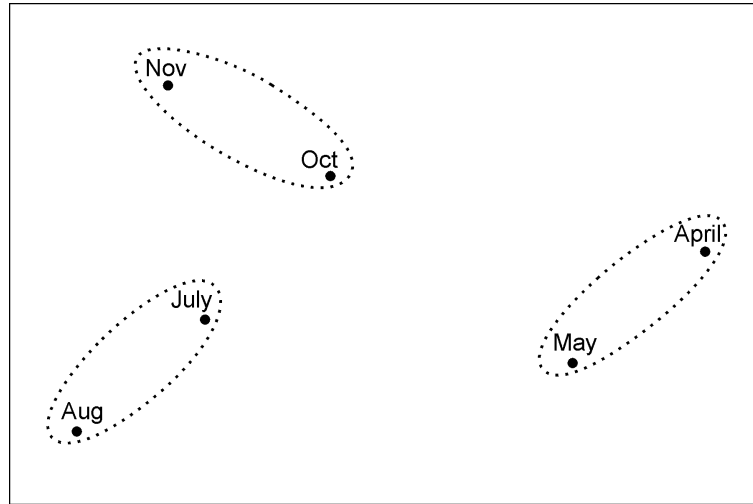|	April	May	July	August	October	November
Abundance (N)	63,526	45,673	60,734	73,913	46,448	26,721
Species richness (NO)	27	34	37	37	35	53
Diversity (N1)	1.50	2.49	4.28	5.08	2.76	4.05
Eveness (J')	0.12	0.26	0.40	0.45	0.29	0.35
Biomass (B)	30.62	76.47	31.87	19.71	58.89	21.90

Fig. 2. MDS plot showing the relationship between samples using the simplified matrices of abundance.

correlations were identified. Changes in amphipods and polychaetes abundance seemed to follow those of eelgrass aboveground biomass (Fig. 3a and b).

Discussion

The four major groups that constitute the epifaunal community in San Quintin Bay played different roles in characterizing the community: mollusks were the most abundant; polychaetes and crustaceans both had the largest numbers of spe-

Table 3. Species that determine 50% of sample similarity based on abundance (individuals per trawl).

| Seasonal Group	Taxon	Contribution (%)	Cumulative %
Spring	A. dubiosa	20.15	20.15
	H. californiensis	10.83	31.33
	E. brasilensis	5.93	37.26
	C. baconi	5.60	42.86
	Rhachotropis inflata	5.54	48.4
	Amphilochus neapolitanus	5.35	53.75
Summer	A. dubiosa	14.05	14.05
	H. nigra	9.14	23.19
	A. plumosa	8.13	31.32
	C. baconi	7.18	38.50
	E. brasiliensis	6.24	44.74
	R. inflata	5.75	50.49
Autumn	A. dubiosa	14.25	14.25
	H. californiensis	8.43	22.68
	E. crenulata	7.04	29.72
	H. nigra	6.68	36.40
	A. plumosa	6.20	42.60
	C. baconi	4.81	47.41
	P. bicanaliculata	4.61	52.02
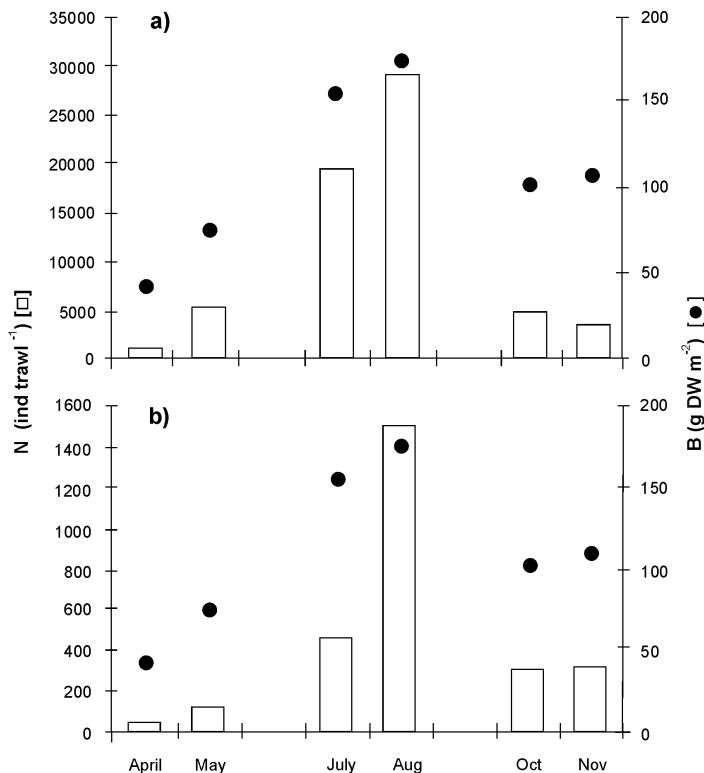
Fig. 3.   Seasonal patterns of (a) amphipods abundance (individual trawl^{-1}) [□], and eelgrass biomass (g DW m^{-2}) [●]; (b) polychaete abundance (individual trawl^{-1}) [□], and eelgrass biomass (g DW m^{-2}) [●].

cies; and crustaceans and fishes had the highest biomass. Community composition differed over time, with the summer assemblage having the highest similarity. Finally, amphipod and polychaete abundances seemed to follow the seasonal variations in eelgrass aboveground biomass.

Mollusks represented 71% of total abundance in San Quintin Bay. Similar high percentages have been reported in other eelgrass beds (e.g. Marsh 1973; Thayer et al. 1975), as well as in beds of other seagrass species (e.g., Virnstein and Howard 1987; Nakaoka et al. 2001). As an example, in the eelgrass beds of North Carolina, gastropods represented up to 72% of the total numbers of epifauna found in the ecosystem (Thayer et al. 1975).

We found high species richness for polychaetes, and crustaceans (Table 1). Reish (1963), Calderón-Aguilera (1992), and Díaz-Castañeda and Rodríguez-Villanueva (1998) report similar results for polychaetes in San Quintin Bay. Similar results were reported by Gambi et al. (1992), Colognola et al. (1984), and Mazella et al. (1989) in a *Posidonia oceanica* bed in the Gulf of Naples. Crustaceans were the second group with high species richness in our study site. A high crustacean richness (46%) was also reported for San Quintin Bay by Villareal (1995), and by for a mixed *Zostera* bed in Otsunhi, Japan (56%) by Nakaoka et al. (2001).

The high contribution of crustaceans to epifaunal biomass that we found during

this study, about 37%, has also been noted for other sites. For the *Heterozostera tasmanica* beds in Western Port, Australia, Edgar et al. (1994) found that the large contribution of crustaceans to biomass was influenced by the presence of eight large filter-feeding brachiopods.

Seasonal differences in epifaunal community abundance in eelgrass beds, with peak values during summer, have been reported by Thayer et al. (1975), Heck and Orth (1980b), and Orth and Heck (1980). Edgar (1990) reported a similar pattern in *Amphibolis* beds, and Coles et al. (1993) found the same trend for eight species seagrass beds in Cairns Harbour, Australia. With the limited data set that we have at present for San Quintin Bay we are unable to describe seasonal variations; however, the MDS test on total abundance identified three groups corresponding to spring, summer and autumn respectively (Fig. 2), with the summer group having the highest similarity (ANOSIM test).

During our study, amphipods made an important contribution to the definition of the summer group, as they reached their maximum abundance and biomass during this season (Table 3). This seasonal pattern differs from the one reported by Nelson (1979), in Beaufort, North Carolina, who found amphipod density, number of species, and diversity to be low in July–August, and higher in January–February. Nelson (1979) suggested that the observed amphipod change was the result of predation by the pinfish *Lagodon rhomboides*. In San Quintin Bay, *S. leptorhynchus* has been described as the most abundant fish species, attaining its maximal abundance in May and November (Rosales-Casián 1997). This difference in life cycle between the fish (predator) and the amphipods (prey) could help explain the differing periods of peak abundance and biomass for these two localities.

Applying univariate community measures in the intertidal *Zostera novazelandica* beds in northern New Zealand, Turner et al. (1999) found few consistent seasonal or annual trends over a two-year period. Multivariate analysis (Canonical Correspondence Analysis) applied at the scale of the patches revealed that spatial structure explained 1–2% of the variation in species abundance, environmental variables explained 3–4%, temporal variability explained 12–14%, and 75% of the variation remained unexplained. Turner et al. (1999) attributed the large contribution of temporal variability to the explained variance as a reflection of the seasonal and annual trends in the number of individuals, and in the species present. Our data for San Quintin Bay also seem to reflect a high temporal variability and could indicate the existence of ephemeral assemblages that change in response to a complex set of physical and biological variables, including the annual variations in eelgrass aboveground biomass.

The high abundance of a few dominant species that we found during this study, with six species accounting for 93% of the total abundance, is similar to what has been reported for other seagrass beds. For example, Marsh (1973) in the eelgrass beds of the York River, Virginia, found that the five most abundant species accounted for about 60% of the total. Heck and Orth (1980a) in the eelgrass beds of the Lower Chesapeake Bay, found that six species of macroinvertebrates made up nearly 68% of the total.

We cannot compare our absolute values of epifaunal abundance and richness with those reported by other authors, because sessile, creeping or walking epifauna are not collected reliably by trawling (Heck and Orth 1980a). As a consequence,

our values represent underestimations of abundance and richness. A further limitation we faced was the reduced number of trawls and the lack of replicates to assess the within-month variability. As a result, the information provided in this study should be considered preliminary.

While some authors have found a good relationship between plant-animal density and biomass (e.g. Heck and Orth 1980b; Orth and Heck 1980; Stoner 1980; Lewis and Stoner 1983; Edgar and Robertson 1992; Webster et al. 1998), others have not (e.g. Virnstein and Howard 1987; Edgar 1999). For San Quintin Bay, Sinicrope-Talley et al. (2000) found a correlation between the presence of *Zostera* and a few taxa of macrofauna, but only in combination with sediment properties. Our data show a significant positive correlation between epifaunal diversity and eelgrass aboveground biomass. Amphipod and polychaete seasonal trends seemed to match the seasonal change in eelgrass aboveground biomass (Fig. 3a and b). These results seem to indicate an association between the above-mentioned epifaunal species and eelgrass leaves, and can be compared with the diverse, leaf-associated faunal assemblage that Edgar and Robertson (1992) described in the *Amphibolis* beds at Seven Mile Beach, Australia, which was negatively affected by seagrass thinning. For mixed seagrass beds in North Carolina, Hovel et al. (2002) found that seagrass shoot biomass strongly influenced shrimp densities in 1992, but no correlation was found the previous year. We are aware of the extreme variability of the above-mentioned relationships for San Quintin Bay, and of the need for repeated samplings to establish reliable plant-animal associations. Hovel et al. (2002) found that different faunal species or species groups may respond to different aspects of seagrass habitats, and concluded that the high variability in seagrass landscape structure does not necessarily correspond to variability in faunal abundance. Rather, myriad processes operating at a variety of scales make relationships between fauna and environmental variables complex and difficult to predict.

Conclusions

The epifaunal community in San Quintin Bay was characterized by the high abundance of a few dominant species. Different assemblages were present throughout the study period, reflecting the seasonal changes of the various species present, as well as the changes in environmental conditions. The summer group had the highest similarity. Polychaetes and amphipods seemed to follow the seasonal changes in eelgrass aboveground biomass.

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