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Oceanographic conditions and diversity of sea stars (Echinodermata: Asteroidea) in the Gulf of California, México

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Abstract: Species richness is one of the best indicators of biodiversity. However, there are few investigations on concordance of diversity patterns and environmental settings for marine regions. The objectives of this study were to correlate species richness of shallow water (< 200 m deep) sea stars with key oceanographic factors in the Gulf of California, México, and to predict species richness of Asteroidea using multiple regressions. In these analyses the Gulf was divided into nine sections of one degree in latitude (from 23 - 31° N), at each section we recorded: continental shelf area (at 100 and 200 m depth), temperature mean and range at three depth levels (0, 60 and 120 m), thermocline depth, surface nutrient concentrations (nitrates, phosphates and silicates), surface photosynthetic pigment concentration, and integrated productivity. Sea star species richness at each latitudinal section was estimated from literature data, new collections and museum records. Species were assigned to one of the following feeding guilds: predators of small mobile invertebrates (I), detritivores (D), predators of colonial organisms (C), generalist carnivores (G), and planktivores (P). There are 47 shallow water asteroid species in the Gulf of California (16 I, 15 D, eight C, six G, one P and one not assigned). Total species richness and guild species richness showed strong latitudinal attenuation patterns and were higher in the southernmost Gulf, an area characterized by a narrow shelf, high temperature, and low nutrient concentrations. Species diversity for each guild was correlated to a set of oceanographic parameters: temperature, nitrate concentration, and integrated productivity were linked to richness in must cases. We detected that nutrients and surface pigments always presented negative relationships with species richness, indicating that productive environments limit asteroid diversity in the study area. Finally, the postulated regression models to estimate species richness from oceanographic data were significant and highly precise. We conclude that species richness of Asteroidea in the Gulf of California is related to oceanographic conditions and can be estimated from regional oceanographic information. Rev. Biol. Trop. 53(Suppl. 3): 245-261. Epub 2006 Jan 30.

Keywords: Asteroidea, Gulf of California, Biogeography, Oceanography, Species Richness, Multiple Regression.

Biogeography in the Gulf of California has been studied almost exclusively from a descriptive point of view (Briggs 1974, Laguna 1990). A key conclusion of many studies is that the Gulf has a relatively high level of endemism and thus can be considered an independent province within the Eastern Pacific (Briggs 1974, Brusca and Wallerstein 1979, Wickstein 1989, Bernard *et al*. 1991). Thus it is implied that local environmental conditions are the selective forces that favour speciation, and thus the latter may control distribution and variety of taxa. However, no actual relationships between oceanographic factors and species distributions or richness have been determined, although sea temperature and primary productivity have been invoked to explain biogeographic zonation in the region (Santamaría del Angel *et al*.

1994, Thomson *et al*. 2000). Continental shelf area can also influence diversity of warm-water marine faunas (Bellwood and Hughes 2001), but that study was conducted on such a large scale that its applicability might be limited. One of the best ways to look for relationships between species richness and oceanographic conditions is to analyze more than one factor at the same time, and also to study marine taxa with the potential to occupy a variety of niches, that are well-known taxonomically, as well as those for which reliable information on their natural history is available.

Sea stars (Echinodermata: Asteroidea) are invertebrates of great importance in marine ecosystems because, among other things, some act as key species due to their predatory activities (Menge 1982). Asteroids of the Gulf of California are taxonomically well known (Caso 1986, Cintra-Buenrostro 2001); however, to date, distribution patterns of the group have not been explored in the detail they deserve. The objectives of this study were: a) to correlate species richness of shallow water (< 200 m deep) sea stars (total and for four feeding guilds) with several key oceanographic factors along the Gulf of California, México, and b) to predict species richness of Asteroidea using multiple regressions, which will explain the distribution patterns observed. We discovered that total richness, as well as richness of feeding guilds display a latitudinal attenuation pattern, and richness of each guild of Asteroidea is correlated to certain oceanographic factors, of which nitrates, temperature and productivity were the most important. All the multiple regression models applied were significant and highly precise. We conclude that species richness of sea stars of the Gulf of California is closely related to oceanographic conditions, and it can be estimated efficiently from regional information on properties of the marine environment.

General oceanographic setting of the study area

The Gulf of California (Fig. 1) is a semi-closed sea about 1 000 km long and 150 km wide (Brusca 1980), and a unique evaporation basin in the Eastern Pacific for being located between two arid areas of western México (Robles and Marinone 1987). Circulation in the Gulf is complex because of the combination of diverse oceanic factors such as winds, tides, remote effects, and local physiography (very shallow areas in the northern Gulf and deep in the south; Lavín *et al*. 1997). Another relevant characteristic of this inner sea is its high productivity, which in certain areas (at 28-29° N) is comparable to that of the western coast of Africa and the Pacific side of the Baja California Peninsula (Zeitzschel 1969, Millán-Núñez & Lara-Lara 1995). The exceptional values of chlorophyll are a result of fluxes of deep, nutrient-rich water from local upwelling and tide flows (Alvarez-Borrego *et al*. 1978, Valdez-Holguín and Lara-Lara 1987). Mean sea surface temperature in the Gulf of California increases southwards (Soto-Madrones *et al*. 1999) and varies significantly during the year; it is as low as 14º and 20ºC during February, and as high as 27º and 31ºC in August (at latitudes 30° and 24° N, respectively). Nutrient profiles show a well-developed cline within the euphotic zone, with surface concentrations increasing from the southern to the center of the Gulf (Alvarez-Borrego *et al*. 1978, Lara-Lara and Valdez-Holguín 1988), or along the coast (Zuria-Jordán *et al*. 1995). Surface chlorophyll *a* concentration is patchy and has low values in the south and it is much higher northwards, especially in the northern Gulf and the Midriff Islands (Gendrop *et al*. 1978, Lara-Lara *et al*. 1993, Valdez-Holguín *et al*. 1995).

MATERIALS AND METHODS

This study is based on a taxonomic revision of all nominal species of Asteroidea that have been reported from shallow waters (0-200 m) of the Gulf of California (Cintra-Buenrostro 2001). Once the status of all species and their synonyms was defined, we conducted an exhaustive literature search to determine the distribution of the species, and complemented the information with revision of specimens from the Laboratorio de Sistemática y Ecología de Equinodermos of the Instituto de Ciencias del Mar y Limnología of the Universidad Nacional Autónoma de México (México City, México), and the Museo de Historia Natural and the Laboratorio de Ecología del Bentos, Universidad Autónoma de Baja California Sur (La Paz, México). In addition, we obtained further material from over 20 locations of the Gulf of California (from 23-28° N), and made observations of feeding mode of the species in the field. Species were sorted according to latitudinal degree as well as according to five feeding guilds: generalist carnivores, predators of colonial organisms (sponges, bryozoans, corals), predators of small mobile invertebrates (mollusks, crustaceans), detritivores, and planktivores (after Jangoux 1982, Blake 1990). Latitudinal species distributions were put jointly with several environmental parameters that are known to determine species richness of marine organisms.

Environmental parameters here utilised were: a) continental shelf area (km^2) between 0-100 m, 100-200 m and 0-200 m; b) average thermocline depth (m); mean, maximum, minimum and range; c) surface, 60 m, and 125 m temperature (ºC); d) nutrient concentrations (µM NO_3^-, PO_4^{-3}, and SiO_4) from 0 to 200 m (pooled); e) integrated productivity (gC/m^2/d) from 0 to 200 m; and f) surface pigments (mg/m^3), for which median value was also used. References are presented in Appendix 1. Although, other factors (*e.g.* salinity, sediment type, and particular conditions in the islands) influence distribution of several organisms, including echinoderms (Thomson and Gilligan 1983, Blake 1990) they were not considered in the numerical analyses due to the lack of enough quantitative information for the scale and level used in the present study.

The first step of the numerical analyses was to calculate a correlation coefficient between sea star richness and values of the oceanographic variables, for all sections of 1° of latitude. Although, a variety of multivariate statistical techniques (*e.g.* niche partitioning, PCA) could be used to explain species richness based on the analysed parameters, our goal was to predict it, and thus we decided to perform correlation and regression analyses, the former allowed to detect autocorrelated variables while the second helped to eliminate them. The likelihood of introducing highly correlated terms and generating erroneous estimates of regression coefficients due to multicollinearity increased with the inclusion of several variables in our analyses. Thus, ridge regression was performed to identify and eliminate variables generating unstable regression coefficients (Cornell and Karlson 1996). Between the correlation coefficients (Spearman and Pearson) used, we selected the second because similarity of correlations, but most important due to robustness of parametric over non-parametric statistics. A Kolmogorov-Smirnov test was used to test data normality. Once confirmed, Pearson correlation was applied to total species richness and to richness of four of the five feeding guilds given that there is just one planktivore species. Then, we applied three multiple model II ($\alpha = 0.05$, without constant use) regression models to check which factors were most related to richness:

a) Model I. All variables were considered, but their relevance to species richness was determined with a forward ridge stepwise regression, an appropriate model when analysis is applied to similar variables (*e.g.*, mean and minimum temperature in a site), and thus the problem of multicollinearity exists (Sokal and Rohlf 1997). The stepwise routine is a way to optimize and select factors, which explain most of the variance of the response variable (Zar 1996).

b) Model II. Only average values of the main oceanographic parameters were included in the regression of species richness, and for the multiple regression models we selected only those that were significantly correlated to species richness, according with the Pearson coefficient. This approach was followed to establish an equation based on the usual way to report information in biogeographic studies.

c) Model III. Only total shelf area (0 to - 200 m) and surface temperature values were considered. Both factors were selected because they are the most common parameters used to explain species distribution and diversity patterns in the ocean (Briggs 1974, Brusca and Wallerstein 1979, Rosen 1988a, Bernard *et al*. 1991).

RESULTS

A total of 47 species of Asteroidea, belonging to 17 families and 28 genera, have been registered in the Gulf of California. These species represent five feeding modes: a) generalist carnivores (forcipulatids, n = 6), b) predators of colonial organisms (echinasterids and *Acanthaster planci* (Linnaeus,1758; n = 8), c) predators of small invertebrates (paxillosids, n = 16), d) detritivores (most valvatidans, n = 15), and e) planktivores (brisingids, n = 1). There was a southward trend of increasing total species richness, and richness of all feeding groups (Fig. 1 and 2), reaching a species richness peak in the southernmost latitudinal section (42 species, Fig. 1).

The results of the multiple stepwise regressions will be presented in order.

Total species richness, Model I

A total of 21 oceanographic variables were significantly related to asteroid species richness in the Gulf of California (Table 1). From these, the stepwise procedure selected only two: maximum concentration of nitrates ($MaxNO_3^-$ in µM) and surface temperature range (STr in °C) (Equation 1). The regression line is shown in Fig. 3a.

Equation 1:

$$\text{Total richness} = -1.22\,(STr) + 3.04\,(MaxNO_3^-)$$
$$r^2 = 0.96,\ p < 0.001$$

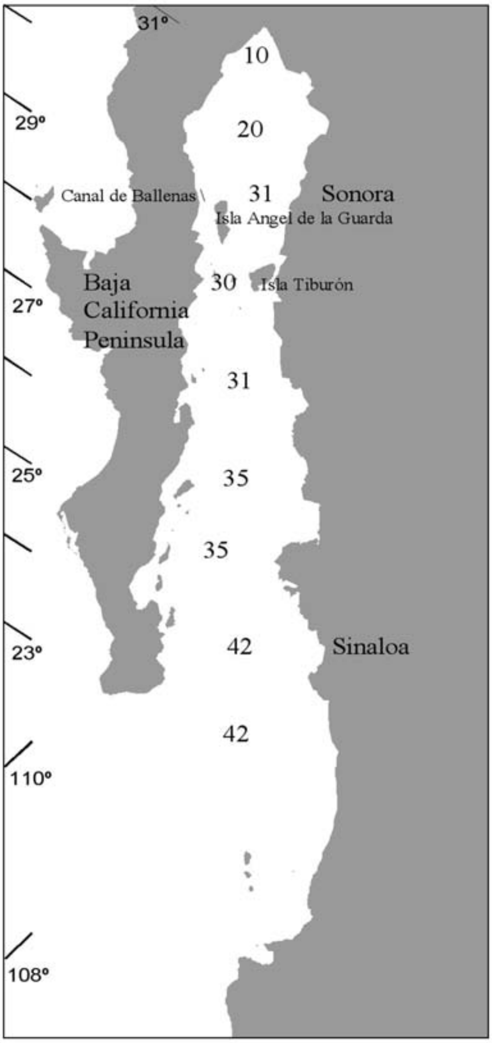

Fig. 1. Study area and total species richness of sea stars by degree of latitude (after Cintra Buenrostro *et al*. 2002).

Fig. 1. Área de estudio y riqueza total de especies de estrellas de mar por grado de latitud (basado en Cintra Buenrostro *et al*. 2002).

Total species richness, Model II

Highest correlation values among total species richness and average values of the oceanographic factors came from temperature at 60 m (AvgT2 in ºC), temperature at 125 m (AvgT3 in ºC), silicate concentration ($AvgSiO_4$

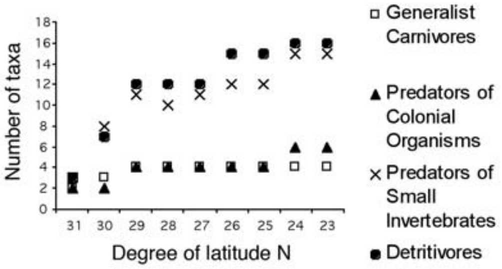

Fig. 2. Number of species represented by each sea star feeding guild by degree of latitude.

Fig. 2. Número de especies representadas por cada hábito alimenticio de las estrellas de mar por grado de latitud.

TABLE 1

Simple linear correlation values between total species richness and the analyzed variables[1]

CUADRO 1

Correlación linear simple entre los valores totales de riqueza de especies y las variables analizadas[1]

Variable	n	r	p
Surface temperature range	9	- 0.82	0.007
Maximum temperature at 60 m	9	- 0.90	0.001
Temperature range at 60 m	9	- 0.91	0.001
Mean temperature at 60 m	9	- 0.84	0.004
Minimum temperature at 125 m	8	- 0.96	0.0001
Maximum temperature at 125 m	8	- 0.87	0.005
Mean temperature at 125 m	8	- 0.93	0.001
Maximum nitrate concentration	8	0.84	0.009
Maximum silicates concentration	8	- 0.85	0.007
Range of silicate concentration	8	- 0.85	0.007
Mean silicate concentration	8	- 0.83	0.009
Minimum concentration of surface photosynthetic pigments	9	- 0.85	0.004
Median concentration of surface photosynthetic pigments	9	- 0.82	0.006
Minimum integrated productivity	9	- 0.92	0.0004
Mean integrated productivity	9	- 0.84	0.005

[1] Only significant relations where $r > 0.80$ are shown, n = degrees of latitude.

in µM), weighted averages of surface photosynthetic pigments (Avgpigw in mg/m^3), and integrated productivity (Avgprod in $gC/m^2/d$) (Equation 2 and Fig. 3b).

Equation 2:

$$\text{Total richness} = 2.11\,(\text{AvgT2}) + 2.43\,(\text{AvgT3}) - 1.32\,(\text{AvgSiO}_4) + 2.04\,(\text{Avgpigw}) - 12.75\,(\text{Avgprod})$$
$$r^2 = 0.96,\ p < 0.001$$

Total species richness, Model III

Ridge regression among total species richness, average surface temperature (AvgST in ºC) and total continental shelf area (TCSA in km^2), produced equation 3; the estimated species richness from this equation appears in Fig. 3c. This model was significant even when neither of these oceanographic variables by itself showed a significant correlation with the total richness (Table 1).

Equation 3:

$$\text{Total richness} = 1.79\,(\text{AvgST}) - 0.001\,(\text{TCSA})$$
$$r^2 = 0.90,\ p < 0.001$$

As clearly observed in the graphics and the statistical results, a reduction in the number of variables in the models makes them less precise. However, in all cases ridge regressions were significant and they explain more than 90% of the variance, which makes them useful to predict species richness at each degree of latitude in the Gulf of California.

Generalist carnivores, Model I

The stepwise analysis showed that the best factors to model richness were: average temperature at 60 m (AvgT2 in °C), maximum value of nitrates ($MaxNO_3^-$ in µM), and continental shelf area at 100 m (CSA100 in km^2) (Equation 4). The regression line is shown in Fig. 4a.

Equation 4:

$$\text{Generalist carnivore richness} = 0.13\,(\text{AvgT2}) + 0.05\,(\text{MaxNO}_3^-) - 0.0001\,(\text{CSA100})$$
$$r^2 = 0.96,\ p < 0.001$$

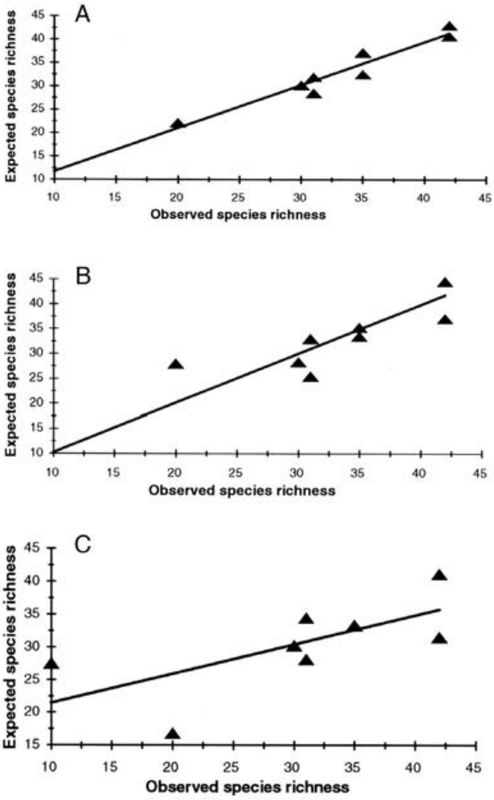

Fig. 3. Model I Stepwise (a), Model II (b) and Model III (c) for total species richness.

Fig. 3. Modelo I Stepwise (a), Modelo II (b) y Modelo III (c) para el total de riqueza de especies.

Generalist carnivores, Model II

From the correlation among species richness of generalist carnivore sea stars and the average values of oceanographic factors, the following variables were selected: temperature at 60 m (AvgT2 in ºC), and nitrate concentration ($AvgNO_3^-$ in µM). Equation 5 was obtained and estimated richness appears in Fig. 4b.

Equation 5:

$$\text{Generalist carnivores richness} = -0.04\,(AvgT2) + 0.32\,(AvgNO_3^-)$$
$$r^2 = 0.96,\ p < 0.001$$

Generalist carnivores, Model III

Ridge regression analysis among species richness of generalist carnivores, average surface temperature (AvgST in ºC), and total continental shelf area (TCSA in km^2) resulted in equation 6. The estimated richness from this equation is shown in Fig. 4c. Again, this model was proposed even when neither of the two oceanographic variables showed a significant correlation with the total richness (Table 2).

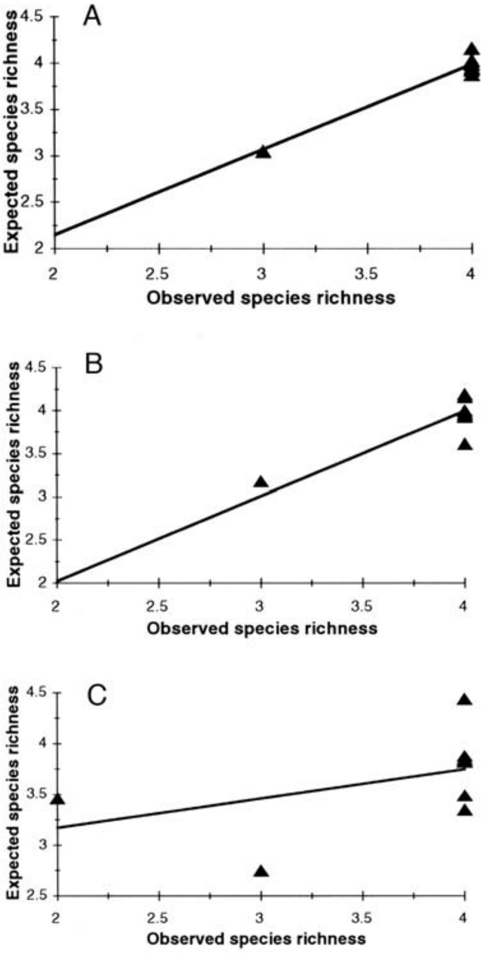

Fig. 4. Model I Stepwise (a), Model II (b) and Model III (c) for generalist carnivore sea star species richness.

Fig. 4. Modelo I Stepwise (a), Modelo II (b) y Modelo III (c) para la riqueza de especies de estrellas de mar carnívoras generalistas.

TABLE 2

Simple linear correlation values between species richness of generalist carnivores sea stars and the analyzed variables[1]

CUADRO 2

Correlación linear simple entre los valores de riqueza de especies de las estrellas carnívoras generalistas y las variables analizadas[1]

Variable	n	r	p
Maximum temperature at 60 m	9	- 0.80	0.009
Mean temperature at 60 m	9	- 0.90	0.001
Maximum concentration of nitrates	8	0.89	0.003
Mean concentration of nitrates	8	0.82	0.010
Minimum concentration of surface photosynthetic pigments	9	- 0.94	0.0001
Minimum integrated productivity	9	- 0.80	0.009

1 Only significant relations where $r > 0.80$ are shown, n = degrees of latitude.

Equation 6:

$$\text{Generalist carnivores richness} = 0.18\,(\text{AvgST}) - 0.0001\,(\text{TCSA})$$
$$r^2 = 0.93,\ p < 0.001$$

Predators of colonial organisms, Model I

The stepwise analysis showed that the best factors to model richness were: maximum value of nitrates (MaxNO_3^- in µM) and surface temperature range (STr in °C) (Equation 7). The regression line with those components is shown in Fig. 5a.

Equation 7:

$$\text{Richness of predators of colonial organisms} = -\,1.7\,(\text{STr}) - 11.63\,(\text{MaxNO}_3^-)$$
$$r^2 = 0.96,\ p < 0.001$$

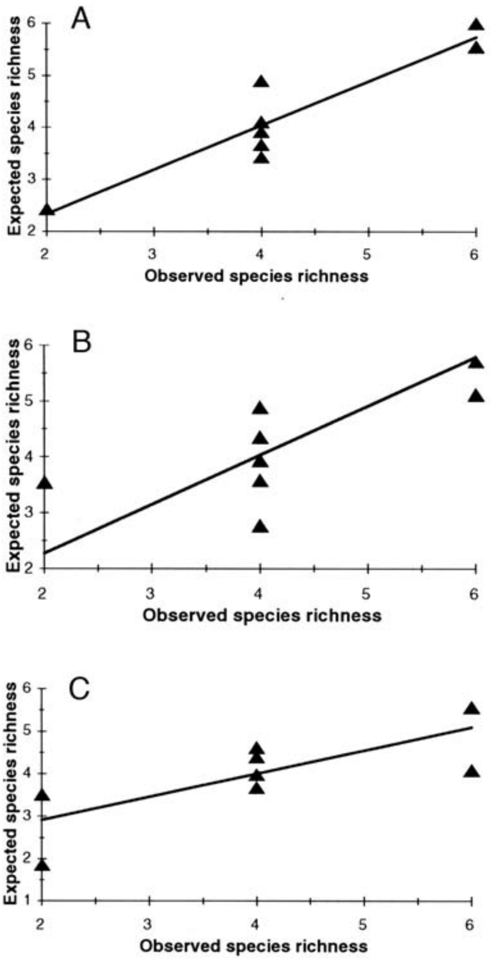

Fig. 5. Model I Stepwise (a), Model II (b) and Model III (c) for colonial organisms predator sea star species richness.

Fig. 5. Modelo I Stepwise (a), Modelo II (b) y Modelo III (c) para la riqueza de especies de estrellas de mar que depredan en organismos coloniales.

Predators of colonial organisms, Model II

From the correlation among species richness of predatory sea stars on colonial organisms, and the average values of the oceanographic factors, the following variables were selected: temperature at 60 m (AvgT2 in ºC), temperature at 125 m (AvgT3 in ºC), silicate concentration (AvgSiO_4 in µM), and integrated productivity (Avgprod in $\text{gC/m}^2\text{/d}$). Equation 8 was obtained and the estimated richness appears in Fig. 5b.

Equation 8:

$$\text{Richness of predators of colonial organisms} = 0.68\,(\text{AvgT2}) - 0.29\,(\text{AvgT3}) - 0.11\,(\text{AvgSiO}_4) - 1.01\,(\text{Avgprod})$$

$$r^2 = 0.90,\ p < 0.001$$

Predators of colonial organisms, Model III

Ridge regression analysis among species richness of predatory asteroids of colonial organisms, average surface temperature (AvgST in ºC), and total continental shelf area (TCSA in km^2) produced equation 9. The estimated richness from this equation is shown in Fig. 5c. Again, this model was significant even when neither of the two oceanographic variables showed a significant correlation with the total richness (Table 3).

TABLE 3

Simple linear correlation values between species richness of sea stars that prey on colonial organisms and the analyzed variables [1]

CUADRO 3

Correlación linear simple entre los valores de riqueza de especies de estrellas de mar que depredan organismos coloniales y las variables analizadas[1]

Variable	n	r	p
Minimum surface temperature	9	0.81	0.009
Range of surface temperature	9	- 0.86	0.003
Maximum temperature at 60 m	9	- 0.88	0.002
Range of temperature at 60 m	9	- 0.89	0.001
Minimum temperature at 125 m	8	- 1.0	0
Maximum temperature at 125 m	8	- 0.85	0.008
Mean temperature at 125 m	8	- 0.88	0.004
Minimum integrated productivity	9	- 0.84	0.005
Mean integrated productivity	9	- 0.80	0.009

[1] Only significant relations where $r > 0.80$ are shown, n = degrees of latitude.

Equation 9:

$$\text{Richness of predators of colonial organisms} = 0.25\,(\text{AvgST}) - 0.0002\,(\text{TCSA})$$

$$r^2 = 0.90,\ p < 0.001$$

Predators of small invertebrates, Model I

The stepwise analysis was significant and proposed that the factors that better explain the variance in species richness were: nitrates range (NO_3^-r in µM) and minimum of integrated productivity (Minprod in gC/m^2/d) (Equation 10). The regression line with those components is shown in Fig. 6a.

Equation 10:

$$\text{Richness of predators of small invertebrates} = 0.89\,(NO_3^-r) - 9.27\,(\text{Minprod})$$

$$r^2 = 0.96,\ p < 0.001$$

Predators of small invertebrates, Model II

From the correlation among species richness of predatory sea stars on small invertebrates, and the average values of the oceanographic factors, the following variables were selected: temperature at 60 m (AvgT2 in ºC), temperature at 125 m (AvgT3 in ºC), silicate concentration (AvgSiO$_4$ in µM), weighted average values of surface photosynthetic pigments (Avgpigw in mg/m^3), and integrated productivity (Avgprod in gC/m^2/d). Equation 11 was obtained and the estimated richness appears in Fig. 6b.

Equation 11:

$$\text{Richness of predators of small invertebrates} = 0.92\,(\text{AvgT2}) + 0.51\,(\text{AvgT3}) - 0.39\,(\text{AvgSiO}_4) + 0.87\,(\text{Avgpigw}) - 5.44\,(\text{Avgprod})$$

$$r^2 = 0.96,\ p < 0.001$$

Predators of small invertebrates, Model III

Ridge regression analysis among species richness of predatory asteroids of small

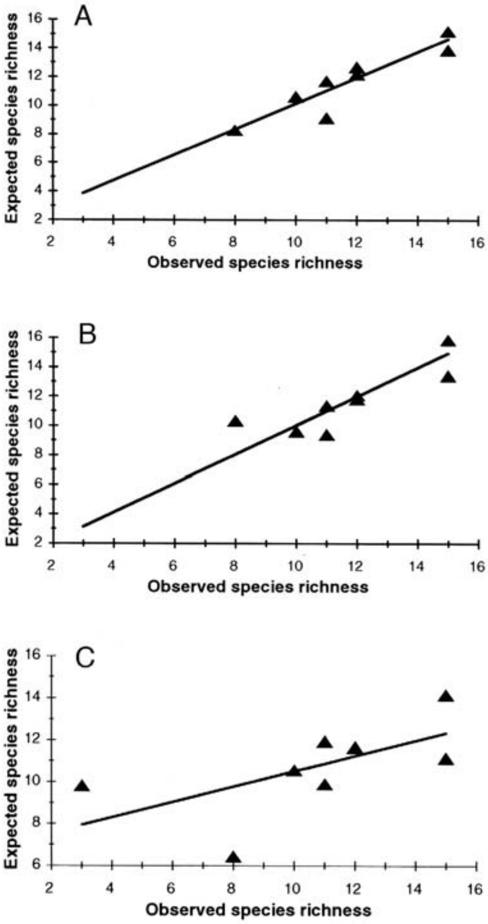

Fig. 6. Model I Stepwise (a), Model II (b) and Model III (c) for small invertebrates predator sea star species richness.

Fig. 6. Modelo I Stepwise (a), Modelo II (b) y Modelo III (c) para la riqueza de especies de estrellas de mar que depredan en pequeños invertebrados.

invertebrates, average surface temperature (AvgST in ºC), and total continental shelf area (TCSA in km^2) produced equation 12. Estimated values of richness are shown in Fig. 6c. This model was proposed even when none of the two oceanographic variables showed a significant correlation with the total richness (Table 4), and it was significant this time.

TABLE 4

Simple linear correlation values between species richness of carnivores of small invertebrates sea stars and the analyzed variables[1]

CUADRO 4

Correlación linear simple entre los valores de riqueza de especies de los carnívoros de invertebrados pequeños y las variables analizadas[1]

Variable	n	r	p
Surface temperature range	9	- 0.83	0.006
Maximum temperature at 60 m	9	- 0.87	0.002
Range of temperature at 60 m	9	- 0.89	0.001
Mean temperature at 60 m	9	- 0.82	0.007
Minimum temperature at 125 m	8	- 0.96	0.0001
Maximum temperature at 125 m	8	- 0.87	0.005
Mean temperature at 125 m	8	- 0.95	0.0004
Maximum silicate concentration	8	- 0.84	0.009
Range of silicate concentration	8	- 0.87	0.005
Mean silicate concentration	8	- 0.81	0.020
Minimum concentration of surface photosynthetic pigments	9	- 0.87	0.003
Median concentration of surface photosynthetic pigments	9	- 0.80	0.009
Minimum integrated productivity	9	- 0.89	0.001
Mean integrated productivity	9	- 0.83	0.005

[1] Only significant relations where r > 0.80 are shown, n = degrees of latitude.

Equation 12:

$$\text{Richness of predators of small invertebrates} = 0.61\ (\text{AvgST}) - 0.0004\ (\text{TCSA})$$
$$r^2 = 0.90,\ p < 0.001$$

Detritivores, Model I

The stepwise analysis showed that the best factors to model richness were: maximum value of nitrates (MaxNO$_3^-$), and minimum integrated productivity (Minprod) (Equation

13). The regression line calculated using those components is shown in Fig. 7a.

Equation 13:

$$\text{Detritivore richness} = 1.3\ (\text{MaxNO}_3^-) - 6.94\ (\text{Minprod})$$
$$r^2 = 0.96,\ p < 0.001$$

Detritivores, Model II

From the correlation among species richness of detritivore sea stars and the average values of the oceanographic factors, the following variables were selected: temperature at 60 m (AvgT2 in ºC), temperature at 125 m (AvgT3 in ºC), silicate concentration (AvgSiO_4 in µM), weighted average values of surface photosynthetic pigments (Avgpigw in mg/m^3), and integrated productivity (Avgprod in $\text{gC/m}^2\text{/d}$). Equation 14 was obtained and the estimated richness appears in Fig. 7b.

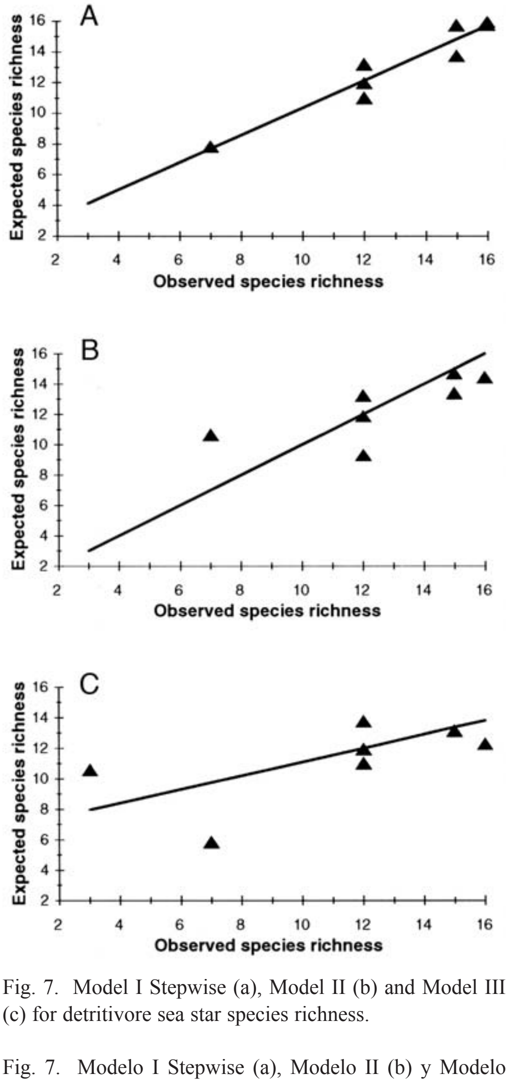

Fig. 7. Model I Stepwise (a), Model II (b) and Model III (c) for detritivore sea star species richness.

Fig. 7. Modelo I Stepwise (a), Modelo II (b) y Modelo III (c) para la riqueza de especies de estrellas de mar detritívoras.

Equation 14:

$$\text{Detritivore richness} = 0.88\ (\text{AvgT2}) + 0.9\ (\text{AvgT3})$$
$$-\ 0.53\ (\text{AvgSiO}_4) + 0.34\ (\text{Avgpigw}) - 3.07\ (\text{Avgprod})$$
$$r^2 = 0.94,\ p < 0.001$$

Detritivores, Model III

Ridge regression among detritivores species richness, average surface temperature (AvgST in ºC), and total continental shelf area (TCSA in km^2) produced equation 15. The estimated richness from this equation appears in Fig. 7c. This model was significant but none of the oceanographic variables analyzed individually showed a significant correlation with the total richness (Table 5).

Equation 15:

$$\text{Detritivore richness} = 0.73\ (\text{AvgST}) - 0.006\ (\text{TCSA})$$
$$r^2 = 0.90,\ p < 0.001$$

DISCUSSION

We will start this section by analyzing each kind of multiple regression model applied. Model I (Fig. 3a, 4a, 5a, 6a, 7a), is considered the most complete to explain the relationships among species richness and oceanographic factors since it considered all of them, and selected those which best explained richness patterns based on the amount of variance explained and test robustness. Model II (Fig. 3b, 4b, 5b, 6b, 7b) that included only mean values of all analyzed factors, is less precise than the previous one given the reduction in tested variables, which led to a decrease in explained variance;

TABLE 5

Simple linear correlation values between species richness of detritivore sea stars and the analyzed variables[1]

CUADRO 5

Correlación linear simple entre los valores de riqueza de especies de las estrellas de mar detritívoras y las variables analizadas[1]

Variable	n	r	p
Maximum temperature at 60 m	9	- 0.90	0.001
Temperature range at 60 m	9	- 0.90	0.001
Mean temperature at 60 m	9	- 0.86	0.003
Minimum temperature at 125 m	8	- 0.87	0.005
Maximum temperature at 125 m	8	- 0.81	0.010
Mean temperature at 125 m	8	- 0.87	0.005
Maximum nitrate concentration	8	0.87	0.005
Maximum silicate concentration	8	- 0.85	0.008
Range of silicate concentration	8	- 0.82	0.010
Mean silicate concentration	8	- 0.85	0.008
Minimum concentration of photosynthetic pigments	9	- 0.87	0.002
Minimum integrated productivity	9	- 0.94	0.0002
Mean integrated productivity	9	- 0.83	0.006

[1] Only significant relations where $r > 0.80$ are shown, n = degrees of latitude.

however, it is still very accurate. Finally Model III (Fig. 3c, 4c, 5c, 6c, 7c), which included only average surface temperature (ºC) and continental shelf (km^2) from 0-200 m depth, was the least precise probably because these factors taken independently do not relate much to sea star richness (Tables 1-5). Thus, the interaction of oceanographic factors must be considered when relationships among species richness and oceanographic factors are to be estimated. Nevertheless, we calculated the regressions because average surface temperature and total continental shelf area are commonly used as proxies of marine organism distributions (Briggs 1974, Brusca and Wallerstein 1979, Thomson and Gilligan 1983, Wickstein 1989, Hendrickx 1995). The good results obtained in the presented numerical analyses nevertheless have to be taken cautiously because the utilised scale is rather coarse (1° in latitude). Consequently their biological interpretation is still tentative until more detailed studies and other statistical analyses are conducted to know in much more detail the oceanographic setting of the Gulf of California (specially in coastal areas), and the distribution and richness of Asteroidea.

The initial observation from the Pearson correlation analyses is that most of the oceanographic parameters were inversely correlated to species richness of sea stars in the Gulf of California (Tables 1-5). This may indicate that, individually, they may act primarily as limiting factors controlling species number in the Gulf, and a situation like that would be expected in a transitional zone like the Gulf of California, which presents strong seasonal changes in environmental conditions. The relevance of limiting factors shows that local species richness in the Gulf (at scale of 1° in latitude) is apparently not proportional to regional richness, and thus that a certain “saturation” of species richness may occur in the study area (Cornell 1993, Loreau 2000).

Detailed discussion of all tested oceanographic factors is beyond the scope of this paper. Here we will focus only on the major ones as revealed by the ridge and stepwise models: surface temperature, nitrate concentration and integrated productivity. Surface temperature range was a key factor in determining total richness and richness of predators on colonial organisms (Eqs. 1 and 7). The coefficient of the regression was negative, which means that the smaller the variation on surface temperature, the greater the number of species. Temperature has been considered as a direct determinant in the distribution of numerous animal and plant taxa (Briggs 1974, Brusca and Wallerstein 1979, Rosen 1988a, Bernard *et al.* 1991), which is expected because it has direct effects on the physiology and reproduction of the organisms (Lawrence and Lane 1982, Ross-Ellington 1982, Lawrence 1987). Consequently, extreme changes in temperature cause effects at both population and assemblage levels, as it occurred when the 1982-83 and 1997-98 El Niño-Southern Oscillation impacted the western coast of the Americas, and other areas of the Pacific Ocean (Glynn 1988, Goreau *et al*. 2000). In the case of asteroids, changes in temperature affect locomotory activity, feeding, and metabolic rates, and most importantly, severely diminishes their reproductive output (Lawrence 1987).

Surprisingly, mean sea surface temperature did not returned as relevant to determine species richness (total or of any feeding guild), although mean temperature at 60 m appeared in the stepwise model for generalist carnivores (Fig. 4a). As mentioned, temperature has been traditionally considered a key factor in the distribution of marine taxa, however, the relations were not statistically tested because most of the studies were based exclusively on surface measurements, or their relevance was not compared against that of other oceanographic factors, maybe because of data accessibility. One good explanation of our results is that as asteroids have wide bathymetric distribution ranges in the Gulf of California (with depth distribution midpoints usually around 70-120 m; Maluf 1988a, Cintra-Buenrostro 1997), most populations are not under the influence of the surface temperature, and consequently species richness is not much affected by this parameter. The relative independence may result from the fact that thermocline depth in the Gulf of California is very shallow, and rarely exceeds 50 m depth (Gendrop *et al*. 1978). On the other hand, very few asteroid species live in the intertidal or the very shallow subtidal, and although in this case surface temperature is crucial, the number of species that occupy this kind of habitats is low and consequently they did not affect the general patterns observed. The presented information points out the need to consider that all oceanographic factors change with depth, when conducting biogeographic analyses of marine taxa. Thus, discussion based only on surface data have to be taken with a grain of salt!

In the multiple regression models, nitrates were the foremost factor of importance. This result is interesting for two reasons; first, post-metamorphic sea stars cannot obtain this nutrient directly, but only in particulate form (Bamford 1982, Lawrence and Lane 1982), although they are able to absorb amino acids from the environment by epidermic absorption and by intermittent oral feeding (Bamford 1982). On the other hand, nitrates are usually low in concentration in the tropical and subtropical Eastern Pacific region especially in areas of very high sea temperature such as southern México (less than 1 µM). However, the level increases remarkably in upwelling areas (Gulfs of Papagayo and Tehuantepec) and at the equator or nearby areas (2-6 µM; Anonymous 1998). In the Gulf of California nitrates are high, especially north of 26° N (Anonymous 1998), and Alvarez-Borrego *et al*. (1978) mentioned that their concentration is also high in upwelling areas of the Gulf. Nutrient availability in the water is of uttermost importance for larval and juvenile forms of the sea stars, which consume dissolved and particulate organic matter in the water column. Also, juvenile individuals depend on proteins, amino acids, and other nitrogenated material deposited in the detritus (Jangoux 1982). We suggest that nitrates presented a positive relationship with richness because they favor the establishment of species benefiting survival of individuals in their initial development stages. This hypothesis may also help to explain why the richest zones in echinoderm species (including sea stars) in the Eastern Tropical Pacific are located in upwelling areas as California and the West coast of Baja California (Maluf 1988a, b).

Integrated productivity was the third important factor in determining the species richness. Although it was only relevant for consumers of small invertebrates and detritivore sea stars (Eq. 10 and 13). This factor represents the available carbon per unit of area per unit of time (Gaxiola-Castro and Alvarez-Borrego 1986), which can be incorporated by heterotrophs into the trophic web, and is expected that as productivity increases (and consequently more plant biomass exists), a larger number of individuals and species of heterotrophs can be supported by the system (Begon *et al*. 1996). Sea stars rarely prey on phytoplankton (there is only one species of this kind in the Gulf, *Astrolirus panamensis* (Ludwig, 1905), which inhabits only the southernmost portion of the Gulf up to 24° N; Cintra-Buenrostro 1997). However, they consume organic material deposited in the sediments (detritivores) or prey on organisms that use plankton as food, for example, consumers of colonial species (sponges, bryozoans, etc.) and on small invertebrates like bivalves (Jangoux 1982). There was a negative relationship between minimum integrated productivity and richness of either detritivore or consumers of small invertebrates sea stars in the Gulf of California. In other words, species richness was higher in areas where productivity can be extremely low during the year (independently of the mean or maximum value). A possible explanation for this pattern is that it is an artifact resulting from the relation of richness and other factors like temperature, because the lowest values of productivity occur in the southern Gulf (Santamaría del Angel *et al*. 1994). On the other hand, high productivity zones also have elevated densities of pelagic predators (Hendrickx 1995), which can cause a decrease in asteroid larval survivorship, and consequently a reduction on their richness. This finding has no easy explanation and needs to be further tested. However, it is relevant to notice that the same effect (more productivity, less richness) has also been observed in the Gulf of California brachyurans and echinoids (Correa-Sandoval and Carvacho-Bravo 1992, Cintra-Buenrostro and Reyes Bonilla, in prep.), an indication that our results are not so exceptional for this region.

In this study, perhaps the least expected result was the exclusion of the continental shelf area as an important factor in the determination of total sea star richness in the Gulf, because theoretically the size of an area is indicative of habitat variability (Rosenzweig 1997). This does not always happen (Brown 1988, Rosen 1988b, Hallam 1994, O'Hara and Poore 2000); in the present study we found that in the northern Gulf (where more shelf area is available) less species were present. Probably, as most shallow areas of this region have sandy bottoms (Byrne and Emery 1960, Van Andel 1964) they may present a low variety of habitats and consequently, low species richness. It is also important to notice that the northern Gulf is a very dynamic area and presents strong annual changes in salinity, temperature and nutrients (Lavín *et al*. 1997). All these characteristics must hamper the existence of sea stars, which are susceptible to temperature changes and substrate type (Thandar 1989, Blake 1990) and produce the lack of relation between these variables.

O'Hara and Poore (2000) is the only other echinoderms study, that we are aware of, in which a test for certain oceanographic (mainly temperature), physiographic (area of continental shelf), and historic factors was attempted. Thus, ours is the first American paper to test the relevance of oceanographic traits on species richness, and our results may be considered tentative, particularly when alternative analytical methods can and will be tested. However, they are encouraging and allow us to conclude that sea star species richness of the Gulf of California (total and by each of the four feeding guilds presented) is closely related to several oceanographic factors, most importantly nitrate concentration, productivity and surface temperature range. This situation permits the construction of multiple regression models that were highly accurate to predict local species richness, and which may eventually be used to estimate changes of species richness of this marine group, according to predictions from global change models.

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RESUMEN

La riqueza específica es uno de los mejores indicadores para estimar biodiversidad. Sin embargo, para los ambientes marinos existen pocas investigaciones que contrastan los patrones de biodiversidad con las condiciones ambientales. Los objetivos del presente estudio fueron el determinar la correlación existente entre la riqueza específica de estrellas de mar de aguas someras (< 200 m de profundidad) y diversos factores oceanográficos claves en el Golfo de California, México; y predecir la riqueza específica de Asteroidea mediante el uso de regresiones múltiples. Para el análisis se dividió al golfo en nueve secciones de un grado de latitud (desde los 23-31º N), y para cada sección obtuvimos la siguiente información: área de plataforma continental disponible (100 y 200 m); intervalo y promedio de temperatura a tres profundidades (0, 60, y 120 m); profundidad de la termoclina; concentración superficial de nutrientes (nitratos, fosfatos y silicatos); concentración superficial de pigmentos fotosintéticos; y productividad integrada. La riqueza específica de asteroideos por grado de latitud fue estimada con datos provenientes de literatura, trabajo de campo y colecciones museográficas. Cada especie fue asignada a uno de los siguientes grupos tróficos: depredadores de invertebrados pequeños (I), detritívoros (D), depredadores de organismos coloniales (C), carnívoros generalistas (G), y planctotróficos (P). Existen 47 especies de asteroideos de aguas someras en el Golfo de California (16 I, 15 D, ocho C, seis G, uno P, y uno indeterminado). Tanto la riqueza específica total como la riqueza por grupo trófico mostraron una fuerte atenuación latitudinal y fueron mayores en las partes sureñas del golfo; área con estrecha plataforma continental, alta temperatura, y baja concentración de nutrientes. La temperatura, concentración de nitratos y productividad integrada fueron los parámetros oceanográficos que mostraron mayor frecuencia en las correlaciones con la riqueza específica de cada grupo. Se observó una correlación negativa en todos los casos entre la riqueza específica y los nutrientes, así como con los pigmentos superficiales, lo que sugiere que ambientes con alta productividad limitan la diversidad de asteroideos en la zona. Por último, todos los modelos de regresión postulados para determinar la riqueza específica de asteroideos usando datos oceanográficos fueron significativos y tuvieron un nivel de precisión elevado. En conclusión, la riqueza específica de Asteroidea en el Golfo de California está relacionada con las condiciones oceanográficas y puede ser estimada con la información oceanográfica regional disponible.

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