1. **Predicting changes to macrobenthic communities due to fishing**

2. **disturbance in a shrimp fishing ground of the Mexican central Pacific**

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9. Abstract

10. We test predicted short-term structural changes in the macroinvertebrate assemblages of a shrimp fishing ground in the tropical Mexican Pacific subject to low effort with seasonal closures. During two years, five cruises were carried out sampling seven sites and four depths (20, 40, 60 and 80 m) along 100 km of coastline. A series of community structure descriptors were used to determine the ecological effects of fishing disturbances: ABC curves, W-statistic, normalized species size distribution as biomass spectra, spatial segregation index, Shannon-Wiener diversity index, species richness and biomass. Theoretical predictions of the effects of fishing on these indices were tested by comparisons of samples collected from successive open and close fishing seasons. ABC curves show fishing has produced a state of chronic disturbance in the macroinvertebrate community. Short-term effects could be masked by natural seasonal and interannual environmental changes. Results of the analyses of short-term effects are not in agreement with the fishing disturbance theories; only in 31% of the cases the results obtained of comparisons between successive cruises to test the different hypotheses about the effects of fishing were in agreement with theory. The temporal trend of increase of the biomass and the decline of species richness, could evidence interannual effects. The complexity of the sources of variability in a exploited community forces to focus on temporal and spatial gradients to understand the community structural processes.

11. Key words: biomass spectra, diversity, fishing disturbance, macroinvertebrate community structure, dominance, species-area curve, spatial segregation, shrimp fisheries, trawl, tropical shelf ecosystems.

12. Introduction

13. Natural disturbance events are important factors that determine the structure of benthic communities (Grassle & Sanders, 1973; Kaiser et al., 2000) and the magnitude of their effect is dependent on their scale (Hall et al., 1994). Fishing is one of the most important anthropogenic disturbance sources to marine benthic ecosystems and has been occurring for centuries (De Groot, 1984). At present, mobile bottom fishing gear is used in almost every shelf in the world (Collie et al., 2000).

14. Trawl fisheries are characterised by their highly pernicious effects in marine ecosystems, mainly due to the low selectivity of gears (Pascoe, 1997) and their impacts on the sea floor (Collie, 1998). The low selectivity of the fishing gear and high level of by-catch are particularly important in shrimp or prawn fisheries in temperate and tropical zones (Stobutzki et al., 2001). In these fisheries, most of the by-catch is discarded at sea, and it is composed of species that are the target of other commercial or recreational fisheries or that are endangered or vulnerable, e.g. marine turtles (Stobutzki et al., 2001). In the shrimp trawl fisheries of the Mexican Pacific, juvenile fish such as snappers caught by the artisanal fleet (Saucedo-Lozano et al., 1998), and turtles are part of the by-catch. The magnitude of the mortality induced by the shrimp trawl fishery in the Mexican Pacific to the non-target species remain unknown as well as their spatial and temporal variation, and the impact of fishing effort alone does not explain the high catch variability of the commercial shrimps fluctuations (López-Martínez et al., 2002).

15. Identifying impacts produced by fisheries is often obfuscated by the lack of environmental-impact assessment procedures in fisheries management. (Thrush et al., 1998), besides that biological effects are difficult to identify due to the complexity and variability in benthic communities (Hall, 1994). There are several studies of soft-bottom commercial fishing that have identified experimentally evidence of small-scale local disturbance (e.g. Eleftheriou and Robertson 1992; Thrush et al., 1995; Currie and Parry, 1996), however local conclusions can not be extrapolated to broad scales. According to Thrush el al. (1998), experiments occur on much smaller scales

in space and time whereas fishing occurs in broad spatial scales and in some cases permanently. Besides, recovery rates of benthic organisms are extremely dependent upon the proximity to recruit source areas for recruitment. Therefore, isolated and small experimental disturbances do no mimic fishing disturbances. Small-scale disturbances events, even when frequent, are masked by the background of large-scale disturbances (Kaiser and Spencer, 1996). Experimental studies comparing conditions before and after trawling are focused on short-term (acute) impacts ignoring long term (chronic) effects (McConnaughey et al., 2000). Large-scale natural disturbances, such as seasonal storms and strong tidal currents form a background against which other smaller disturbances such as those induced by predation occur (Hall et al., 1994), and the impact intensity of the storms and tidal currents could be related with depth (Thrush et al., 1998).

16. Comparisons between impacted areas and closed fishing areas has been the most frequent strategy to assess fishing disturbance (e.g. Thrush et al., 1995; Collie et al., 1997), however undisturbed areas of a significant scale are scarce around the world or the period protected has been brief, due that the time scales of disturbance and recovery could be on the order of 5 to 10 yr (Collie et al., 1997). The impact and recovery rates of organisms depend of species, scale of disturbance, habitat and gear type (Collie et al., 2000). Works that analyse catch time series or long time monitoring, are focused to detect trends of catch or changes in assemblage composition as fishing disturbances evidences (e.g. Greenstreet and Hall, 1996; Fried et al., 1999; Greenstreet et al., 1999; Rogers et al., 1999). Accurate long-term databases of exploited communities are not frequently available.

17. The original, pre-fishing, faunal composition is difficult to be estimated in most ecosystems because data gathered prior to the era of intensive bottom fishing are sparse and intensively fished areas are likely to be maintained in a permanently altered state (Collie et al., 2000). The experimental comparison of the impact of fishing is in most cases very difficult due to the large scale of the effects and lack of adequate controls. Due to this fact, the effect of trawling in demersal and benthic communities is often deduced by changes over time and respect to theoretical undisturbed communities in the species composition and relative abundance of fishes and macroinvertebrates (e.g. Greenstreet and Hall, 1996; Kaiser and Spencer, 1996; Kaiser et al., 2000) and by the effects on individual size frequency distributions as biomass spectra (e.g. Duplisea and Kerr, 1995; Duplisea et al., 1997; Jennings et al., 2001; Macpherson, and Gordoa, 1996).

18. Spite of hydroclimatic seasonality is known as the main recomposition force of the marine communities, which act on large scales, however, it is not frequent to consider it as part of the explanation of changes of the target population levels or community composition in fishing disturbance surveys. The first working hypothesis of our approach is that there exist several sources of disturbance scale-dependent; natural and anthropogenic, that act concurrently and permanently to model the community, and their effect on the community should start to be elucidated. The present paper assesses the short-term effects of fishing on soft-bottom macroinvertebrate community structure in shrimp fishing grounds. Short-term effects are defined as the occurring between subsequent close and fishing seasons. Different community parameters were evaluated and the performance of these indices assessed against theoretical predictions.

19. **Material and Methods**

20. *Description of the fishery*

21. The continental shelf of the central Mexican Pacific supports a relatively low intensity shrimp trawling fishery, which has been operating in the study area during decades. There is no statistics about spatial and temporal trends of catches and effort, and fishing could be considered the only important human impact in the area. A small fleet operates almost permanently in this area, and the fleet from the most important fishing grounds in the Mexican Pacific coast (Gulf of California and Gulf of Tehuantepec, see Fig 1) when they are crossing the study area switching between fishing grounds. Although accurate statistics of fishing effort do not exist, in the last 10 years effort has been growing slightly. Fishery regulations close the fishery between May and October, and permanently exclude fishing in bays and enclosed coastal bodies. Fishers are also required to use turtle exclusion devices (TEDs). The commercial fleet operates mainly from 25 to 100 m deep (authors personal observation and information provided by fishers).

22. *Experimental fishing samplings*

23. The study area is located on the continental shelf in the Mexican central Pacific (Fig. 1), between 10 and 90 m isobaths, from Punta Farallón (Jalisco) at the mouth of the Cuitzmala River to Cuyutlán (Colima). Five cruises (DEM 1 to DEM 5) were

conducted aboard the research vessel BIP-V of the University of Guadalajara, covering the different hydroclimatic and fishing seasons (Fig. 2). Seven sites were selected along the coast to be sampled during each cruise according to the spatial distribution of soft bottoms and to the commercial shrimp fleet preferences. Four depth strata were selected (20, 40, 60 and 80 m) for each site making a total of 28 sampling stations per cruise. Each tow lasted 0.5 h at a mean velocity of 2 knots corresponding to an average of one hectare trawled by sampling station. Samples were taken with two shrimp trawl nets (one by hand of the boat), with a mouth opening of 6.9 m, a calculate headline height of 1.15 m and a stretched-mesh size along the bottom and the seine of 38 mm. In each cruise, the sampling order of the seven sites was randomly selected. All the samples (the four depth strata) from the same site were taken the same night. In the present study, the dominant invertebrate groups in catches, both infauna and epifauna (cnidarians, molluscs, crustaceans, and echinoderms) are considered (a detailed analysis of assemblages is in Godínez-Domínguez et al., in review).

24. According to spatial patterns obtained from previous analyses of assemblage data, depth strata were pooled in two categories (shallow: 20 and 40 m, and deep: 60 and 80, respectively) because an important discontinuity in community structure occurs between 40 and 60 m deep (Godínez-Domínguez and Freire, submitted; Godínez-Domínguez et al, submitted). Data from the seven sites were considered independently and used as replicates in all data analyses. We assume that the extent (about 100 km of coastline) is enough to be considered as a broad scale (adequate to measure the effects of fishing) and it is not too large to assume the existence of a latitudinal source of variability.

25. Data analysis strategy

26. Macrobenthic community is subject to a large number of potential sources of variability (Table 1). In the present study no interannual trends are expected in the temporal behavior of the community descriptors (detailed below), and only seasonal-cyclic patterns are expected to reflect both fishing and hydroclimatic effects. However ANCOVA tests were used to determine the significance of the potential linear time trends. Significant linear trends of community descriptors could determine interannual disturbance patterns and their possible causes according to the proposed framework of disturbance interactions (Table 2). The ANOVA procedure was used for a priori single comparisons between successive close and

open seasons of several descriptors of community structure in each depth strata. The ANOVAs and ANCOVAs mentioned above were carried out with community descriptors data estimated by a Jack-knife procedure. Pseudovalues obtained with the Jack-knife method are assumed to follow a normal distribution (Zahl, 1977).

27. *Descriptors of community structure (DCS) and hypothesis on fishing disturbance*

28. Abundance biomass curves (ABC)

29. According to Clarke and Warwick (1994), changes in the dominance pattern of the abundance and biomass of benthic macrofaunal communities could be a good disturbance indicator. In this sense, the ABC curves are expected show communities in heavily fished areas are dominated by high abundances of small-bodied organisms, whereas less intensely fished and disturbed areas are dominated by fewer, larger-bodied biota (Kaiser et al., 2000). When the biomass curve is above the abundance curve, the sum of the B_i-A_i values across the ranks *i* will be strongly positive. In contrast, this sum will be strongly negative for cases where abundance and biomass curves are transposed. Intermediate cases in which *A* and *B* curves are interwined will tend to give $\sum(Bi\text{-}Ai)$ values near zero (Clarke and Warwick, 1994). The W-statistic is a synoptic descriptor of an ABC curve and is recommended when the number of sites, times or replicates is large (Clarke, 1990; Clarke and Warwick, 1994), as is the present case:

$$W = \sum_{l=1}^{s} (B_i - A_i) \,/\, [50(S\text{-}1)]$$

30. where B_i and A_i are the biomass and abundance for each rank (*i*) in an ABC curve, and *S* is the number of species. We hypothesize that a) the community should have an overall negative value of $\sum(Bi\text{-}Ai)$, because it has been perturbed for a long time by fishing, and b) values of the index should be lower during open fishing seasons *than* in the previous or consecutive close seasons (Table 2). ANOVA tests based in W-statistic were performed to determine differences between successive cruises in each depth strata

31. Biomass size spectra

32. The body size of marine biota follows a regular pattern. The relationship between size classes and total normalized biomass (biomass in a class interval divided by the interval width) has been defined as a consequence of energy flow from prey to predators (Jennings et al., 2001). The slope of the spectrum can provide a broad indication of the intensity of exploitation that modifies predator-prey relationships (Pope et al. 1988; Rice and Gislason 1996). Normalized species size distributions (NSSD) are obtained by regressing the $\log_2$ of the relative biomass in a size class (= biomass in size class / biomass in all size classes) against the $\log_2$ of the middle body size in the class. The slopes of the linear regressions characterize biomass trends across the size spectrum and can be used to compare different data sets (Kerr, 1974; Rasmussen, 1993; Sheldon et al., 1977; Sprules and Munawar, 1986). Steeper slopes suggest heavy exploitation, and many studies have reported that fishing causes a shift from non-exploited communities where biomass is dominated by large-sized species to exploited communities dominated by small-sized organisms (Collie et al., 2000).

33. In our case, biomass size spectra were constructed from the distribution of the average individual wet weight for each species, and the normalized spectra was estimated across size classes ranging from 8 to 1024 g. Species with individual average weight lower than 8 g were not considered to avoid biases caused by net selectivity. Following the predictions of the effect of fishing in biomass spectra, NSSD slopes for open season data sets should be steeper than those corresponding to closed seasons (see table 2). ANOVA tests were employed to determine the significance of the differences among the jack-knifed pseudovalues of slopes (Manly, 1997) in successive fishing seasons for both depth strata.

34. Spatial segregation

35. Competition can cause spatial segregation and fishing can reduce competition acting as a top-level predator and promoting coexistence between competing species (Blanchard, 2001). Spatial segregation among species within a community could be estimated using species-area curves (Rosenzweig, 1995).

36. $S = a\, A^{\beta}$

37. where S is the species richness, A the trawled area, the intercept a is related to overall species richness and the slope β constitutes an index of spatial segregation.

If fishing promotes increases in local coexistence, then spatial segregation caused by competition would be expected to decrease with increasing fishing pressure (Blanchard, 2001). In our case, communities during close fishing seasons should have slopes of species-area curves steeper than those in previous or successive open seasons (see table 2). ANOVA tests were conduced to compare successive fishing seasons using jack-knifed pseudovalues of slopes in both depth strata.

38. Shannon index of diversity and species richness (Magurran, 1988)

39. Local information suggest that the fishing effort applied during the last years in the study area has been moderate, and for this reason we hypothesized that fishing have generated increases in diversity according to the intermediate disturbance hypothesis (Connell, 1978). In the short term, the Shannon index and species richness will increase after a fishing season (see table 2). For each cruise and depth strata, the mean value and confidence intervals of the Shannon index and the species richness were estimated according to Zahl (1997), and following the procedures described by Heltshe and Forrester (1983) and Routledge (1980). ANOVA tests were carried out to determine differences among successive fishing seasons by depth strata using the jack-knife diversity and richness pseudovalues.

40. Biomass

41. During the fishing season a gradual shift of the community biomass ($g \cdot ha^{-1}$) is expected due to short-term biomass removal effects as consequence of the fishing effort. It is expected that average biomass by depth strata will be higher during close than open fishing season. ANOVA tests were carried out to compare successive fishing seasons using as input the jack-knifed pseudovalues of the estimates of mean biomass for each cruise and depth strata.

42. **Results**

43. Long term fishing disturbances: ABC curves

44. The biomass and abundance curves show the community is in a permanent state of disturbance in both depth strata (Fig. 3). The fact that abundance curves are under biomass curves or both are close indicate a gross to moderate perturbation state (Clarke and Warwick, 1994). Important differences were also evident among cruises and depth strata.

45. Short-term fishing disturbances: Comparison of successive open and close fishing seasons

46. A low percentage (31%) of comparisons carried out between successive open and close seasons for the different DCS showed results in agreement with theoretical predictions about the effects of fishing disturbances. The W-statistic (in both depth strata), spatial segregation (shallow stratum) and species richness (shallow stratum) were the descriptors with less agreements recorded (14.3%), and the most successful was the biomass (in deep stratum; 57.1%, and in shallow 42.9%) followed by Shannon index (42.9% in both depth strata). Comparisons of cruises DEM 2 and DEM 4 showed the higher percentage of agreements with hypothesis with 83.3 % of agreement in deep stratum and 33.3% in the shallow one. In the opposite extreme, DEM 1 vs. DEM 3 and DEM 4 vs. DEM 5 showed no agreements in the shallow stratum and DEM 1 vs. DEM 3 in a deep stratum.

47. Interannual trends in DCS

48. No patterns were observed in the significance of the interannual trends (Table 3). The W-statistic and NSSD slope, did not show significant trends, although the other DCS showed a significant trend in at least one depth stratum. The spatial segregation index, biomass and species richness, showed significant linear fits ($P<0.05$) in the deep stratum, whereas in the shallow strata a significant trend was observed only for the Shannon index and biomass (Fig. 4).

49. **Discussion**

50. A permanent moderate to strong state of disturbance was detected in our study area using ABC curves. In other trawled seabed grounds chronic fishing has caused a shift to communities dominated by small-body fauna, reaching an alternative stable state (Kaiser et al., 2000), that is independent of the level of the fishing effort applied.

51. A biomass size spectrum is the distribution of biomass per unit area as a function of body size in an ecosystem (Schwinghamer, 1981) and it is a considered temporally stable property, in absence of major disturbances (Duplisea and Kerr, 1995; Duplisea et al., 1997; Pope et al., 1988; Sheldon et al., 1972, 1973). In our data,

stability was only observed on the shallow stratum. In the deep stratum differences between successive open-close fishing seasons were detected in most of cases, which suggest a continuous modification of the species size structure, but no clear trend was evidenced. The steepest value of the slope estimate of the NSSD was recorded during DEM 4, when the highest biomass was also recorded. A steep slope value could evidence strong fishing on large sized organisms and/or the increase of small-sized organisms. In this work, a proliferation of the small-sized species combined with a reduction of average body size of most of the dominant species, determined the steep NSSD slope value and the highest biomass during DEM 4. The steep slope during this period could not be attributed to fishing effects, because the cruise was carried out at the end of the close season.

52. The effects of trawling disturbance on body-size structure-production relationship is poorly understood (Jennings et al., 2001). However, it is reasonable to expect trawling disturbance to affect size structure and production, because trawling-induced mortality is positively correlated with body size (Bergman and van Santbrink, 2000; Lindeboom and De Groot, 1998), and because there are close relationships between body size distributions and production (Brey, 1999). There are consistent links between body size and life history characteristics. Increased body size is correlated with lower natural mortality, slower growth, lower annual reproductive output, increased longevity and lower intrinsic rates of natural increase (Brey, 1999; Charnov, 1993), and as conclusion, production to biomass ratios (P:B) are inversely related to the body size (Brey, 1999). This suggests that intensive trawling may favour smaller species and, since these have higher P:B ratios, they may be more productive and compensate for the loss of production from larger species (Jennings et al., 2001). In spite of some studies that suggested that trawling disturbance produces an effect of "farming the sea" ploughing the seabed to boost production (Jennings et al., 2001), the positive relation between fishing effort and benthic productivity is far to be established, and the hypothesis most accepted actually is that trawling is assumed to damage key functional processes (Jennings and Kaiser 1998, Jennings et al., 2001).

53. Biomass levels varied several times in DEM 4 cruise respect to the rest of the cruises, which could not be explained by an increase of the macroinvertebrate production rate attributed to anthropogenic causes. This biomass variation could be related to alterations in seasonal patterns probably associated to interannual processes. It is not possible to assume that a production rate increase, however,

environmental disturbance could favour locally the increase of population growth of a few species or the movement and concentration of these species on shallower waters. The life histories of benthic organisms are closely linked to the natural disturbance regime (Grassle and Sanders, 1973). Large-scale natural disturbances, such as seasonal and strong tidal currents, form a background against which other smaller disturbances, such as those induced by predator feeding occur (Hall et al., 1994). In spite of predation disturbance is considered as small-scale source of disturbance, Hall et al. (1994), suggest that predator disturbance has a considerable additive influence on benthic communities.

54. Interannual trends were more evident in the deep stratum especially in descriptors such as spatial segregation, Shannon diversity index, biomass and species richness (Fig. 4). The trend in the slope of the spatial segregation suggests that fishing effects are not important over time, and confirm a relaxation of fishing disturbance. According to Levine (1976) and Vandermeer (1980), in communities regulated by interspecific interactions, a high intensity of predation can alter the strength of competitive interactions and allow for increased coexistence of competitive species, and thus Blanchard (2001) proposes that exploitation by fishing would have similar effects. A strong trend of increasing species dominance, as it is showed, could preclude the detection of a decreased coexistence in successive close-open fishing seasons. The Shannon index show in both strata a negative trend suggesting a loss of diversity due to a decline in richness and a consequent decline in evenness. This evidence is stronger in the deep than the shallow strata, and could suggest a community shift where the dominance pattern of a few species is emphasized, whereas the biomass is growing constantly.

55. In general the immediate impact of fishing disturbance on benthic communities vary significantly with gear type, habitat and taxa (Collie et al., 2000). It has been possible to demonstrate short-term changes in benthic fauna using relatively small-scale field studies with experimental trawling (Bergman and Hup, 1992; Kaiser and Spencer, 1996; Thrush et al., 1995; Tuck et al., 1998), however the conclusions generated could not be applied to the large-scale disturbance regime imposed by a commercial fishing fleet (Kaiser et al., 2000). Apparently the small-scale disturbance events, even frequent, are either masked by the background of large-scale disturbances, or that the scale of disturbance is small enough to allow rapid recolonization such that large-scale effects never become apparent (Kaiser and Spencer, 1996). The small spatial scale of most of the trawl impact studies make it

likely that much of the recolonization was through immigration into disturbed patches, rather than reproduction within patches (Collie et al., 2000). In our study we assume that the seasonal bathymetric movement pattern could mask the open-close fishing effects. However besides of the scale factors and the limitations of the methods, the stronger signals due to seasonal and interannual natural changes restrict the possibility of finding evidence of fishing impact in a open-close experimental design and of making short-term forecasts of fishing effects.

56. It is clear that fishing has produced a chronic state of disturbance on the macroinvertebrate community of the Mexican Tropical Pacific in spite of short-term fishing evidences being masked by natural seasonal and interannual variability. However the role of fishing as a cause of variability in the seasonal pattern in a community has not been understood. It is probable that size structured interactions occur between the benthic fishes and the benthic invertebrates (Boudreau and Dickie, 1992), and, due to a differential survival rate after capture by trawls between teleost species (90% die) and other taxa such as crustaceans (much lower mortality) (Hill and Wassenberg, 1990; Wassenberg and Hill, 1989), fishing alterations enhance the natural-caused population fluctuations that originate peaks in the biomass of the small-sized species following peaks in fish predator species, in a unknown delayed pattern.

57. **Acknowledgements**

59. **References**

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124. **Figure Caption**

125. Figure 1. Location of the study area and sampling sites. Shaded rectangles represent the depth range of the sampling zones.

126. Figure 2. Timing of the cruises in relation to the main hydroclimatic events and seasonality of the shrimp fishery in the study area. Sea-surface temperature (SST) is taken from Filonov et al., (2001) and non-published oceanographic data.

127. Figure 3. Abundance-biomass curves (ABC) for each cruise and depth strata.

128. Figure 4. Temporal trends of the descriptors of community structure along the five cruises in each depth strata. Mean and 95% confidence interval are represented. a) W-statistic, b) biomass spectra, c) spatial segregation, d) Shannon diversity, e) biomass, and f) species richness.
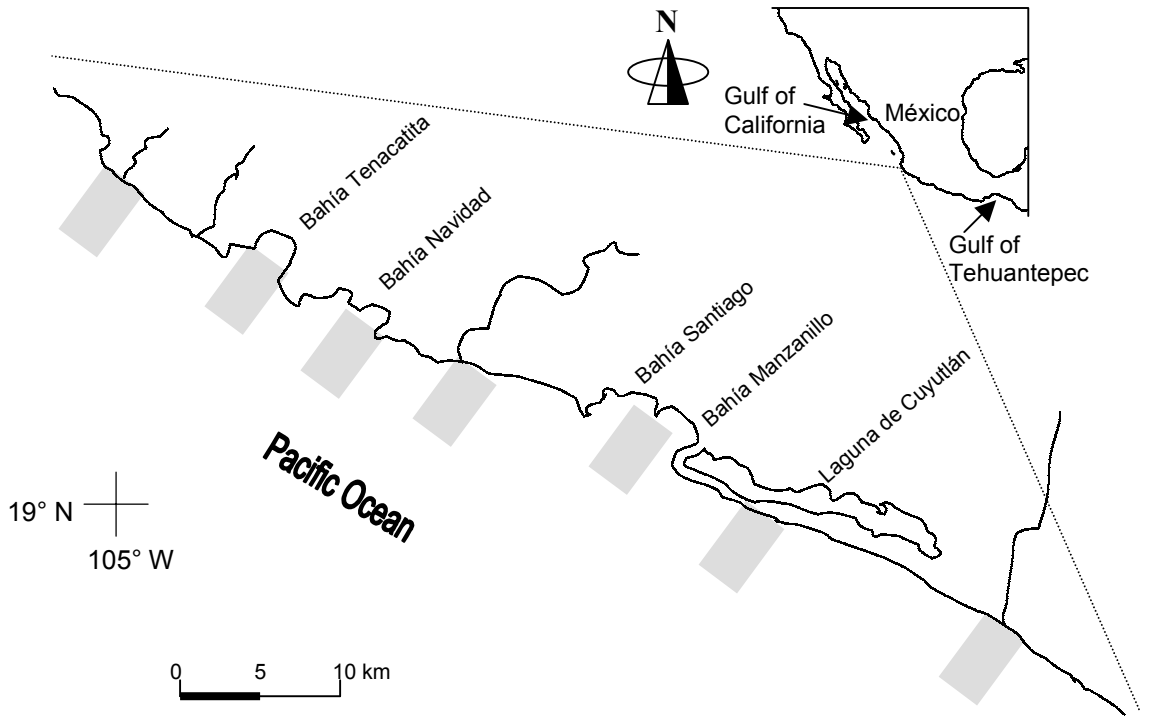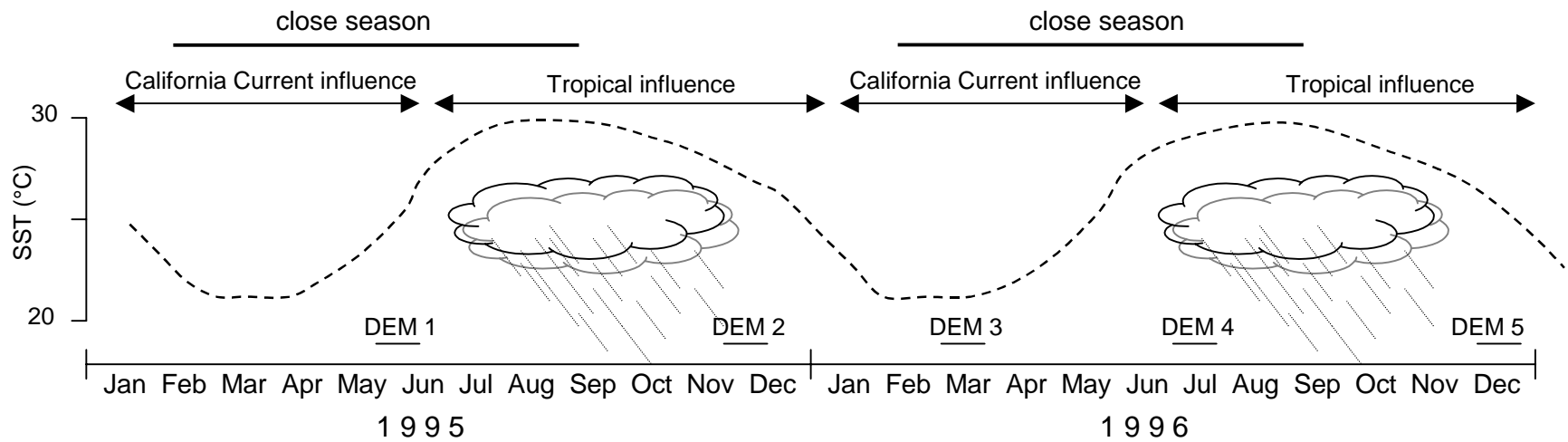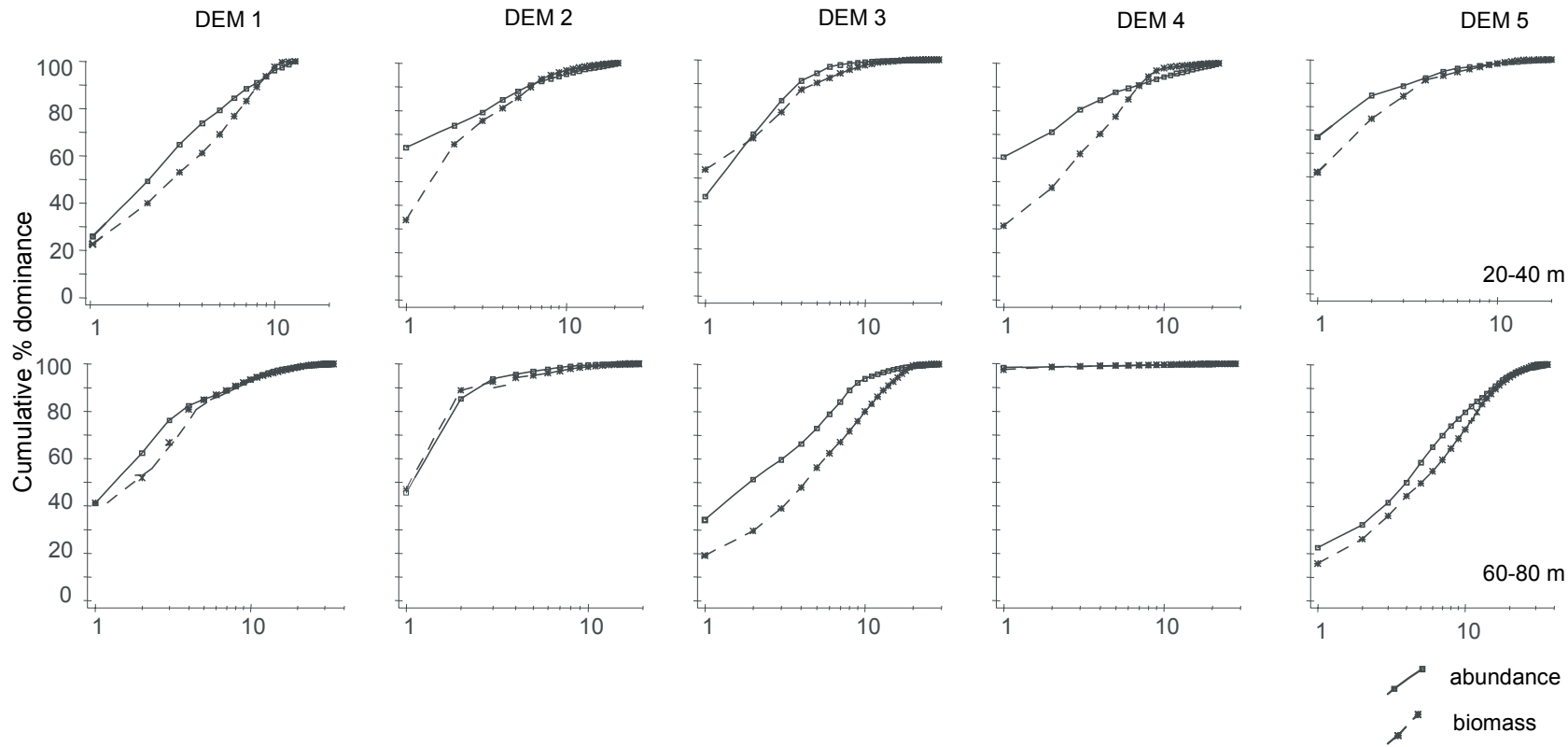
Figure 1. Godínez-Domínguez

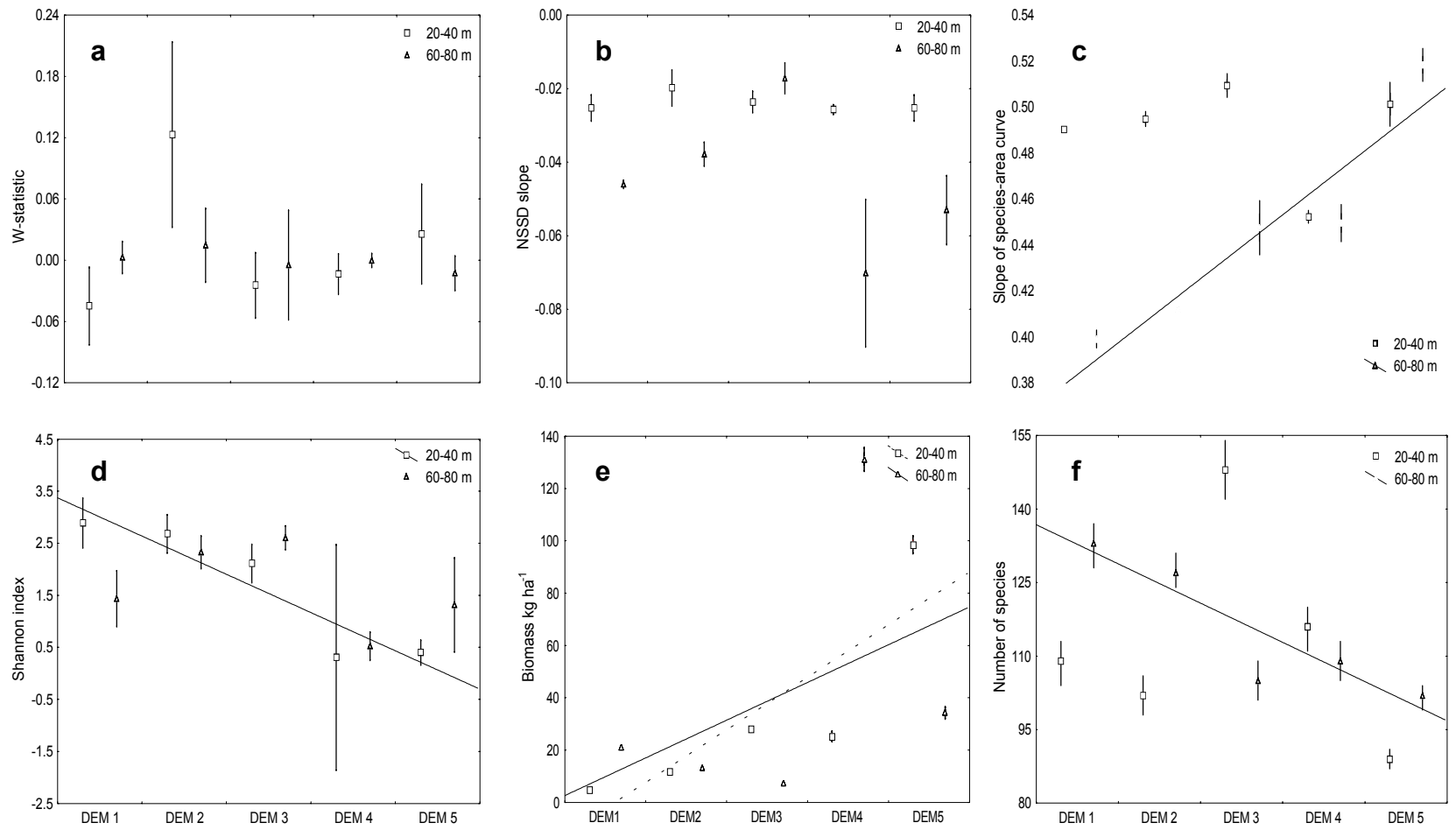Figure 2. Godínez-Domínguez et al.

Figure 4. Godínez-Domínguez et al

Table 1. Main potential sources of variability in the benthic communities in the study area, arranged according to their cause and time scale. For each category, the characteristics and information available respect to the study area are provided and hypothesis about their effects in benthic communities are stated. DCS = descriptors of community structure.

Time scale

	Seasonal	Interannual
Natural	Hydroclimatic season*: -Tropical (June-December) -Subtropical-Temperate (January-May) **Hypothesis**: Cause seasonal fluctuations in DCS.	It is still unknown the ENSO effect in local communities, however is considered an important source of disturbance in soft bottom habitats. The study was carried out during an interENSO event, previous to strongest (1997-1998) anomalous event of the 20th century **Hypothesis**: Interannual natural disturbances cause long-term trends in DCS
Anthropogenic	Fishing is an important disturbance source that could modify natural seasonal patterns.The vulnerability to fishing is depends on structural community features and life histories (Jennings et al., 2001). **Hypothesis**: Seasonal fishing disturbances cause changes in DCS between succesive open and close seasons. See table 2 for details.	No important changes in communities are expected. Unavailable information about the unfished community. An slight stable of chronic disturbance is expected. **Hypothesis**: Interannual fishing disturbances cause, 1) chronic change in ABC curves, and 2) long-term trends in DCS.

Causes

*Seasonal pattern showed on zooplankton (Franco-Gordo et al., 2001 a;b; 2002), coastal fishes (Godínez-Domínguez et al., 2000), soft bottom macroinvertebrates (Godínez-Domínguez and González-Sansón, 1998; 1999) and dynamics of coastal masses of water (Filonov, et al., 2000).

Table 2. Short-term expected responses of community structural descriptors to fishing distrurbances. Pairs of cruises represent succesive open and close fishing seasons. The significance and sign of the expected effect are showed, in agreement with the hypotheses proposed about the effects of the fishing in each descriptor. (=) no changes between cruises are expected (>) a higher value of the response parameter is expected from the first than the second cruise, and vice versa (<).

Cruises	Fishing season	W-statistic	NSSD slope	Species-area curves slope	Shannon index	Species richness	Biomass
DEM 1 vs. DEM 2	close vs. open	>	<	>	<	<	>
DEM 1 vs. DEM 3	close vs. early close	=	=	=	=	=	=
DEM 2 vs. DEM 3	open vs. early close	<	>	<	>	>	<
DEM 2 vs. DEM 4	open vs. late close	<	>	<	>	>	<
DEM 3 vs. DEM 4	early close vs. late close						
DEM 4 vs. DEM 5	late close vs. open	>	<	>	<	<	>

Table 3. Results of ANCOVAs carried out with each community descriptor and depth stratum to test the existence of a linear temporal trend during the five cruises.

	20-40 m		60-80 m	
	F	P-level	F	P-level
W-statistic	0.02	0.96	0.87	0.35
NSSD slope	1.11	0.29	2.78	0.11
Species-area curves slope	1.21	0.27	269	<0.001
Shannon index	19.8	<0.001	4.14	0.04
Species richness	38.04	<0.001	111.14	<0.001
Biomass	179.21	<0.001	17.91	<0.001

Table 4 Results of ANOVAs carried out to compare the descriptors of community structure in succesive open-close fishing season.

	DEM 1 vs. DEM 2				DEM 1 vs. DEM 3				DEM 2 vs. DEM 3				DEM 2 vs. DEM 4				DEM 3 vs. DEM 4				DEM 4 vs. DEM 5				agreements (%)
	F	P-level	observed	expected	F	P-level	observed	expected	F	P-level	observed	expected	F	P-level	observed	expected	F	P-level	observed	expected	F	P-level	observed	expected	
W-statistic																									
20-40 m	11.21	<0.001	<	>	0.64	0.42	=	>	9.06	<0.001	>	<	8.31	<0.001	>	<	0.33	0.56	=		2.14	0.15	=	>	1 (14.3)
60-80 m	0.35	0.55	=	>	0.06	0.79	=	>	0.34	0.56	=	<	0.62	0.43	=	<	0.02	0.86	=		1.86	0.18	=	>	1 (14.3)
NSSD slope																									
20-40 m	0.14	0.71	=	<	0.04	0.84	=	=	0.02	0.86	=	>	0.22	0.64	=	>	0.07	0.79	=		0.003	0.95	=	<	2 (28.6)
60-80 m	22.2	<0.001	<	<	5.57	0.02	<	=	6.5	0.03	<	>	13.8	<0.001	>	>	15.02	<0.001	>		0.49	0.51	=	<	2 (28.6)
Slope of Species-area curve																									
20-40 m	6.49	0.01	<	>	50.11	<0.001	<	=	21.63	<0.001	<	<	369.4	<0.001	>	<	360.5	<0.001	>		91.4	<0.001	<	>	1 (14.3)
60-80 m	32.2	<0.001	<	>	57.1	<0.001	<	=	33.6	<0.001	<	<	79.9	<0.001	<	<	0.07	0.78	=		91.4	<0.001	<	>	3 (42.9)
Shannon index																									
20-40 m	0.45	0.5	=	<	6.41	0.01	>	=	4.57	0.04	>	>	4.48	0.04	>	>	2.59	0.11	=		0.007	0.93	=	<	3 (42.9)
60-80 m	7.99	<0.001	<	<	15.45	<0.001	<	=	1.92	0.17	=	>	73.31	<0.001	>	>	132.2	<0.001	>		2.68	0.11	=	<	3 (42.9)
Biomass																									
20-40 m	1688	<0.001	<	>	1971	<0.001	<	=	905.7	<0.001	<	<	174.7	<0.001	<	<	5.73	0.2	=		1392	<0.001	<	>	3 (42.9)
60-80 m	281.8	<0.001	>	>	1133	<0.001	>	=	346.3	<0.001	>	<	2716	<0.001	<	<	30221	<0.001	<		1466	<0.001	>	>	4 (57.1)
Speceis richness																									
20-40 m	892.8	<0.001	>	<	25.15	<0.001	<	=	2317	<0.001	<	>	5.68	0.02	<	>	1359	<0.001	>		117.7	<0.001	>	<	1 (14.3)
60-80 m	3239	<0.001	>	<	2029	<0.001	>	=	120.4	<0.001	>	>	389.8	<0.001	>	>	904.5	<0.001	<		113.6	<0.001	>	<	2 (28.6)
agreements 20-40 m (%)	0				1 (16.7)				3 (50)				2 (33.3)				5 (41.7)				0				
agreements 60-80 m (%)	3 (50)				0				2 (33.3)				5 (83.3)				4 (33.3)				1 (16.7)				