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# Long-term stability of eelgrass fish assemblages in two highly developed coastal estuaries

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**Abstract** Changes in fish assemblages were tracked in representative eelgrass (*Zostera marina* L.) beds within two estuaries on the urbanised coast of southern California, USA, San Diego Bay and Mission Bay, from 1987 to 2010. Assemblages were sampled twice yearly (spring and summer) at day and night using beach seines. Assemblage stability was examined over time along with changes in assemblage structure across time of day and season, including the influence of temporally variable abiotic variables. Only the occasionally occurring fish, those present in <70% of samples, in Mission Bay appeared to be shifting to a new assemblage. Although season and sampling time significantly affected assemblages, correlations with abiotic factors were low. Given the long history of urban development of these estuaries, community shifts may have occurred prior to the onset of sampling, giving the appearance of stability. Alternatively, eelgrass habitat may be providing a refuge from long-term disturbances.

**KEY WORDS:** eelgrass, estuary, fish assemblage, stability, urbanisation.

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## Introduction

Biological communities change over space and time from the interplay of abiotic and biotic factors (Sousa 1984; Ricklefs 1987; Collins 2000; Rehage & Loftus 2007). Changes in community members or their abundances may be temporary and result from single pulse disturbances, after which stable communities may return rapidly to equilibrium (Bender *et al.* 1984; Yount & Niemi 1990). By contrast, long-term changes in ecosystem condition, termed press disturbances, may sustain community shifts (Bender *et al.* 1984; Yount & Niemi 1990). In this scenario, the press disturbance may lead to a new state with a different equilibrium community (Bender *et al.* 1984; Ives & Carpenter 2007). Density decreases in multiple migrant juvenile fish guilds as a result of long-term sediment contamination (e.g. Courrat

*et al.* 2009) are an example of an assemblage change due to a press disturbance. Changes in community composition are a valuable metric for ecosystem health, defined as proximity of structural and functional properties to a reference or undisturbed state, because communities respond to environmental changes and, thus, are indicative of shifts or disturbances in habitat health (Cairns *et al.* 1993; Bond *et al.* 1999).

Coastal estuaries are highly productive, primarily marine (low freshwater inflow) ecosystems that provide habitat to numerous commercially and recreationally important fishes (Jenkins & Wheatley 1998; Forrester & Swearer 2002; Lugendo *et al.* 2005). These habitats are often used as nurseries for coastal fishes as they provide shelter from predation and high-energy ocean conditions, as well as greater access to prey items (Barry & Cailliet 1981; Tupper & Boutilier 1997; Beck *et al.* 2001; Fodrie

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*et al.* 2009). Moreover, eelgrass, *Zostera marina* L., that frequently grows on soft substrate within these coastal estuaries increases three-dimensional habitat structure, providing protection for juvenile fishes (Hoffman 1986). Habitats that provide nursery function are vital for fish populations because they can alleviate the bottlenecks that often occur in early life-stages by decreasing predation risk and increasing growth rates (Irlandi & Crawford 1997; Limburg 2001). Thus, because juvenile fish and later stages of certain fish species are dependent on these seagrass beds for survival, changes in fish assemblages in particular provide a biologically meaningful measure of habitat health as well as insight into habitat productivity.

In southern California, estuaries and lagoons historically covered approximately 220 km<sup>2</sup> of the coastline. Throughout California, population growth and development throughout the 20th century has resulted in the reduction of wetland habitat area by over 90% (Zedler 1996; Larson 2001). The remaining habitats are anthropogenically altered by waste inputs, shoreline manipulation and invasive species, resulting in diminished water quality, habitat fragmentation and changes in species composition. While there is no estimate of historic eelgrass coverage throughout southern California's bays and estuaries, decreased water quality, channel dredging to depths below the limits of eelgrass survival and construction of docks and piers that shade eelgrass habitat have eliminated much of its historic habitat. In impacted systems such as these, it is likely that previously diverse biological communities have changed directionally towards dominance by tolerant and generalist species (Weaver & Garman 1994; Bilkovic & Roggero 2008). Under these chronic, or press, disturbances, community change is likely to occur over many years rather than as an immediate transformation after a catastrophic incident, or pulse disturbance, such as an oil spill (Konrad & Booth 2005). Development over the past century of southern California estuaries may have slowly changed the fish assemblage (e.g. Marvier *et al.* 2004; Devictor *et al.* 2008). In addition, projections of climate change and persistent population growth suggest anthropogenic pressures on California coastal ecosystems will only continue to intensify and influence biological communities (Whitfield & Elliott 2002; Harley *et al.* 2006). Understanding how communities respond to the long term, diverse pressures in urbanised systems will aid in focusing management efforts and offsetting these impacts, as well as in developing their use as indicators of habitat health.

Long-term community data are invaluable for establishing a system's biological baseline to understand the consequences of anthropogenic impacts (Connell *et al.*

2008) and for examining environmental changes over time (Perry *et al.* 2005). Unfortunately, because of the time and resources required, such datasets are relatively rare in the literature. An additional benefit of long-term data is the ability to analyse stability, defined as resistance to changes in composition over time, as an indicator of changes in ecosystem health (Cairns *et al.* 1993; Fleeger *et al.* 2003; Rohr *et al.* 2006). Univariate response variables, such as species diversity and species richness, may be too coarse to describe complex long-term community dynamics (Collins *et al.* 2008). Instead, multivariate techniques are used to tease apart more complex community changes (Hewitt *et al.* 2005). Fish assemblages are ideal candidates for long-term studies of habitat health because they typically encompass a range of life histories, trophic levels and functional guilds that may express variable responses to stressors (Araújo *et al.* 2000; Harrison & Whitfield 2004). In addition, many fish are relatively long lived, can disperse away from stressed habitats and have economic and recreational importance (Whitfield & Elliott 2002). In this study, an eelgrass bed fish assemblage was sampled in two adjacent, impacted estuaries twice annually during both day and night for 24 years to examine long-term dynamics and assemblage stability in two estuarine eelgrass beds with densely populated and urbanised surroundings. In both bays, fish assemblages are hypothesised to show directional change over time as development increases around these estuaries.

## Methods

### Study site

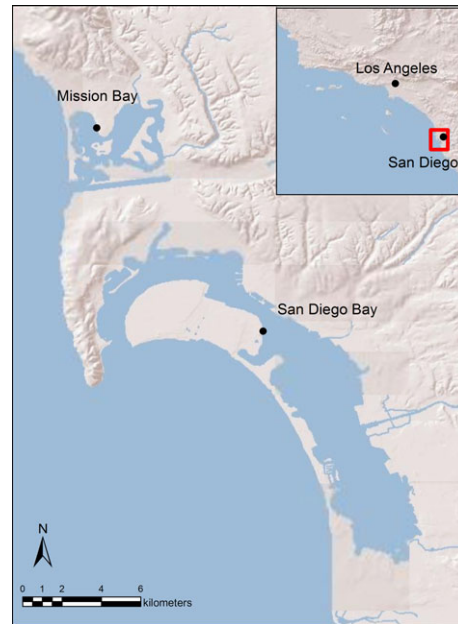
Data were collected in San Diego Bay and Mission Bay, two highly developed coastal estuaries located in San Diego, California, USA. San Diego Bay (32.68 N, 117.15 W) abuts downtown San Diego and has a surface area of 49 km<sup>2</sup>. It is located within the Pueblo, Sweetwater and Otay watersheds that total approximately 1150 km<sup>2</sup>. The primary land uses within these watersheds are urban or residential with an estimated 950 000 residents total. San Diego Bay is primarily influenced by mixed semidiurnal tidal flux as freshwater input is mostly limited to rain events. It also serves as a major seaport for the US Navy as well as many recreational vessels. Water quality was severely compromised in San Diego Bay during the early and mid-20th century from sewage discharge, industrial waste and oil leaks (Peeling 1974). Regulations enacted in the 1960s through 1990s improved water quality, although anthropogenic toxins remained in the sediments for decades and continue to be present in those locations that have not been subject

to mandated contaminant remediation (Fairey *et al.* 1998). Eelgrass is abundant in southern portions of San Diego Bay where little dredging has occurred but is relatively sparse in northern sections of the bay that are more developed and have been deepened for large vessels. Total eelgrass coverage in San Diego Bay was estimated at 5.3 km<sup>2</sup> in 2008 (Merkel & Associates, Inc 2009).

Mission Bay (32.78 N, 117.23 W) is a 17.1 km<sup>2</sup> coastal estuary several miles north of downtown San Diego. It is located within the Mission Bay Watershed that is 174 km<sup>2</sup> and contains approximately 236 000 residents. The primary land uses in the watershed are residential, commercial/industrial and parkland. Freshwater input into Mission Bay is also limited mainly to rain events and, thus, is primarily influenced by mixed semi-diurnal tidal flux. Once a tidal marsh, dredge and fill activities changed Mission Bay into an aquatic recreational park with over 5 000 000 visitors annually, although a few remnant marshes are still present (Gabrielson 2002). Total eelgrass coverage in Mission Bay was estimated at 4.0 km<sup>2</sup> in 2013 (Merkel & Associates, Inc. 2013). While it never received the industrial pollution of San Diego Bay, Mission Bay does receive urban run-off and disturbance from recreational activities and private boat storage. Despite these disturbances, the eelgrass beds in each bay have proven resilient and represent a large proportion of eelgrass habitat in southern California (Olsen *et al.* 2014).

### Sampling methods

Sampling of nearshore fish assemblages was conducted during spring and summer months in San Diego and Mission Bays from 1987 through 2010. Samples were taken at one location in each bay: north of the Coronado Bridge on the western coast of San Diego Bay (32.69, -117.16) and the eastern coast of Sail Bay in Mission Bay (32.79, -117.24; Fig. 1). Eelgrass beds were persistent at each site throughout the sampling period (R. Hoffman, personal observation), although no data were taken on areal extent or density. Fishes were sampled using a 25-m beach seine (mesh size 5 mm) in nearshore (<40 m from shore) eelgrass beds. The seine was moved perpendicular to the shoreline starting from the bayward extent of the sampling area to the shoreline. A steeper intertidal/shallow subtidal slope in Mission Bay reduced the area available for sampling, resulting in shorter haul lengths compared with San Diego Bay. Thus, haul lengths were recorded for each event and catch was converted to fish ·25 m<sup>-2</sup> to standardise data. Sampling took place during consecutive daytime and night-time low tides because previous research has shown diel



**Figure 1.** Sampling locations in Mission Bay and San Diego Bay, California.

changes in fish assemblages that are associated with different foraging patterns (Robblee & Zieman 1984; Clark *et al.* 2003). All fishes were measured for standard length (mm), weighed (g), identified to species (with the exception of Gobiidae) and released. Gobiidae were only identified to the family level due to difficulty in reliable field identification. In some sampling events, topsmelt, *Atherinops affinis* (authorities for all fishes collected in this study are in Table 1), and shiner surfperch, *Cymatogaster aggregata*, were too abundant for the sampling crew to count efficiently. In these cases, a random subset of 100 individuals was measured and weighed. The mean weight was then divided into the total weight of the uncounted fish to estimate the total number of individuals (Hoffman 1986).

### Abiotic metrics

Environmental parameters included in the analysis were sea surface temperature (SST), salinity and precipitation as well as the climate indices North Pacific Gyre Oscillation (NPGO, DiLorenzo *et al.* 2008), El Niño (ENSO) and Pacific Decadal Oscillation (PDO, Mantua *et al.* 1997). Water temperature and salinity were included because they typically limit distribution in marine organisms. Salinity and SST data were obtained from the Scripps Pier long-term dataset available from the Southern California Coastal Ocean Observing System (2010). These data were considered to be accurate estimates of conditions at the sampling sites because both sites were close

**Table 1.** Mean densities of fish caught (fish·25 m<sup>-2</sup>) in each bay across each season and sampling time from 1987 to 2010

Species	Common name	Mission bay	San Diego bay
<i>Atherinops affinis</i> (Ayres)	Topsmelt	21.63	39.32
<i>Leuresthes tenuis</i> (Ayres)	California grunion	0	6.68
<i>Engraulis mordax</i> Girard	Northern anchovy	<0.01	3.76
<i>Cymatogaster aggregata</i> Gibbons	Shiner surfperch	0.8	1.44
Gobiidae	Goby family	0.78	1.43
<i>Anchoa compressa</i> (Girard)	Deepbody Anchovy	0.01	1.72
<i>Heterostichus rostratus</i> Girard	Giant kelpfish	0.45	1.15
<i>Syngnathus leptorhynchus</i> Girard	Bay pipefish	0.47	0.48
<i>Paralabrax nebulifer</i> (Girard)	Barred sand bass	0.18	0.34
<i>Anchoa delicatissima</i> (Girard)	Slough anchovy	<0.01	0.41
<i>Seriphus politus</i> Ayres	Queenfish	<0.01	0.27
<i>Micrometrus minimus</i> (Gibbons)	Dwarf perch	0.43	<0.01
<i>Paralabrax maculatofasciatus</i> (Steindachner)	Spotted sand bass	0.07	0.18
<i>Leptocottus armatus</i> Girard	Staghorn sculpin	0.13	0.14
<i>Hypsoblennius gentilis</i> (Girard)	Bay blenny	0.12	0.05
<i>Embiotoca jacksoni</i> Aggasiz	Black perch	0.14	0.02
<i>Albula vulpes</i> (Linnaeus)	Bonefish	0	0.05
<i>Hypsopsetta guttulata</i> (Girard)	Diamond turbot	0.01	0.05
<i>Gibbonsia elegans</i> (Cooper)	Spotted kelp fish	0.04	0.02
<i>Paralichthys californicus</i> (Ayres)	California halibut	0.03	0.02
<i>Paralabrax clathratus</i> (Girard)	Kelp bass	0.04	0.01
<i>Fundulus parvipinnis</i> Girard	California killifish	0.05	<0.01

enough to the mouth of the bay to receive adequate flushing (J. Largier, personal communication). Further from the mouth, both of these estuaries become hypersaline (Largier *et al.* 1997). Precipitation was included as a surrogate for pollution because the primary mode of contaminant introduction into these estuaries is urban run-off (e.g. nutrients resulting in bacterial blooms and pesticides) and not point sources (DiGiacomo *et al.* 2004). Precipitation data were obtained from a compilation of historic National Weather Service data for San Diego (Stokes 2010). Because these data are from a personal site and not a government or academic institution, results from 1987 to 2006 were validated with the Western Regional Climate Center database (2006). Data from the Western Regional Climate Center were not used in the analysis because data only extended to 2006. Climate indices (NPGO, ENSO, PDO) were included because the data were collected on a large enough time scale that they may influence changes in fish assemblages. Pacific Decadal Oscillation data were taken from the University of Washington Joint Institute for the Study of the Atmosphere and Ocean (Mantua & Hare 2010). ENSO data were taken from the National Oceanic and Atmospheric Administration (2010) and the NPGO index from DiLorenzo *et al.* (2008).

#### Data analysis

The length of each seine haul varied among sampling events; therefore, data were standardised by dividing

catch by sampling distance to give densities for each species. As sampling efforts were identical, data of night and day samples in both seasons were pooled within year to create a mean annual record for each sampling location. To examine coarse assemblage changes over time, means were used to calculate standard univariate diversity measures including the Shannon–Wiener index and species richness density, which was used because variable seine lengths would bias absolute species richness values.

All data were analysed using the R programming language (version 2.15.3, R Core Team 2013). The effects of seasonal and diel sampling time as well as sampling location on assemblage structure were analysed using a two-way analysis of similarity (ANOSIM), a non-parametric permutation procedure. This procedure is used to test for differences between or among predetermined sampling groups by determining the distance (similarity) among these groups based on the relative abundance of species. A Bray–Curtis dissimilarity matrix was created using fourth root transformed relative fish abundance data. ANOSIM was performed on the Bray–Curtis dissimilarity matrix with time of day and season as factors. The test statistic, *R*, is constrained between  $-1$  and  $1$ , where positive values indicate differences among groups. To determine species-specific contribution to differences in the fish assemblage, a Similarity Percentages (SIMPER; R Package ‘Vegan’; Oksanen *et al.* 2013) procedure was performed on the assemblage relative

abundance data using time of day and season as factors. This procedure returns the species most responsible for assemblage differences between sampling groups. The effect of sampling location on assemblage structure was examined using a non-metric multidimensional scaling plot (NMDS; package 'Vegan'; Oksanen *et al.* 2013). This plot displays the relative association among species assemblages in each sample. The process of fitting multi-dimensional assemblage data into only a few axes (ordination) may cause a deviation in results. The measure of this distortion is 'stress', and it ranges from 0 to 1 where lower values indicate less distortion. The non-parametric BIO-ENV procedure (Clarke & Ainsworth 1993) was used to determine the effect of environmental data on assemblage structure. This method calculates the Spearman rank correlation ( $\rho$ ) between ranked fish assemblage and environmental similarity matrices based on Bray–Curtis distance. The correlation coefficients show the best combination of environmental variables that explain the biotic assemblage. All combinations of the environmental variables described above were included in the BIO-ENV analysis. Because assemblages from day and night samples were found to be different using ANOSIM ( $P = 0.002$ ,  $R = 0.08$ ), day and night data were analysed separately in the BIO-ENV procedure. Although there were also differences between spring and summer assemblages, they were analysed together because the environmental variables in the analysis should capture the seasonal changes. That is, the model incorporates variables such as temperature and salinity that vary seasonally and may drive assemblage changes. Only those species present in >15% of all sampling events were included in these analyses to reduce bias from rare species (McCune & Grace 2002). Density of those species in <15% of samples was compared before and after 2000 to determine whether any substantial changes occurred during the sampling period that would not have been evident in multivariate analysis.

Community stability over time was assessed with mean rank shift and time lag analysis. Mean rank shift measures the change in species rank abundance over time using the following equation:

$$\text{MRS} = \sum_{i=1}^n (|R_{i,t+1} - R_{i,t}|) / n \quad (1)$$

where  $n$  is the number of years,  $t$  is the year, and  $R_{i,t}$  is the relative rank of species  $i$  in year  $t$  (Collins *et al.* 2008). In unstable communities, species will exhibit high variation in relative abundance and therefore increased values of mean rank shift. This analysis is non-statistical but effectively illustrates relative stability (Robinson & Yakimishyn 2013), with lower values of mean rank shift

indicating a more stable community (e.g. <4; Collins *et al.* 2008). Estuarine fish assemblages are typically dominated by a subset of core species that may conceal changes in other species. Therefore, species found in over 70% of years were considered core species and analysed separately from occasional species (those found in <70% of years) in the mean rank shift analysis (Magurran & Henderson 2003; Robinson & Yakimishyn 2013).

Time lag analysis (Collins 2000) provides a statistical test for directional community change over time. Euclidean distance is calculated using mean annual density between each year combination within an estuary, then plotted against each time lag (the time difference between compared assemblages) from the sampling period. The results are used in a linear regression with Euclidean distance as the dependent variable and the square root of time lag length as the independent variable. The square root of the time lag is taken to reduce the effect of fewer data points at higher time lags. A significantly positive slope indicates the community is undergoing directional change towards a novel community, while a significantly negative linear regression line indicates the community is undergoing directional change towards the structure of a previously sampled assemblage (Collins *et al.* 2008). A non-significant regression suggests stochastic variation.

## Results

A total of 209 299 individuals of 50 species were caught during 168 sampling events in San Diego Bay and Mission Bay from 1987 to 2010. Densities were typically between 15 and 100 fish · 25 m<sup>-2</sup> in both sites. Fish density in Mission Bay fluctuated little throughout the sampling period, while fish density in San Diego Bay was more variable over time, increasing from 1998 through 2003, then decreasing through the conclusion of sampling in 2010 (Fig. 2). The density increase was related to higher catch of *A. affinis*, *Leuresthes tenuis*, *Anchoa delicatissima* and *Engraulis mordax*, although *A. affinis* was the only species with consistently high density during those years. A spawning event of *L. tenuis* at the sampling site and large schools of *A. delicatissima* and *E. mordax* were the other causes of density increase in San Diego Bay during that time period. Such schools were likely to be present in all years, but not encountered during sampling. *Atherinops affinis* was the most abundant species in both estuaries (Table 1). *Leuresthes tenuis* and *E. mordax* were almost exclusively found in San Diego Bay and only in a few samples. *Cymatogaster aggregata*, Gobiidae, *Heterostichus rostratus*, *Syngnathus leptorhynchus* and *Paralabrax nebulifer* were all common at both sampling sites.

Species richness density was generally higher and exhibited greater fluctuations in Mission Bay than in San Diego Bay (Fig. 3), although this may have been an artefact of shorter seine hauls; it is possible that the number of species in each haul from San Diego Bay and Mission Bay was similar, but that the increased length of San Diego Bay hauls decreased richness density. In contrast, and with only a few exceptions, Shannon–Wiener diversity was similar at both sampling sites over time and fluctuated together (Fig. 4). As most samples were dominated by a few species, the Shannon–Wiener index values were typically low, ranging between 0.5 and 1.

Assemblages differed significantly between seasons and sampling time for both San Diego Bay (two-way ANOSIM,  $P = 0.002$ ,  $R = 0.08$ ) and Mission Bay ( $P = 0.001$ ,  $R = 0.1$ ) and also differed between sampling sites ( $P = 0.001$ ,  $R = 0.07$ ; Fig. 5). SIMPER analysis found that *A. affinis*, *C. aggregata* and Gobiidae were typically responsible for the assemblage differences among the sample groups at the compared sampling times (Tables 2 and 3). In the analysis of rare fish in San Diego Bay, *Anchoa delicatissima* ( $0.57 \text{ fish} \cdot 25 \text{ m}^{-2}$ ), *Seriphus politus* ( $0.42 \text{ fish} \cdot 25 \text{ m}^{-2}$ ) and *Engraulis mordax* ( $1.22 \text{ fish} \cdot 25 \text{ m}^{-2}$ ) decreased from the first to the second sampling period, while *Anchoa compressa* ( $1.85 \text{ fish} \cdot 25 \text{ m}^{-2}$ ) increased. In Mission Bay, only *Micrometrus minimus* ( $0.81 \text{ fish} \cdot 25 \text{ m}^{-2}$ ) decreased

substantially, and no fish present in <15% of all samples increased notably.

According to BIO-ENV analyses, the correlation between abiotic factors and fish assemblage structure was low for all four combinations of season and estuary (San Diego Bay day and night, Mission Bay day and night; Table 4). Salinity, precipitation and water temperature were the most frequent factors influencing assemblages, although their effects were weak ( $0.058 \leq \rho \leq 0.291$ ; Clarke & Ainsworth 1993). Climatic variables were not considered important in structuring these assemblages, as the single significant climatic factor, ENSO, was only included in the best model output for the San Diego Bay day assemblage. However, small changes likely related to climate did occasionally occur. For example, the tropical species, *Albula vulpes*, was collected San Diego Bay following the strong ENSO event of 1998 but was absent in every other year.

In San Diego Bay, the core and occasional fish assemblage did not undergo directional change over the course of sampling, as indicated by an insignificant, though negative, linear regression in the time lag analysis (Fig. 6a and 6b; Core:  $F_{1,208} = 1.11$ ,  $P = 0.293$ ,  $\text{Adj } R^2 = 0.001$ ; Occasional:  $F_{1,208} = 2.502$ ,  $P = 0.115$ ,  $\text{Adj } R^2 = 0.007$ ). The core fish assemblage in Mission Bay also showed no directional change (Fig. 6c,  $F_{1,252} = 0.053$ ,  $P = 0.819$ ,  $\text{Adj } R^2 = -0.004$ ), but time lag analysis indicated the

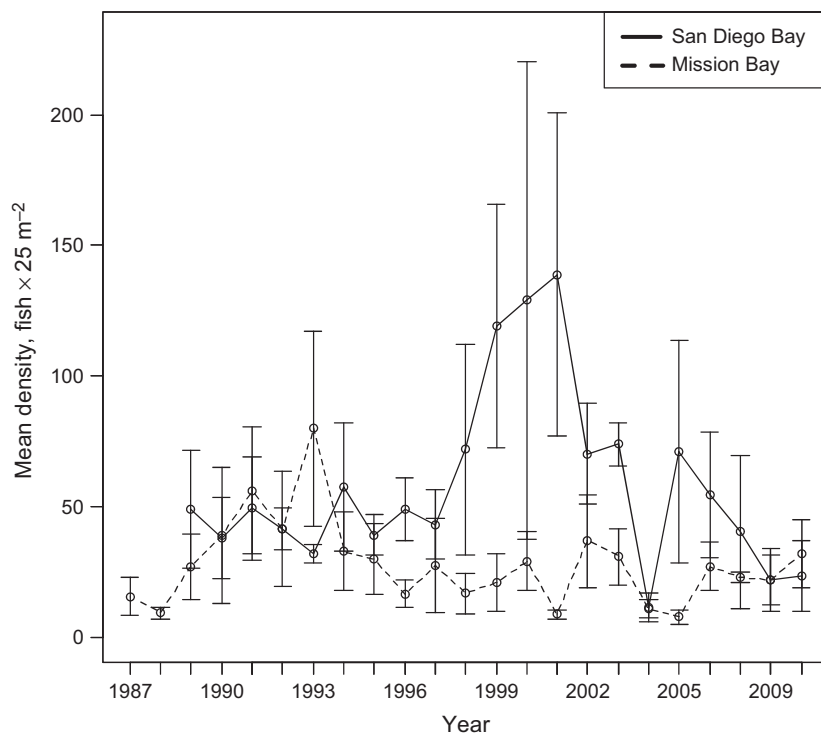


Figure 2. Mean total fish density per year in Mission Bay and San Diego Bay. Vertical bars are standard error.

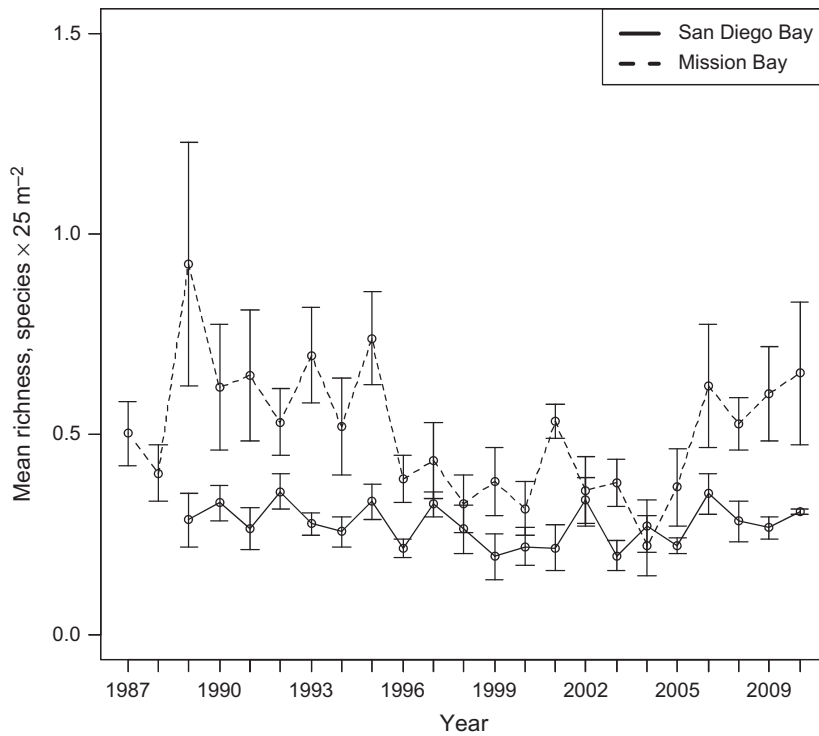


Figure 3. Mean fish species richness density each year in Mission Bay and San Diego Bay. Vertical bars are standard error.

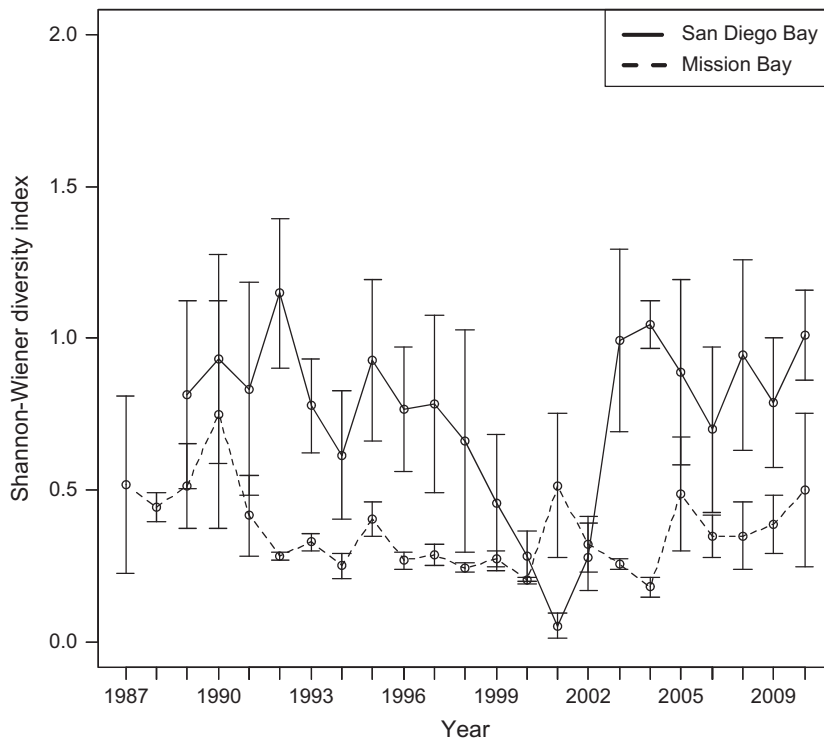


Figure 4. Mean Shannon-Wiener diversity index in Mission Bay and San Diego Bay, vertical bars are standard error.

occasional fish assemblage underwent directional change towards a new assemblage structure (Fig. 6d,  $F_{1,251} = 46.88$ ,  $P < 0.001$ , Adj.  $R^2 = 0.154$ ; Collins

2000). Mean rank shift, the measure of species abundance rank changes within a community over time, was similar for the core fish assemblages in Mission Bay and San



**Table 2.** San Diego Bay SIMPER results of pairwise comparison of assemblage composition during spring and summer seasons and day and night time sampling periods

Species	Spring day	Spring night	Contribution (%)
<i>Atherinops affinis</i>	0.723	0.539	40.36
<i>Cymatogaster aggregata</i>	0.095	0.209	23.55
Gobiidae	0.055	0.088	11.47
Total Abundance	39999	29447	

Species	Spring day	Summer day	Contribution (%)
<i>Atherinops affinis</i>	0.723	0.761	38.54
<i>Cymatogaster aggregata</i>	0.095	0.017	13.17
<i>Anchoa compressa</i>	0.011	0.052	8.77
<i>Heterostichus rostratus</i>	0.03	0.057	8.44
Total Abundance	39999	31348	

Species	Spring day	Summer night	Contribution (%)
<i>Atherinops affinis</i>	0.723	0.848	41.53
<i>Cymatogaster aggregata</i>	0.095	0.035	18.04
Gobiidae	0.055	0.014	9.82
<i>Heterostichus rostratus</i>	0.03	0.052	8.98
Total Abundance	39999	35050	

Species	Spring night	Summer day	Contribution (%)
<i>Atherinops affinis</i>	0.539	0.761	39.41
<i>Cymatogaster aggregata</i>	0.21	0.117	21.06
Gobiidae	0.088	0.014	8.94
Total Abundance	29447	31348	

Species	Spring night	Summer night	Contribution (%)
<i>Atherinops affinis</i>	0.539	0.848	44.97
<i>Cymatogaster aggregata</i>	0.21	0.035	23.8
Gobiidae	0.088	0.014	10.14
Total Abundance	29447	35050	

Species	Summer day	Summer night	Contribution (%)
<i>Atherinops affinis</i>	0.761	0.848	41.39
<i>Heterostichus rostratus</i>	0.057	0.052	11.27
<i>Anchoa compressa</i>	0.052	0.002	10.77
<i>Anchoa delicatissima</i>	0.053	0.001	10.71
Total Abundance	31348	35050	

Diego Bay, with a maximum value of 2.6 (Fig. 7). The occasional fish assemblage exhibited more variation than the core assemblage, with greater mean rank shift in both San Diego and Mission Bay and most values between two and six. From 2001 to 2005, mean rank shift in San Diego

**Table 3.** Mission Bay SIMPER results of pairwise comparison of assemblage composition during spring and summer seasons and day and night time periods

Species	Spring day	Spring night	Contribution (%)
<i>Atherinops affinis</i>	0.663	0.683	35.51
<i>Cymatogaster aggregata</i>	0.075	0.112	18.6
Gobiidae	0.061	0.054	11.55
Total Abundance	6784	9215	

Species	Spring day	Summer night	Contribution (%)
<i>Atherinops affinis</i>	0.663	0.911	43.21
<i>Cymatogaster aggregata</i>	0.075	0.005	11.78
Gobiidae	0.061	0.017	10.32
Total Abundance	6784	18140	

Species	Spring day	Summer day	Contribution (%)
<i>Atherinops affinis</i>	0.663	0.795	39.06
<i>Syngnathus leptorhynchus</i>	0.062	0.077	13.44
<i>Cymatogaster aggregata</i>	0.075	0.008	10.5
Total Abundance	6784	7745	

Species	Spring night	Summer night	Contribution (%)
<i>Atherinops affinis</i>	0.683	0.911	43.33
<i>Cymatogaster aggregata</i>	0.112	0.005	19.34
Gobiidae	0.054	0.017	8.82
Total Abundance	9215	18140	

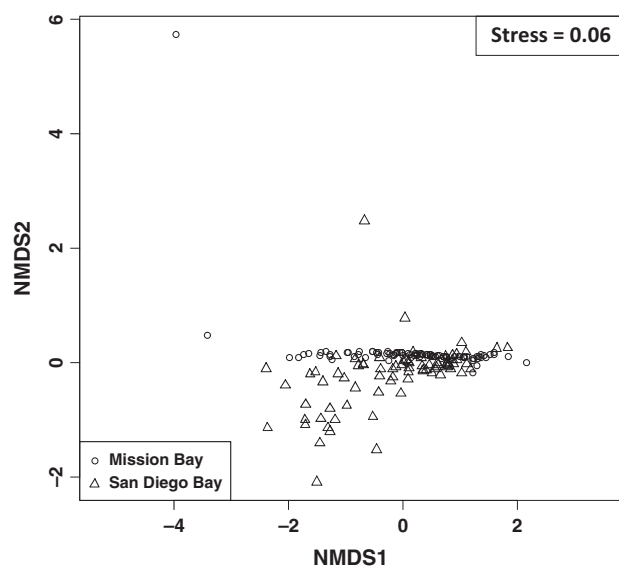
Species	Spring night	Summer day	Contribution (%)
<i>Atherinops affinis</i>	0.683	0.795	37.68
<i>Cymatogaster aggregata</i>	0.112	0.008	16.13
<i>Syngnathus leptorhynchus</i>	0.023	0.077	10.84
<i>Micrometrus minimus</i>	0.019	0.058	9.37
Total Abundance	9215	7745	

Species	Summer night	Summer day	Contribution (%)
<i>Atherinops affinis</i>	0.911	0.795	40.79
<i>Syngnathus leptorhynchus</i>	0.012	0.077	17.92
<i>Micrometrus minimus</i>	0.01	0.058	14.32
Total Abundance	18140	7745	

Bay was >5 and substantially higher (mean difference = 2.69) than Mission Bay.

## Discussion

Despite increasing urbanisation around both Mission Bay and San Diego Bay through the duration of



**Figure 5.** Non-metric multidimensional scaling plot of assemblage structure between San Diego Bay and Mission Bay.

**Table 4.** Best-fit models determining the explanatory role of environmental variables in fish assemblage composition using the BIO-ENV procedure; E = ENSO, P = precipitation, S = salinity and T = temperature

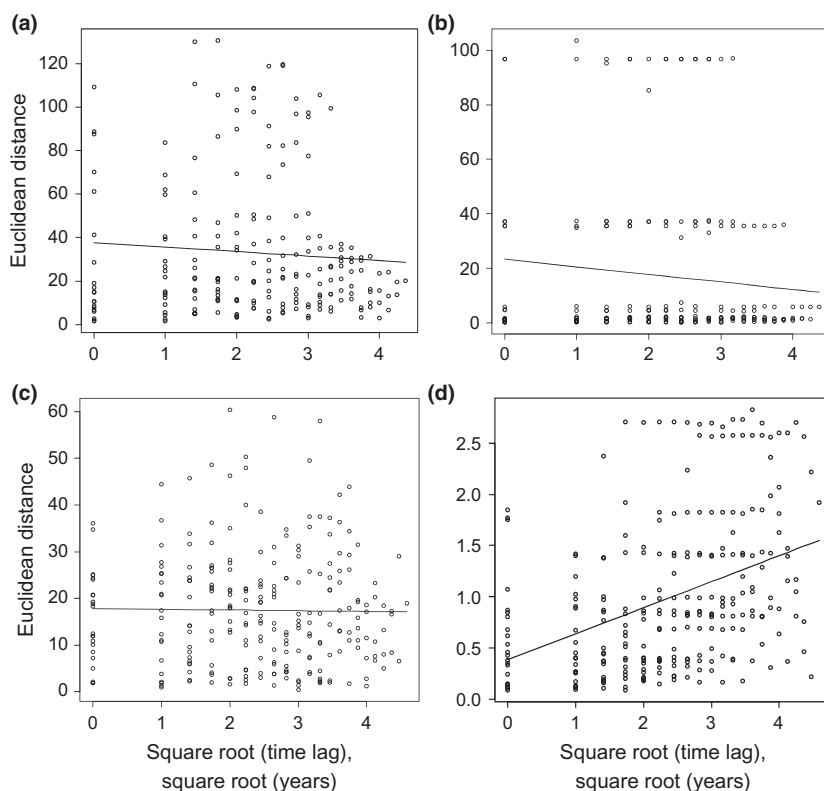
Location	Time of day	Correlation	Variables
San Diego Bay	Day	0.184	S, E
San Diego Bay	Night	0.291	P, T, S
Mission Bay	Day	0.058	P
Mission Bay	Night	0.241	P, T

sampling (Table 5), fish assemblages did not show large impacts or instability in richness, diversity or assemblage composition at either site with the exception of the occasional fish assemblage in Mission Bay. In fact, the fishes recorded during these sampling events were typical of other nearshore southern California estuarine assemblages (Allen *et al.* 1983, 2002). However, this is not a guarantee of habitat health as there are no pristine estuaries in southern California to serve as a baseline or reference. Six of the ten (e.g. *A. affinis*, *C. aggregata*, *E. mordax*) most common species encountered in this study were shared with other sampling efforts in San Diego Bay, suggesting a degree of similarity among studies, although they are not statistically comparable because data were collected using different methods (Allen *et al.* 2002). Relatively high flushing rates in both estuaries are likely to reduce local variation in physical conditions such as temperature and salinity and stressors such as pollution (Largier *et al.* 1997); thus, it is expected that assemblage structure will be more strongly driven by large-scale processes than local variability. As such,

eelgrass fish assemblages at these sites may be subject to similar disturbances as other eelgrass habitats within each of these systems. However, this study is not a comprehensive comparison of fish assemblages in each estuary, but instead an exploration of assemblage stability in two estuarine eelgrass beds with highly urbanised watersheds.

The persistence of eelgrass habitat throughout sampling in both the Mission Bay and San Diego Bay sites may have promoted stability by providing a productive, sheltered habitat for juvenile and adult fishes in spite of increasing urbanisation in the watershed and associated anthropogenic stressors. Substantial shifts occurred in demersal fish assemblages over 50 years of anthropogenic impacts in Lake Ponchartrain, Louisiana, where changes in nearshore fish assemblages were less pronounced and more diffuse, and the effects of development were more pronounced in deeper benthic habitat (O'Connell *et al.* 2004). In San Diego and Mission Bays, nearshore communities may be subject to less direct disturbance than deeper channels that are routinely dredged and, thus, may be more stable. However, it is possible that press disturbances are affecting these eelgrass assemblages, but changes in structure have remained undetected due to substantial time lags (Fitzgerald *et al.* 1998; Borja *et al.* 2010). In addition, future community changes may be accelerated by the combination of climate change with continued alteration of habitat and water quality. However, these data suggest that significant change has not occurred during the course of this study.

The long-term community change that occurred in the occasional fish assemblage of the Mission Bay sampling site, but not at the San Diego Bay sampling site, may be due to the longer history of human impacts in San Diego Bay. Thus, it is possible that the San Diego Bay fish assemblages had already undergone a major shift; unfortunately, baseline fish assemblage structure data prior to 1987 are not available. Both sampling locations are in urbanised estuaries that receive contaminated run-off (e.g. excess nutrients, pesticides), fishing pressure and continued coastal development. San Diego Bay, however, is likely a more disturbed system as it supports a major port complex, a large portion of the US Navy Pacific Fleet and has a substantially greater percentage of altered shoreline. In contrast, Mission Bay has historically been used for residential, commercial and recreational purposes. Despite improvements in water quality from the mid 20th century (Peeling 1974), sediments in the vicinity of the San Diego Bay sampling site are more toxic than those in the vicinity of the Mission Bay sampling site (Fairey *et al.* 1998). As a result, it is also possible that the fish assemblage in this vegetated section of



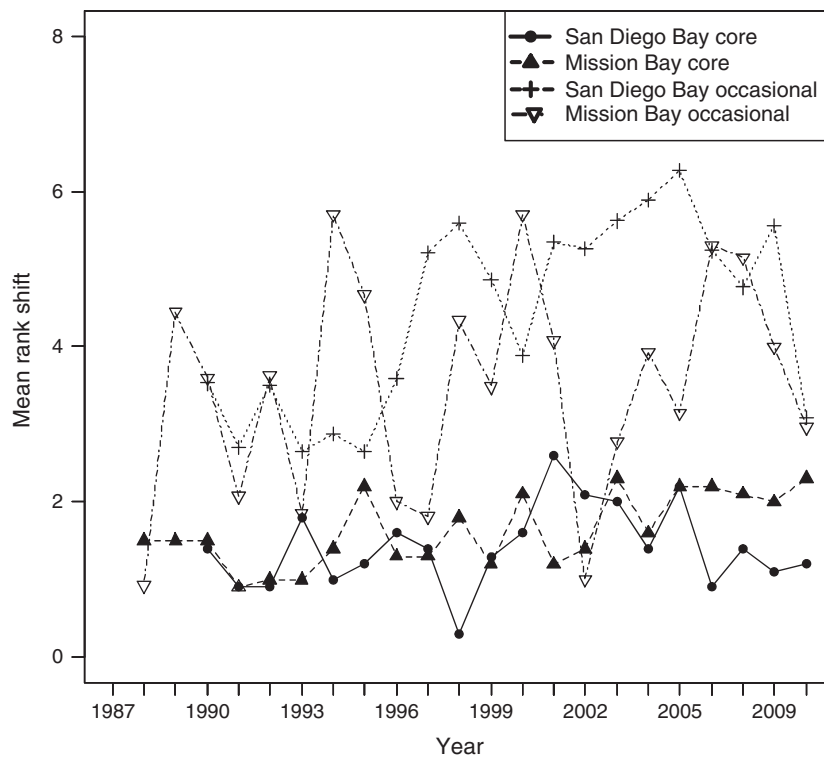
**Figure 6.** Time lag analysis of fish assemblages based on mean annual density for (a) the San Diego Bay core assemblage, (b) San Diego Bay occasional assemblage, (c) Mission Bay core assemblage and (d) Mission Bay occasional fish assemblage. Euclidean distance of each sample is plotted against the square root of time lag.

San Diego Bay shifted to its current composition before sampling commenced. The fish assemblage of the Mission Bay eelgrass habitat may still be changing towards a new assemblage.

Temporal variation in community assemblage is common in estuarine habitats (Rountree & Able 1993; Wilson & Sheaves 2001). Diel differences in both Mission Bay and San Diego Bay fish assemblage composition suggest differential habitat use, consistent with findings in other temperate and even tropical seagrass beds (Robblee & Zieman 1984; Yáñez-Arancibia *et al.* 1988; Guest *et al.* 2003; Ribeiro *et al.* 2006; Unsworth *et al.* 2007). Diel differences are attributed to increased foraging in seagrass beds at night. Data in this study support this hypothesis, as larger piscivores such as *Paralabrax* spp., which have been found to be nocturnal (Hobson & Chess 1986) and forage in eelgrass beds (Mendoza-Carranza & Rosales-Casián 2002), were more abundant at night. They were not abundant enough in the samples to be considered important in SIMPER analyses, although this result is notable because it suggests eelgrass is an important habitat for foraging in several recreationally important species. Studies in tropical habitats have shown that fishes move diurnally between seagrass beds

and mangroves or coral reefs (Unsworth *et al.* 2007). The only analogous habitats in the vicinity of the study area would be artificial reefs and breakwaters. These habitats are not native to coastal estuaries, but it is possible fishes have adapted diurnal movements to and from these habitats during the short time the structures have been in proximity to eelgrass. This hypothesis is consistent with a tracking study of adult *Paralabrax clathratus* that showed individuals exhibit a small home range and prefer high-relief habitat (Lowe *et al.* 2003). Therefore, it is possible that piscivorous fishes in these estuaries exhibit a narrow home range between heterogeneous habitat such as artificial reefs and eelgrass beds. Seasonal differences shown in fish composition were likely due to recruitment, which is more difficult to document as many of the fishes in eelgrass beds are juveniles regardless of season. While it is difficult to interpret these results in the context of urbanisation, they do provide important baseline for comparison with future studies in estuaries with similar urban settings.

Low influence of measured environmental parameters suggests biological controls may have greater importance structuring both assemblages. Low correlations between abiotic factors and fish assemblages (e.g. Malavasi *et al.*



**Figure 7.** Mean annual rank shift of core and occasional fish assemblages in Mission Bay and San Diego Bay.

2004; Arthington *et al.* 2005) have previously led researchers to suggest that biological variables often play a strong role in driving fish assemblage dynamics (Marshall & Elliott 1998). Alternatively, the abiotic variables included may not have encompassed the factors driving fish assemblage dynamics. Incorporation of additional variables into our model, such as water quality (e.g. dissolved oxygen, turbidity) and sediment (contaminant and nutrient concentration), may have increased model fit (e.g. Maes *et al.* 2004; Akin *et al.* 2005). The influence of salinity and temperature on San Diego Bay and Mission Bay fish assemblages, though not strong, corroborates similar findings in other temperate estuarine fish assemblages (Marshall & Elliott 1998; Malavasi *et al.* 2004). By contrast, precipitation is not often seen as a driver of assemblage structure. Its unexpected importance may relate to the structure of these habitats as well as the relative infrequency of precipitation. Because hydrodynamics in these estuaries are dominated by tidal flow and not riverine or freshwater input (Largier *et al.* 1997), infrequent pulses of freshwater input may have a disproportionate effect on fishes. In addition, these estuaries are surrounded by large areas of impervious surfaces. Therefore, precipitation may have a large effect on water quality (e.g. increase in pesticides, nutrient inflow and bacterial blooms) in comparison with rainfall volume (Ackerman & Weisberg 2003), which may

contribute to shifts in fish assemblages, most likely to an assemblage comprised of generalist species (Noble *et al.* 2003; Bilkovic & Roggero 2008). This suggests that the reduced water quality from urban run-off may have a short-term effect, as captured in the BIO-ENV, on fish assemblages in San Diego Bay and Mission Bay. Extension to other assemblages indicative of eelgrass bed habitat quality, such as nekton (Ralph *et al.* 2013), or vegetation type (e.g. presence of macroalgae; Dean *et al.* 2000; Murphy *et al.* 2000) may provide an additional means by which to detect habitat changes. Overall, the relatively low importance of environmental factors suggests that future research examining fish assemblage changes over time should include biological variables such as seagrass and macroalgal characteristics including both density and areal extent to provide a more complete examination of potential predictor variables.

While these assemblages show similarities to other estuarine habitats, it is difficult to draw conclusions on relative habitat health, as all southern California estuarine systems are affected by urbanisation. Moreover, as San Diego Bay is such a large system, it has been divided into four distinct ecoregions (Allen *et al.* 2002). Although Mission Bay is not as large, it is still likely that assemblages in the eastern portions of the estuary differ from those closer to the entrance channel. An examination of assemblage stability at a consistent location in each estuary, as was

**Table 5.** Compilation of metrics illustrating habitat and land-use changes in San Diego Bay and Mission Bay including their watersheds that may adversely affect fish habitat

Metric	Change	Range	Source
Watershed urban land use	12 536 ha increase (39%)	1985–2002	American Forests (2003)
Watershed grassland	9436 acre decrease (32%)	1985–2002	American Forests (2003)
Watershed shrubland	1056 acre decrease (7%)	1985–2002	American Forests (2003)
Population (City of San Diego)	1 283 917 person increase	1900–2010	Sandiegohistory.org, San Diego Association of Governors
San Diego Bay dredge projects (count)	23	1979–2010	NMFS EFH Files
Mission Bay dredge projects (count)	12	1979–2010	NMFS EFH Files
San Diego Bay eelgrass mitigation projects (count)	27	1976–2010	California Eelgrass Mitigation Policy (U.S. Department of Commerce, National Marine Fisheries Service 2014), NMFS EFH Files
Mission Bay eelgrass mitigation projects (count)	11	1982–2010	California Eelgrass Mitigation Policy (U.S. Department of Commerce, National Marine Fisheries Service 2014), NMFS EFH Files
San Diego Bay intertidal habitat	84% decrease	1859–2007	San Diego Integrated Natural Resources Plan
San Diego Bay soft shoreline	74% decrease	1859–2007	San Diego Integrated Natural Resources Plan
San Diego Bay shallow subtidal habitat	41% decrease	1859–2007	San Diego Integrated Natural Resources Plan

Changes in land use from 1985 to 2002 were calculated in GIS using satellite imagery and covered both San Diego Bay and Mission Bay watersheds. Population change was taken from US Census data. A count of dredge projects within each bay was assembled from National Marine Fisheries Service (NMFS), Southwest Regional Office Essential Fish Habitat (EFH) consultation files. NMFS has an obligation to provide recommendations through the EFH consultation process to avoid, minimise or offset impacts from development projects funded, authorised or performed by federal agencies that may adversely affect the waters or substrate necessary to fish for spawning, breeding, feeding or growth to maturity. Similarly, the same EFH consultation files were the source of eelgrass mitigation projects in San Diego Bay and Mission Bay. The San Diego Integrated Natural Resources Plan (U.S. Department of the Navy, Naval Facilities Engineering Command Southwest & Port of San Diego 2013) compared a 2007 aerial photograph with an 1859 chart to discern habitat changes within San Diego Bay.

completed in this study, may be scaled up to much larger sections of each estuary because these sites may be considered representative habitats within each system under similar anthropogenic stressors.

Teasing apart changes to fish assemblages is inherently difficult, yet extremely important in estuaries exposed to myriad impacts from urbanisation. Long-term datasets, such as those analysed here, are rare and useful in finding effects typically missed in short-term studies (James *et al.* 2008; Stobart *et al.* 2009). That the fish assemblages have remained stable despite the aforementioned stressors also suggests habitat conservation measures such as eelgrass preservation and water quality standards may have provided a buffer to urbanisation and had a positive influence on fishery resources, although much improvement could still be made. This result, combined with previous work on elevated fishery productivity within seagrass (Hoffman 1986), highlights the need to conserve remaining seagrass habitats. Future research should focus on the effect of more specific aspects of urbanisation on fish assemblages and expand to include biotic independent variables, particularly measures of seagrass area and health. As impacts on estuaries in urban areas are unlikely to dissipate, a focus on responsible development and offsetting measures of habitat impacts for valuable fishery resources will ensure a

productive future for these stressed estuaries. The results of this study and others that identify habitats valuable for conservation may allow resource managers to more efficiently allocate financial resources and habitat protection measures to protect and enhance remaining valuable fish habitat.

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