Shifts in Fish and Invertebrate Assemblages of Two Southern California Estuaries during the 1997-98 El Niño

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Abstract.—Estuarine fish and invertebrate assemblages at Tijuana Estuary and Loss Peñasquitos Lagoon exhibited changes coincident with the 1997–1998 El Niño event. Three fishes [Albula sp. (bonefish), Ctenogobius sagittula (longtail gobs) and Acanthogobius flavimanus (yellowfin goby)] and three invertebrate species [Callinectes arcuatus (arched swimming crab), Penaeus californiensis (Mexican brown shrimp), and Petricola hertzana (bivalve)] were new to estuary monitoring records. In addition, three historically common species exhibited substantial changes in abundance and/or size frequency: Mugil spp. (mullet spp.), Grandidierella japonica (amphipod), and Tagelus californiensis (jackknife clam). Likely mechanisms for the observed patterns include modified ocean currents, altered larval supplies, increased rainfall, and flooding disturbance. Long-term biological monitoring programs (12-yr) provided valuable baseline data for quantifying the changes and recording faunal patterns over interannual-decadal time scales.

Introduction

El Niño events are short-term cycles in the ocean-atmosphere system with a mean recurrence interval of 3–8 years (Haston and Michaelsen 1994). In the coastal waters of the Californias, El Niño is characterized by increases in segurface temperature and sea level. Most El Niño events also produce abnormally high rainfall and streamflows in southern California (Schonher and Nicholson 1989; Kahya and Dracup 1994). Particularly strong historical El Niño events have occurred in 1926–27; 1957–58, 1982–83, 1991–92, and 1997–98 (Hubbs and Shultz 1929; Simpson 1984; Squire 1987; Lynn et al. 1998). The 1997–1998 El Niño was one of the strongest of this century (Hayward et al. 1999).

In California, the biological effects of El Niño conditions have been docimented in many marine habitats. Offshore, these effects include the migration of subtropical or tropical fishes into more northern latitudes (Hubbs and Schulz 1929; Walford 1931; Hubbs 1948; Ketchen 1956; Radovich 1961; Cowen 1988; Squire 1987; Karpov et al. 1995). Enhanced development of a northerly coastell countercurrent (the Davidson current) during El Niño years also results in the northward movement of more southerly pelagic invertebrates (e.g., Pleuroncodes planipes; Squire 1987) and fish larvae (e.g., Semicossyphus pulcher; Cowen 1985). In nearshore waters, growth and canopy cover of giant kelp (Macrocystis pyrifera) declines, with cascading effects on the associated kelp forest community (Dean and Jacobsen 1986; Tegner and Dayton 1987; Dayton et al. 1998). Abun-

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dance and nesting success of some seabirds also plummets in El Niño years, presumably due to modification of the nearshore food web (Massey et al. 1992; Veit et al. 1996).

Few long-term studies have documented El Niño-related effects on estuarine biota in southern California. Estuarine ecosystems are characterized by substantial variability due to their landscape position at the land-ocean interface, where they are influenced both by their terrestrial watersheds and the tidal marine environment. During El Niño years, high rainfall and streamflows in coastal watersheds can result in rapid flooding, strong freshwater pulses, and substantial sediment deposition in southern California's estuaries and lagoons (Onuf and Quammen 1983). El Niño-related sea level increases and sea storms can lead to dune overwash (Nordby and Zedler 1991) and enhanced inundation of the tidal marsh surface. Together with ocean temperature anomalies and altered current patterns, El Niño-induced natural disturbances may result in a cascade of changes to shallow water estuarine systems. Biotic effects may include a reduction in the diversity and abundance of benthic invertebrate and fish communities (Onuf and Quammen 1983; Nordby and Zedler 1991), invasion by exotic and disturbance-colonizing species, and altered patterns of larval recruitment (e.g., Cowen 1985).

The objectives of our study were to identify trends and anomalies in fish and invertebrate populations from two estuaries in San Diego County during the 1997–98 El Niño. Specifically, we used a 12-year monitoring database to identify the appearance and persistence of new species in these systems coincident with the 1997–98 El Niño, while documenting shifts in historical assemblage composition and size frequency.

Materials and Methods

Study Sites

The Pacific Estuarine Research Laboratory (PERL) at San Diego State University has maintained biological monitoring programs at both Tijuana Estuary (TE) and Los Peñasquitos Lagoon (LPL) since the mid-1980's, enabling comparative ecological research on these unique ecosystems (Nordby and Zedler 1991; Desmond et al. in review). Tijuana Estuary (32°34'N, 117°07'W) is located on the U.S.-Mexico border, at the terminus of the Tijuana River's 4403 km² watershed (Fig. 1). At approximately 1024 ha, it comprises one of the largest remaining, intact estuarine habitats of its kind in southern California. It is one of 22 NOAAdesignated National Estuarine Research Reserves (NERRs) in the nation (Zedler et al. 1992). TE is strongly influenced by marine conditions and has historically remained open to tidal flushing, with a few exceptions (Zedler et al. 1992). Rapid development of the watershed and floodplain has contributed to the severity of episodic flooding and sedimentation events, often accompanied by chronic sewage flows (Marcus 1989). The sampling program for the NERR was initiated in 1986 to monitor TE's water parameters, soil conditions, and plant, invertebrate, and fish assemblages (Desmond et al. 1999).

Los Peñasquitos Lagoon (32° 56′ N, 117° 15′ W) is a relatively small coastal estuary (252 ha) in northern San Diego County, situated at the outlet of the 420 km² Peñasquitos watershed (Fig. 1). The lagoon-marsh complex is protected under its designation as a Natural Preserve, and constitutes the northern portion of Tor-

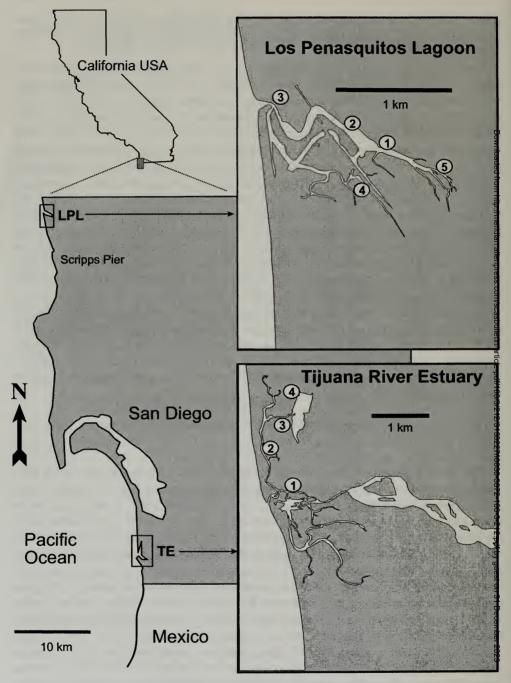


Fig. 1. San Diego coastal region, with insets of estuarine study sites: Tijuana Estuary (TE; 32° 34′ N, 117° 07′ W) and Los Peñasquitos Lagoon (LPL; 32° 56′ N, 117° 15′ W). Estuarine sampling locations are numbered on inset maps.

rey Pines State Reserve under the jurisdiction of California State Parks. Drainages flowing into LPL include Carroll, Los Peñasquitos, and Carmel Valley Creeks, which were historically perennial streams. LPL closes to tidal flushing on an annual basis, a process more recently augmented by hydrologic modifications (including a major reduction in the tidal prism) associated with construction of a railroad through the lagoon (in 1925), a highway across its mouth (in 1933), and sedimentation from human impacts in the watershed. During closed-mouth conditions, waters become vertically stratified, leading to anoxic conditions and fish kills; since 1986 the management approach to these problems has been to reopen the mouth manually, which enhances tidal mixing and flushing (LPL Foundation and State Coastal Conservancy 1985, Zedler 1996; Williams et al. 1999b). Sampling in Los Peñasquitos Lagoon began in 1986 to monitor water parameters, soil conditions, and plant, invertebrate, and fish assemblages (Williams et al. 1999a).

Physicochemical Conditions

Monthly summaries of rainfall data were obtained from the National Weather Service at Lindbergh Field, San Diego (http://nimbo.wrh.noaa.gov/sandiego-/nws.html). Total monthly streamflows of the Tijuana River at the Nestor gauge were obtained from the International Boundary and Water Commission (IBWC) (http://www.ibwc.state.gov/). Intensive water monitoring was conducted at Oneonta Slough, near Seacoast Drive in the north arm of TE, using an automated YSI 6000 upg datalogger which has been operated and maintained continuously since 1996. This unit samples 6 parameters, including salinity and temperature (°C), at 30-minute intervals, 24 hours a day, with sensors located 10 cm off the bottom of the channel.

Biotic Responses

Identical methods were used to sample invertebrate and fish assemblages at TE and LPL (see below), although sample number and frequency differed. The database at TE includes quantitative estimates (species composition, density, and size-frequency) of fishes and invertebrates collected from three stations (TE#1–3) in the north arm of the estuary (Fig. 1) on a quarterly basis (spring = March, summer = June/July, fall = September, and winter = December/January) from 1986–1999. An additional station in a restoration site (TE#4) was added during 1997–99. At LPL, fishes and invertebrates were initially collected from three stations (LP#1–3; Fig. 1) on a quarterly basis. Sampling frequency at LPL decreased to summer and winter for fishes in 1990, and for invertebrates in 1995, while two additional sampling stations (LP#4 and #5) were added in the upper lagoon in 1995.

Two sets of benthic invertebrate samples were collected at low tide from each station. A first set of nine shallow cores was collected by removing the top 5 cm of sediment with a cylindrical "clam gun" (45 cm length; 15 cm diameter; 176 cm² area). The nine cores were combined in groups of three, yielding three replicate samples (0.053 m² ea.) from each station. Samples were seived through a 1-mm screen in the field. Easily identifiable animals were counted and released, while all others were preserved in 95% EtOH for later identification; samples were soaked in a rose bengal solution prior to sorting. A second set of "deep" cores was collected by pushing the same "clam gun" 20 cm into the sediment to

Table 1. Number of fish collected at three Tijuana Estuary sampling stations (see Fig. 1 for locations), 1986-1999. * indicate species discussed in this paper.

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Longtail goby* Longjaw mudsucker 39 Cheekspot goby 45 5	Arrow goby			3795 17	17124 84	8482 5515	5 442		161 58	5856 5	564 1533	3 3775	5 398	556
ibilis Longjaw mudsucker 39 Cheekspot goby 45 5													65	_
Cheekspot goby		39	2	233	4	∞	6 1	1 :	32	3 8	889	17 2	28 123	17
	Cheekspot goby	45	5	2	219	38	2		2	∞	32 7	77	8 12	71
Lepidogobius lepidus Bay goby						2	65							
Quietula y-cauda Shadow goby 3	Shadow goby	3				96								
MUGILIDAE Mugil spp. 3 2	Mullet*	3	2			29	7	24		4	9 1	7 356	6 185	268
PLEURONECTIDAE Hypsopsetta guttulata Diamond turbot 13 33		13		36	3	34	2	5	2	53	24 6	67 4	44 12	45
Pleuronichthys ritteri Spotted turbot 3 1		3	_											

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Table 1. Continued.

Family	Species	Common name 1986 1987 1988 1989 1990 1991 1992 1993 1994 1995 1996 1997 1998 1999	1986 1987	988	686 19	661 06	1 1992	1993	1994	1995	9661	1997	8661	6661
	Pleuronichthys coenosus	C-O turbot							1			4		-
POECILIDAE	Gambusia affinis	Mosquitofish			2									
RHINOBATIDAE	Rhinobatos productus	Shovelnose guitarfish	2											
SCIAENIDAE	Seriphus politus	Queenfish	1											
SERRANIDAE	Paralabrax clathratus	Kelp bass	1	∞					1					
	Paralabrax maculatofasciatus Spotted sand bass	Spotted sand bass												
	Paralabrax nebulifer	Barred sand bass									1	3		
SYNGNATHIDAE	Syngnathus leptorhynchus	Bay pipefish	6 1	2				1		-	-	3		4
TOTAL FISH COLLECTED	TED		9888 3433 8106 21770 9564 6258 4923 13034 11425 3060 7118 10663 4173 13704	3106 2	26 0771	64 6258	3 4923	13034	11425	3060	7118	10663	4173	3704

estimate the abundance of large, deep-dwelling invertebrates (e.g., bivalves, burrowing shrimp). Nine cores, pooled using the same methods as in the shallow series, were taken at each station. Samples were seived through a 3-mm screen in the field. Easily identifiable animals were counted and released, others were preserved as above for later identification. Field observations, including those made of specimens captured during fish seining (see below), provided additional data on large and/or mobile taxa not usually sampled with the cores. Because invertebrate monitoring focused on benthic invertebrates, our protocol for surface macroinvertebrates was to note the presence of the more mobile taxa (e.g. Pach ygrapsus crassipes on banks of channels). When unusual species appeared, their presence was noted and, time permitting, density and/or size data were gathered.

Fishes and mobile surface macroinvertebrates (e.g., decapod crustaceans) were sampled from each station during the slack period of a low neap tide using two blocking nets and one 15-m bag seine with 3-mm square delta mesh. At each study site a linear distance (~9 to 12 m) was measured parallel to the channed and two blocking nets were deployed to confine all fishes within this area. The bag seine was then swept between the two blocking nets and across the channed to the opposite bank (defining 1 pass). Passes were repeated until the number of fish captured per pass was less than 5% of the total catch. The species composition and number of fishes collected was recorded separately for each pass. Subsamples of at least 25 individuals per fish species were measured and then released outside the blocking nets. Individuals that were unique or difficult to identify were preserved as voucher specimens.

Historical data (i.e., Tables 1–3) was used to identify groups of fish and inverge tebrate species that exhibited atypical abundance trends coinciding with the strong 1997–98 El Niño event. Although another fairly strong El Niño event (1991–92) has occurred during our long-term monitoring program, our data indicated ministrational responses to this event among the biotic communities of TE and LPL (Tables 1–3). However, because the 1997–98 event had a striking effect on these two systems, we focused on 1997–98 data from both LPL and TE, identifying species new to the sampling record and reporting long-term trends in abundance (density) and size-structure.

Results and Discussion

Physicochemical Conditions

Monthly multivariate El Niño indices indicate that strong El Niño conditions extended from April 1997 through July 1998 along the southern California coass (Hayward et al. 1999). During this time, sea-surface temperatures were anomal lously warm, averaging from 2–4 °C above long-term means (Lynn et al. 1998). El Niño conditions also produced a substantial increase in mean water levels during this time, with a maximum anomaly of +0.2 m at the Scripps Pier (La Jolla, CA) in November 1997 (Lynn et al. 1998).

Precipitation during the 1997–98 water year (7/1/97–6/30/98) was over 45 cm, which exceeded the long-term average of 25.4 cm yr⁻¹ recorded at Lindbergh Field, San Diego (Fig. 2). An exceptional peak in February 1998 rainfall (19.4 cm) was almost equal to the long-term annual mean. Rain events were accompanied by elevated river flows. At the U.S.-Mexico border in April 1998, Tijuana

Table 2. Number of fish collected at five Los Peñasquitos Lagoon sampling stations (see Fig. 1 for locations), 1986–1999. * indicate species discussed in this paper.

Family	Species	Common name	1986	1986 1987 1988	1988	1989	0661	1961	992 1	993	1989 1990 1991 1992 1993 1994 1995		1996 1997	II .	1998	1999
ATHERINOPSIDAE	Atherinops affinis	Topsmelt	1668	416	1456	6479	-	1262	222	181	2327	842	784	5176	257	963
BOTHIDAE	Paralichthys californicus	California halibut	9	4	7	-		-		2	2	1	15	3	-	3
CENTRARCHIDAE	Lepomis cyanellus	Green sunfish														-
	Micropterus sp.	Unid. bass													_	
COTTIDAE	Leptocottus armatus	Staghorn sculpin	94	23	11	376	3	-	14	15	4	29	14	16		
EMBIOTOCIDAE	Cymatogaster aggregatta	Shiner surfperch										-				
ENGRAULIDAE	Anchoa compressa	Deepbody anchovy	236	Ξ	99	21				13	119	44	2	139	15	21
	Anchoa delicatissima	Northern anchovy						3	_							
FUNDULIDAE	Fundulus parvipinnis	California killifish	26	124	61	237	7	11	137	3	149	45	99	45	13	22
GIRELLIDAE	Girella nigricans	Opaleye	-						-		2			-		
GOBIIDAE	Acanthogobius flavimanus	Yellowfin goby*				9				3	2				32	25
	Clevelandia ios	Arrow goby	17	55	27	236	23	18	_	53	12	6	4	27	99	127
	Ctenogobius sagittula	Longtail goby*													4	
	Gillichthys mirabilis	Longjaw mudsucker	111	298	536	295	7	66	18	7	7	13	21	48	32	4
	Ilypnus gilberti	Cheekspot goby			18	34							3	7	63	7
	Lepidogobius lepidus	Bay goby		6				11								
	Quietula y-cauda	Shadow goby						4			137		838	1671	526	871
MUGILIDAE	Mugil spp.	Mullet*			3						2	9	-	7	163	128
PLEURONECTIDAE	Hypsopsetta guttulata	Diamond turbot	1	3	11				2		16		=	15	13	14
	Pleuronichthys ritteri	Spotted turbot						-								
POECILIIDAE	Gambusia affinis	Mosquitofish	9	7	928	394				-			4	41	c	33
SCIAENIDAE	Menticirrhus undulatus	CA corbina													7	
	Umbrina roncador	Yellowfin croaker										-				
SERRANIDAE	Paralabrax clathratus	Kelp bass									2					
	Paralabrax maculatofasciatus	Spotted sand bass									3					
	Paralabrax nebulifer	Barred sand bass						_								
SYNGNATHIDAE	Syngnathus leptorhynchus	Bay pipefish	13		7			_		∞	16		23	_	9	56
TOTAL FISH COLLECTED	ΓED		2179	950	3659 10779		30	1413	489	1251	2891	1029 1829	1829	7184	1071	2636
1																

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Table 3. Decapods observed at Tijuana Estuary and Los Peñasquitos Lagoon, 1991-1999. * indicate species discussed in this paper.

					Tijuan	Tijuana Estuary	ary						Los I	eñasq	luitos	Los Peñasquitos Lagoon	u		
		1991	1992	993	1994	1995	996	997 1	998 1	1991 1992 1993 1994 1995 1996 1997 1998 1999 1991 1992 1993 1994 1995 1996 1997 1998 1999	991 1	992 1	993 1	994	995 1	966	97 16	1 86	666
CALLIANASSIDAE	Neotrypaea californiensis	X	×		×	×	×	×		×				X	X	×			
CANCRIDAE	Cancer sp.								×										
CRANGONIDAE	Crangon sp.				×										×				
GRAPSIDAE	Hemigrapsus oregonensis	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
	Pachygrapsus crassipes	×				×	×	×						×	×	×	×	×	×
HIPPOLYTIDAE	Hippolyte californiensis					×		×		×						×	×	×	×
OCYPODIDAE	Uca crenulata						×							×	×	×	×	×	
PALEOMONIDAE	Palaemon macrodactylus					×		×		×				×	×	×	×	×	×
PAGURIDAE	Pagurus sp.				×	×		×											
PENAEIDAE	Penaeus californiensis*							×	×								×	×	
PORTUNIDAE	Callinectes arcuatus*								×	×								×	×
	Portunus xantusii							×	×							×	×	×	
UPOGEBIIDAE	Upogebia pugettenis			×						×									
XANTHIDAE	Lophopanopeus bellus							×		×						×			
	Lophopanopeus frontalis															\times			

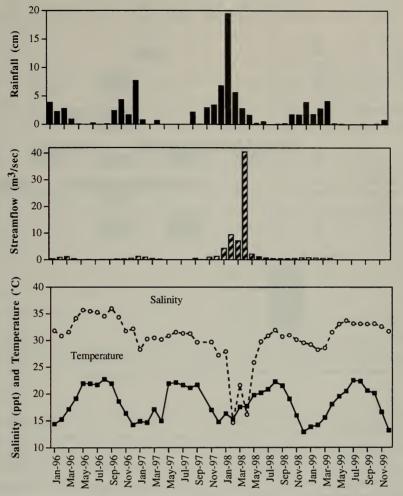


Fig. 2. Total monthly rainfall (cm; top) and mean monthly streamflow (m³ sec⁻¹; middle) in the Tijuana River. Mean monthly salinity and temperature (ppt, °C; bottom) within Tijuana Estuary, as measured by YSI datalogger at station TE#2. El Niño conditions persisted from approximately April 1997–July 1998.

River flows exceeded 40 m³ sec⁻¹; mean daily flow rates at this site (since 1962) were 2.31 m³ sec⁻¹. No river gauges are maintained in the lower watershed of Los Peñasquitos Lagoon.

Exceptional precipitation and river flow-rates also impacted estuarine habitats, where flooding deposited up to 12 cm of sediment over Tijuana Estuary mudflats (Ward 2000). Dramatic declines in mean monthly water salinities at TE#2 during February and April 1998 corresponded with periods of high rainfall and water flows (Fig. 2).

Biotic Responses

Based on differences before and during the 1997-1998 El Niño event, we observed six fish and invertebrate species that were either historically uncommon

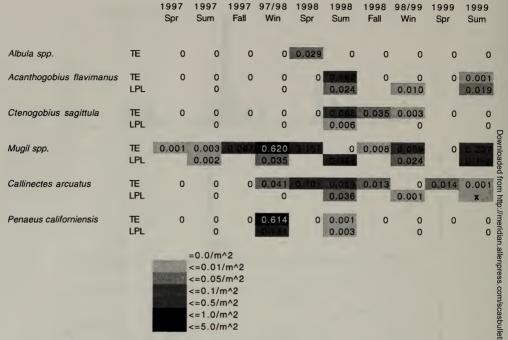


Fig. 3. Mean density (per m²) of species collected with the seine (spring 1997 through summer 1999) that exhibited atypical abundance trends during the 1997–98 El Niño event. "X" indicates that individuals were observed in low numbers, but densities were not quantified.

or completely new to the monitoring record. During 1997–98 we also documented shifts in abundance (increase or decrease) and/or size structure of three species that were common in the historical monitoring record. Descriptive analysis of these species trends includes the date of first collection, density and relative abundance, persistence in the estuary, size frequency, and discussion of life history.

New/uncommon species.—Most of the fish and invertebrate species new to the 12-year monitoring record at TE and LPL in 1997–98 were collected as juveniles. Their appearance altered the relative abundance of common species and increased species richness in lagoon assemblages. New invertebrates were first collected in winter 1997–98, while fishes were collected later in the summer or fall of 1998 either due to differential catchability or real differences in larval arrival/avail-species ability (Fig. 3). Each species exhibited variable periods of persistence in these estuaries. Although it appears that the abundance of several other species (Portunus xantusii—Xantus' swimming crab, Paralabrax nebulifer—barred sand bass, Menticirrhus undulatas—California corbina, and Pleuronichthys coenosus—C-Osturbot) may also be correlated with the 1997–98 El Niño event (Tables 1 and 2), we are not considering these as "new/uncommon species" because they are all regularly found in the local sandy nearshore environment.

Albula sp. (bonefish): A total of 11 Albula spp. leptocephalus larvae were collected at TE in spring 1998 (Table 1; Fig. 3). While not abundant (mean density $< 0.03 \, \text{m}^{-2}$; < 4% relative abundance), Albula spp. leptocephali were collected at 3 of 4 sampling stations, indicating wide distribution throughout the estuary. Albula leptocephali in the Gulf of California grow to lengths of up to 70 mm

standard length (SL) prior to settlement (Pfeiler 1984). Individuals in our collections ranged in size from 38–68 mm total length (TL).

This is the first time this tropical species has been collected at TE since monitoring was initiated in 1986 (Table 1); none have been collected at LPL. No additional *Albula spp.* (larvae, juveniles, or adults) were collected in 1999 or 2000, suggesting that this species did not persist in the estuary either due to outmigration, mortality, or our inability to capture juvenile stages or adults. Unusual recruitment of *Albula spp.* was also observed in 1998 at nearby Mission Bay (Talley 2000) and San Diego Bay (Allen 1998).

Because of current uncertainties regarding the taxonomic identity of bonefish in our region (Pfeiler et al. 1988), we refer to specimens in our collections as *Albula spp*. Bonefish are oviparous and presumably have planktonic eggs; larvae are rare in collections from the California Current region, although they are common and widespread in the Gulf of California (Moser et al. 1993, Charter and Moser 1996). Pfeiler et al. (1988) postulated that *Albula* leptocephali from the Gulf of California have a larval duration of 6–7 months; during winter and spring months the larvae actively move into shallow, lagoon nurseries in the first hours of a nocturnal flood tide, where they metamorphose into juveniles (Pfeiler 1984). *Albula* leptocephali are euryhaline, with a salinity tolerance of 4–52 ppt; they have been reported in both hyper- and hypo-saline lagoon habitats (Pfeiler 1981). Adult bonefish constitute an important recreational fishery in many areas and typically inhabit shallow (<0.5 m) sand and seagrass flats, where they feed on a variety of benthic prey (Mojica et al. 1994, Charter and Moser 1996).

Ctenogobius sagittula (longtail goby): The tropical goby, Ctenogobius sagittula, was first sampled at TE and LPL during summer 1998 (Tables 1 and 2). At TE, 65 C. sagittula were collected from stations TE#2 and TE#3 in channels of moderate depth (0.25–0.6 m on a low, neap tide), with strong tidal flows and bottoms composed of muddy sand or shell hash. Mean density across all stations was <0.09 m⁻² (Fig. 3), with C. sagittula averaging over 20% of the catch. Ctenogobius sagittula persisted in TE for approximately six months, becoming less common in quarterly samples subsequent to summer 1998. Mean densities decreased to 0.035 fish m⁻² by fall 1998 and <0.01 m⁻² by winter 1998–99. Mean C. sagittula sizes rapidly increased from 55.6 mm during summer 1998 (range: 33–78 mm TL), to 123.6 mm by fall 1998 (range: 98–200 mm TL).

Ctenogobius sagittula was less abundant at LPL. During the June 1998 sampling period, a total of four *C. sagittula* measuring 88–93 mm TL were collected from one station (LP#2), which is located in a warm, shallow side-channel near the lagoon interior (Fig. 1). Ctenogobius sagittula made up <2% of the mean catch across all stations, with mean densities of 0.03 fish m⁻² (Fig. 3). This is the only LPL record of *C. sagittula*; no individuals were collected in subsequent samples. Specimens from both locations have been archived in the Scripps Institution of Oceanography vertebrate collections (TE—SIO 98-124; LPL—SIO 98-123).

Ctenogobius sagittula is currently considered rare (Miller and Lea 1972) or extirpated (Swift et al. 1993) in southern California. However, the species is common in the Gulf of California and adjacent waters to Panama (Ruiz-Campos and Castro-Aguirre 1999), with disjunctive records in warmer Pacific coastal lagoons of Baja California, Mexico (e.g., San Ignacio lagoon by De La Cruz-Aguero and

Cota-Gomez 1998, San Quintin Bay by Rosales-Casian 1996). *Ctenogobius sagittula* was also observed during spring and summer of 1998 in Mission Bay marshes (Talley 2000).

Acanthogobius flavimanus (yellowfin goby): Another historically rare goby, the nonindigenous Acanthogobius flavimanus also appeared during summer 1998 sampling at both TE and LPL (Fig. 3). At TE, A. flavimanus was collected at densities of 0.49 m⁻² at one station (TE#2) in the main channel of the north arm. Averaged across all 3 stations, A. flavimanus densities were 0.16 m⁻² (4.9% of the total catch). All A. flavimanus collected at this time were juveniles (<100 mm TL; Baker 1979) with a size range of 28–88 mm TL. This recruitment pulse appeared to be a one-time event at TE; the only A. flavimanus specimen observed since then has been a single 38 mm TL individual collected in June 1999. The absence of adults in subsequent TE collections suggests that A. flavimanus popilations do not persist for long in TE, with recruitment events likely dependent on an influx of larvae supplied from other locations (perhaps San Diego Baya Williams et al. 1998a).

A recruitment pulse of *Acanthogobius flavimanus* was also observed in summed 1998 at LPL, where their mean density was 0.02 m⁻² and they averaged 6.4% of the catch across all stations (Fig. 3). Most of these specimens were collected in the mid-lagoon channels of station LP#1 and LP#2, and ranged in size from 58 mm TL, considerably larger than those collected at TE two weeks later However, *A. flavimanus* were prevalent throughout the lagoon, including upped lagoon stations LP#4 and LP#5 where surface salinities were low (3–5 ppt) and generally reflected heavy freshwater inputs (Fig. 1). The summer 1998 cohort of *A. flavimanus* presumably persisted in LPL through the next year, growing integration and summer 1999 and summer 1999. A new recruitment pulse of juveniles (47–133 mm) TL) also came into the lagoon in summer 1999 at densities averaging 0.02 mm (3.4% of the total catch).

Acanthogobius flavimanus is becoming increasingly common in San Diego County estuaries. Previous studies documented the southern expansion of A. flavimanus to San Diego Bay (32°34′N, 117°5′W) in 1989 (Williams et al. 1998a) However, unpublished records show that a single 96-mm individual was previously collected at TE in 1990 under the NERR fish monitoring program (Table 1). Acanthogobius flavimanus individuals have been collected episodically at LPE during summer sampling periods in 1989, 1993, and 1994 (Table 2) and during fish kills coinciding with extended mouth closure events (G. Williams, pers. obs.) Tolerant to a wide range of salinities and temperatures, this large (to 290 mm TL), opportunistic carnivore may negatively impact native fish assemblages, especially in disturbed habitats (Baker 1979, Usui 1981). While the extending range and increasing abundance of A. flavimanus is apparent, the long-term ramifications of these changes are unclear. However, resource managers should be aware of this species' presence and potential impacts to the ecology of native aquatic communities (Williams et al. 1998a).

Callinectes arcuatus (arched swimming crab): This crab species is typically found in estuarine mud or sand substrates (Garth and Stephenson 1966, Paul 1982a). It was initially collected with the seine at TE in winter 1997–98 (0.041 individuals m⁻²) and at LPL in summer 1998 (0.036 individuals m⁻²) (Fig. 3).

Additional specimens were observed at this time in several nearby estuaries, including the San Diego River channel and Sweetwater Marsh on San Diego Bay (G. Williams and J. West, pers. obs.), as well as Mission Bay (Talley 2000). Southern California represents the northern extension of *C. arcuatus*' known geographic range, which continues south to Peru (Williams 1974).

At TE, *C. arcuatus* was most abundant during the main pulse of the El Niño event (winter 1997–98 through summer 1998; Fig. 3). *Callinectes arcuatus* had peak densities of 0.101 individuals m⁻² during spring 1998, with a mean carapace width (CW) of 61.1 mm (range: 40–119 mm). As *C. arcuatus* densities declined throughout the following year, the population structure shifted to predominantly larger adults. *Callinectes arcuatus* is known to exhibit rapid growth rates of about 8 mm/month, reaching maturity at 80 mm carapace width (CW) (Paul 1982b). By spring 1999, *C. arcuatus* densities had declined substantially (0.014 individuals m⁻²), while the mean size of collected individuals increased to 123.7 mm CW (range: 105–145 mm). None were collected after summer 1999 (Desmond et al. 2000). At LPL, *C. arcuatus* was most abundant in summer 1998 (0.036 individuals m⁻²); densities dropped dramatically by winter 1998–99 (0.001 individuals m⁻²; Fig. 3).

Callinectes arcuatus is considered a euryhaline species tolerant of a wide range of temperatures. In the Gulf of California it occurs in areas with salinities ranging from 1–65 ppt and temperatures from 17.5–34°C (Paul 1982a). In a western Mexico lagoon system, C. arcuatus fed primarily on bivalves (particularly Tagelus affinis), crabs, and fish, while shrimp and gastropods were consumed in lesser amounts (Paul 1981).

Penaeus californiensis (Mexican brown shrimp): Juvenile Peneaus californiensis were collected with the seine at TE and LPL in winter 1997–98 and summer 1998 (Fig. 3). Seine samples were generally made in shallow water ~1 m depth, and all individuals collected were juveniles between 14–37 mm carapace length (CL). There is no previous collecting record of this species at either LPL or TE, although their native range spans the coast from San Francisco Bay to Peru (Dore and Frimodt 1987).

The mean density of *P. californiensis* at TE during winter 1997–98 was 0.614 individuals m^{-2} , yet none were collected the following spring (Fig. 3). LPL densities during winter 1997–98 were lower than at TE (0.131 individuals m^{-2}); LPL was not sampled in spring 1998. By summer 1998, *P. californiensis* densities had declined to < 0.005 individuals m^{-2} at both LPL and TE.

Penaeus californiensis is an important commercial species in Mexico, where it constitutes up to 75% of the Mexican Pacific shrimp catch (Dore and Frimodt 1987; Magallon-Barajas 1987). Newly hatched larvae travel up coastal estuaries into lagoons, where they spend several months growing to a "subadult" stage before returning to sea to mature and spawn (Snyder-Conn and Brusca 1975; McGoodwin 1979). Mature adults, which can reach a maximum size of 210 mm CL, generally occur on muddy bottoms or sandy mud at depths of 25–50 m (Dore and Frimodt 1987). In the Gulf of California, P. californiensis abundance naturally peaks during the winter season, and most individuals live only one year (Snyder-Conn and Brusca 1975). The P. californiensis fishery in the Gulf of California experiences substantial interannual variation in catch per unit effort, likely due to strong recruitment events, which have been positively correlated with elevated

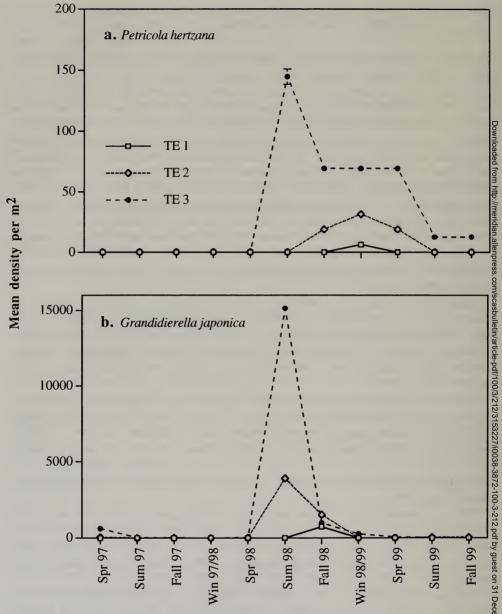


Fig. 4. Petricola hertzana (a) and Grandidierella japonica (b) densities (± SE) at three Tijuan Estuary sampling stations from spring 97 through fall 1999.

sea temperature anomalies characteristic of El Niño events (Morales-Bojorquez and Lopez-Martinez 1999).

Petricola hertzana: The bivalve Petricola hertzana (Petricolidae) was first encountered during summer 1998 in benthic core samples collected at station TE#3, where mean densities reached 145 individuals m⁻² (Fig. 4a). Since this initial collection date, P. hertzana abundance has generally decreased, although the species continues to persist at low densities (~35 individuals m⁻²) at this site. During

fall 1998 *P. hertzana* was also observed at a nearby station, TE#2. The population at this site gradually increased, reaching a peak in winter 1998–99 (45 individuals m⁻²). No *P. hertzana* individuals have been collected at TE#2 since spring 1999 (Fig. 4a).

Petricola hertzana is known to nestle among algae (Coan 1997), and adults range in size from 6–11 mm shell length (SL; McLean 1969). Individuals collected in our samples ranged from 1–11 mm, indicating the presence of both juveniles and adults. The distribution of *P. hertzana* ranges from Santa Monica Bay to Magdalena Bay, Baja California Sur (Coan 1997). Another Petricola species (identified as *P. pholadiformis*, which may in fact be *P. hertzana*) was documented in samples conducted at TE from September 1986 to June 1987 (Duggan 1989).

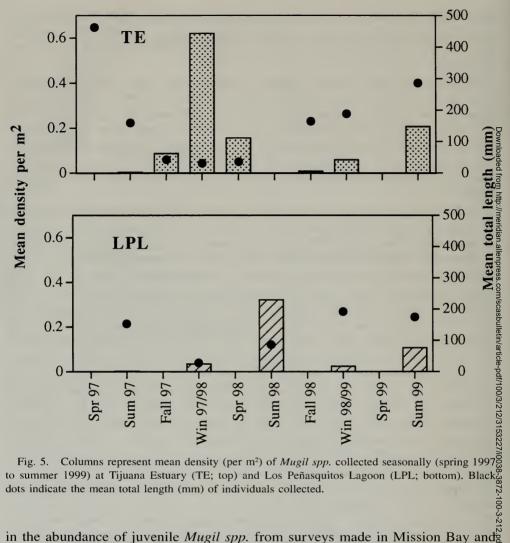
Historically common species.—Several historically common fish and invertebrate species at TE and LPL exhibited a substantial change (increase or decrease) in abundance during 1997–98, often accompanied by shifts in size-frequencies.

Mugil spp. (mullet): Mullet (Mugil spp.) are large, schooling fish with a cosmopolitan distribution that reach maturity at approximately 300 mm TL (2–3 years) (Anderson 1958). Adult Mugil cephalus are common and conspicuous in southern California estuaries and they likely dominate fish biomass in these systems; however, they are generally not sampled effectively due to their size and mobility (Allen 1982, Horn and Allen 1985, Williams et al. 1999a, Desmond et al. 1999). Smaller juveniles, which can be more effectively sampled with most gear (e.g., seines), have historically been rare in these collections (Desmond et al. 1999). Low numbers of Mugil curema (white mullet) have also been collected in southern California waters, and may easily be confused with M. cephalus, especially as juveniles (Lea et al. 1988). We therefore treat mullets as Mugil spp. throughout the remainder of the paper, although M. cephalus is likely the dominant species. In both winter 1997–98 and spring 1998, Mugil spp. juveniles were a major component of catches at TE (22–23% total catch).

Young-of-the-year (YOY) *Mugil spp.* (41–50 mm TL) were first collected in September 1997 throughout TE (3 of 4 stations) at average densities of 0.09 m⁻² (Fig. 3). Small juveniles 18–43 mm TL continued recruitment through December 1997, when they were collected at all four sampling stations at average densities of 0.63 m⁻² (17.7% of catch) (Fig. 5). Thereafter, TE mean densities fluctuated considerably but exhibited a general decline, while mean individual size increased. By September 1998 (one year post-recruitment), average *Mugil spp.* size was 165 mm TL; by June 1999, the average size had increased to 265 mm TL (Fig. 5), indicating a growth rate of between 75 and 125 mm per year at TE.

Under the semiannual sampling schedule at LPL, juvenile *Mugil spp.* were first collected in winter 1997/98 at mean densities of 0.035 m⁻² (Fig. 3; 11.7% of the total catch). Abundance of juvenile *Mugil spp.* peaked the following summer (1998) at 0.32 m⁻², when they were collected at all 5 stations and composed 40.9% of the total catch. Mean size at this time was 76 mm TL (Fig. 5). *Mugil spp.* were still abundant at LPL one year later (summer 1999), but by this time average size had increased to 175 mm TL. A comparison of *Mugil spp.* cohort growth rates from LPL and TE suggests that individuals from LPL may grow at a slower pace.

During the spring of 1998, Talley (2000) and Allen (1998) also noted increases



in the abundance of juvenile *Mugil spp*. from surveys made in Mission Bay and San Diego Bay, respectively. Mugil spp. are found in most warm seas, including the Eastern Pacific from the Galapagos Islands to San Francisco Bay. They are oviparous, with planktonic eggs and larvae (Sandknop and Watson 1996). Adult3 Mugil spp. spawn in surface waters offshore and enter bays and estuaries as juveniles or larvae (Anderson 1958), often moving upstream into freshwater rivers where they develop as yearlings (Follett 1960). Small numbers of mugilid larvae have been collected during annual ichthyoplankton surveys (1951–1984) con-§ ducted in the California Current region; the highest larval concentrations occur in nearshore stations off central and southern Baja California during the summer and fall (Moser et al. 1993, Sandknop and Watson 1996).

Grandidierella japonica: This exotic corophiid amphipod exhibited a population explosion throughout TE during summer/fall 1998. The highest mean G. japonica densities at TE#3 (15,119 individuals m⁻²) and TE#2 (3904 m⁻²) were observed in summer 1998, while TE#1 (1113 m⁻²) peaked in fall 1998 (Fig. 4b). By winter 1998–99, mean G. japonica density across all sites (96.4 m⁻²) had declined substantially, approaching long-term historical densities (mean for 1994–97 = 93.5 m⁻²). LPL populations of *G. japonica* also experienced an abundance peak during the 1997–98 El Niño event. The mean density across all sites in winter 1997–98 was 643 individuals m⁻², three times greater than the long-term average of 203 individuals m⁻² (Williams et al. 1998b). After this substantial peak in abundance, *G. japonica* densities dropped to levels near the long-term average during the following seasons.

The introduction of *G. japonica* into the United States was first reported in San Francisco Bay, California in 1966 (Chapman and Dorman 1975). It was identified in TE samples in 1994, but may have been present and unidentified in TE prior to this. *Grandidierella japonica* is native to Japan and is typically associated with brackish water and soft sediments, where it inhabits U-shaped tubes. In laboratory studies, *G. japonica* is capable of producing 10–12 generations per year (Greenstein and Tiefenthaler 1997), which could explain the dramatic increase in densities that occurred within a relatively short time period.

Rapidly reproducing, opportunistic species increase in abundance following a disturbance if they can take advantage of expanded resources (McCall 1977; Rhoads et al. 1978; Zajac and Whitlatch 1982). El Niño-related winter storms in 1997–1998 caused heavy sedimentation in Tijuana Estuary (Ward 2000), which may have smothered other invertebrates and decreased competition for resources. *G. japonica* densities in Yaquina Bay, Oregon also increased dramatically following a flood event (B. Boese, pers. comm.).

Tagelus californiensis (jacknife clam): This long-time dominant of the invertebrate community at both TE and LPL (Emmett et al. 1991; Desmond et al. 1999; Williams et al. 1999a), exhibited substantial declines at TE during the 1997–98 El Niño event. In spring 1997, the *T. californiensis* population at TE#2 was composed of individuals ranging in size from 28–70 mm shell length (SL) at a mean density of 145 individuals m⁻² (Fig. 6). Densities gradually declined during summer and fall 1997 (57 and 13 m⁻², respectively). No live *T. californianus* individuals were collected (although many empty shells were found) during winter 1997–98 or spring 1998, which coincided with rain and flooding in the estuary. Summer 1998 collections were marked by an influx of new recruits ranging in size from 7–15 mm SL at densities of 138 m⁻² (Fig. 6). Although *T. californianus* densities decreased in the following months (94 m⁻² in fall 1998, 57 m⁻² in winter 1998–99), summer 1999 collections had high densities (270 m⁻²). However, even by the summer of 1999, the population at TE#2 was still composed entirely of juveniles (10–56 mm SL).

Tagelus californiensis has a wide geographic distribution, ranging from Cape San Lucas, Baja California, Mexico to Cape Blanco, Oregon, but it is most abundant from TE to Morro Bay, California (Emmett et al. 1991). Tagelus californiensis occupies a permanent burrow where it feeds on phytoplankton and other suspended particles (Morris et al. 1980). Sexual maturity is reached between 60–120 mm shell length (Merino 1981). Peak spawning of *T. californianus* occurs in spring, with some limited spawning continuing year-round (Emmett et al. 1991).

Summary and Conclusions

Observed changes in the fish and invertebrate assemblages at TE and LPL during 1997-98 were likely related to El Niño-driven ocean anomalies (altered

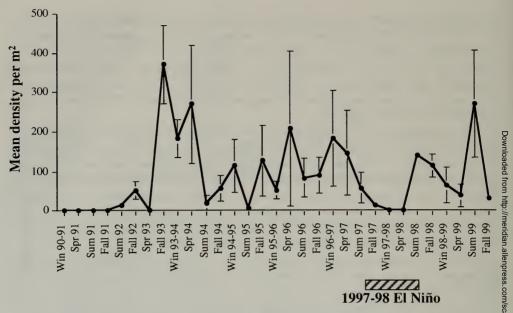


Fig. 6. Mean density of *Tagelus californianus* (jacknife clam) collected seasonally (winter 1990–fall 1999) in 20-cm-deep cores at Tijuana Estuary sampling station TE#2. Error bars represent \pm one standard error.

current patterns, water levels, and increased temperatures) and watershed disturbances (flooding and sedimentation). Altered larval supply, habitat disturbance, and species interactions (e.g., predation and competition) offer several likely mechanisms for the patterns observed. Our analysis of long-term monitoring records is the first documentation of unique changes in estuarine species assemblage composition during El Niño conditions. Continuous monitoring and baseline data are essential to understand the ecology of these estuarine systems and their inherent variability over interannual-decadal time scales. This study also provides the groundwork for future empirical studies to clarify the relationship between El Niño events and species abundance patterns in estuarine habitats, and for developing predictive models to understand change and appropriately manage estuarine resources.

Episodic, El Niño-associated events may affect the composition of fish and invertebrate assemblages in southern California estuaries by modifying larval supply. Of the six new fish and invertebrate taxa appearing in our 1997–1998 collections, most were species with warm-water affinities commonly associated with coastal embayments in southern Baja California and the Gulf of California. Almost all specimens were first collected as juveniles that likely arrived at local estuarine habitats as planktonic larvae, riding northward with warm surface currents. During "typical" years, the southward flowing California current (0–200 m deep) carries most nearshore surface waters equator-ward, while coastal upwelling contributes to offshore transport (Parrish et al. 1981; Simpson 1984). However during "anomalous" El Niño years, upwelling is reduced and a poleward-flowing countercurrent dominates coastal flows, transporting warm, high salinity waters northward and displacing the California current offshore (Simpson

1984; Hayward et al. 1999). Long-duration, anomalous flow conditions can result in episodic pulses of planktonic eggs and/or larvae from southern sources, which are located "downstream" of southern California.

Flow anomalies account for the variable recruitment success of some coastal fisheries stocks (Parrish et al. 1981) and may be important in structuring nearshore benthic communities (Tegner and Dayton 1987). Because long-lived species naturally form age-structured populations and are persistent members of the community, size-frequency analysis provides one of the best indicators of recruitment events. Paralabrax maculatofasciatus (spotted sand bass), a long-lived (≤14 yrs) subtropical species that persists in warm-water bay refugia in southern California, displayed episodic recruitment pulses that matched peaks in summer sea-surface temperatures during 1984-85 and 1989-90 (Allen et al. 1995). High recruitment of Semicossyphus pulcher (sheephead) to temperate reefs at its northern distributional limit (Point Conception, CA) coincided with years of El Niño-associated variation in the coastal current regime (Cowen 1985). From our data we suggest that estuarine populations of Mugil spp., another long-lived species (\leq 15 yrs; Hendricks 1961), also appear to be positively influenced by episodic larval recruitment events (Fig. 5). Furthermore, some portion of the Mugil spp. complex collected during our monitoring efforts may have been Mugil curema, a species also documented in California waters during the 1982-83 El Niño (Lea et al. 1988).

As ocean conditions transitioned to a cool-water, La Niña state in 1998 (Hayward et al. 1999), few warm-water species recruited to TE and LPL. Most of these species have ocean-going larvae which were likely exported offshore and carried southward by the California current, which was then in place. Recruitment did not occur despite reproductive output by some individuals that survived to maturity in local systems. For example, ovigerous female *Callinectes arcuatus* were observed on several dates (G. Williams, pers. obs.), but no juveniles were observed in local lagoons thereafter. However, reproducing individuals from these populations may have contributed larvae to other populations "downstream".

In the absence of additional recruitment events, persistence of many warmwater species appeared to be influenced by the longevity of individuals that recruited during the 1997–98 El Niño. Short-lived species (e.g., *Ctenogobius sagittula* and *Penaeus californiensis*) generally persisted for ≤6 months in estuaries, while longer-lived species (e.g., *Callinectes arcuatus* and *Petricola hertzana*) persisted and grew for more extended periods (up to 2 years). Persistence patterns suggest that these populations are ephemeral and depend on larval replenishment from elsewhere. Short persistence times for some of these tropical species may also be a result of rapid mortality due to low thermal tolerance. However, in our region hydrographic constraints on dispersal likely play a more important role than thermal tolerance in determining faunal distribution and persistence (Cowen 1985).

Changes in the abundance of two historically common benthic invertebrate species may be a response to El Niño-related flooding disturbance and sedimentation events rather than larval availability. *Grandidierella japonica*, an exotic disturbance-opportunist, exhibited extraordinary peaks in abundance following the winter floods, while populations of *Tagelus californiensis*, a native bivalve, plummeted in many areas. Similar impacts were observed at Mugu Lagoon in 1978, when flooding and sedimentation from winter storms resulted in long-term im-

pacts to the distribution and composition of fish and invertebrate assemblages (Onuf and Quammen 1983, Onuf 1985). Sedimentation is an important factor that can lead to both gradual and abrupt changes in community dynamics in coastal estuaries (Onuf and Quammen 1983, Zedler et al. 1992, Desmond et al. in review). Immobile invertebrates in permanent burrows may be buried by catastrophic sedimentation events, leading to suffocation and mortality (Peterson 1985). In contrast, many epibenthic organisms (e.g., capitellid and spionid polychaetes, corophiid amphipods) opportunistically colonize newly deposited sediments, rapidly taking advantage of space and food resources (McCall 1977, Zajac and Whitlatch 1982, Levin et al. 1996).

Sedimentation rates appear to be considerably greater at TE than LPL (G.

Sedimentation rates appear to be considerably greater at TE than LPL (G. Williams, pers. obs.), perhaps due to differential levels of watershed disturbance and area (4403 km² and 420 km², respectively), and differences in impacts were reflected by benthic community responses. Mean sediment accretion on TE tidal mudflats during the winter of 1997–98 was over 8 cm, but reached levels of 12 cm in some areas (Ward 2000). This is higher than long-term TE marsh sedimentation rates of 1 cm yr⁻¹ (Weis 1999), and dramatically more variable than East and Gulf coast sedimentation ranges of 0.1–1 cm yr⁻¹ (Stevenson et al. 1986). Episodic sedimentation events illustrate the extreme influence which storms may have on Tijuana Estuary and point to a need to plan for long-term sediment management solutions (Zedler et al. 1992; Desmond et al. 1999). Furthermore, these impacts indicate the necessity of evaluating the possibilty of habitat shifts related to sedimentation events in future restoration efforts (Zedler 1996).

While the individual impacts of sedimentation and larval recruitment likely exerted major effects on estuarine assemblage composition, their combined, synergistic effects should not be ignored. Interspecific interactions with novel predators or competitors in disturbed habitats can substantially modify feeding patterns and abundance (Moyle et al. 1986, Moyle 1997). While storm-induced sedimentation events may have led to the rapid decline of *Tagelus californiensis* populations, predation by *Callinectes arcuatus* may have also played a role. *Callinectes arcuatus* are active, voracious predators of bivalves (Paul 1981), and the peak in crab abundance coincided with declines of *T. californiensis*. Similar declines in *Penaeus californiensis* numbers may be due to increased competition from *C. arcuatus* juveniles, which utilize similar resources and indirectly compete for food and space (Paul 1981). Related studies show that feeding patterns of some juvenile fish species (e.g., *Paralichthys californicus* and *Clevelandia ios*) shifted during and El Niño years due to accompanying changes in prey abundance patterns at TE (G. Williams et al. in prep.).

This study provides an important record of faunal patterns and variability over interannual-decadal time scales. Furthermore, it suggests that some of southern California's coastal lagoon's may act as a north-south metapopulation for a number of fish and invertebrate taxa. Long-term datasets provided by biological monitoring programs are an irreplaceable resource that allows evaluation of subtle ecosystem responses to climatic cycles (e.g., El Niño events), anthropogenic impacts, exotic species invasions, and other events. Because southern California has an inherently variable environment, complete characterization of a 'normal' year is doubtful (Allen 1982, Desmond et al. in review). Thus, knowledge of temporal variability is needed to understand ecological patterns. Those who wish to test

hypotheses about community membership, population structure, and species persistence in regions influenced by El Niño or other "events" will benefit from the continuation of long-term monitoring programs. In fact, researchers and resource managers cannot expect to understand today's assemblages or conserve their habitats without referring to records of historical composition and change.

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Literature Cited

- Allen, L. G. 1982. Seasonal abundance, composition, and productivity of the littoral fish assemblage in upper Newport Bay, California. U.S. Fish. Bull. 80:769–789.
- Allen, L. G., T. E. Hovey, M. S. Love, and J. T. W. Smith. 1995. The life history of the spotted sand bass (*Paralabrax maculatofasciatus*) within the southern California bight. Calif. Coop. Oceanic Fish. Invest. Rep. 36:193–203.
- Allen, L. G. 1998. Fisheries inventory and utilization of San Diego Bay, San Diego, California: 4th Annual Report, FY 1997–98. Prepared for U.S. Navy, Naval Facilities Engineering Command under Contract No. N68711-94-LT-4033, 25 pp.
- Anderson, W. W. 1958. Larval development, growth, and spawning of the striped mullet (*Mugil cephalus*) along the south Atlantic coast of the U.S. U.S. Fish. Bull. 58:501–525.
- Baker, J. C. 1979. A contribution to the life history of the yellowfin goby (*Acanthogobius flavimanus*) in the San Francisco Bay-Delta area. M.S. Thesis, California State University Sacramento, Sacramento, California, 36 pp.
- Chapman, J. W., and J. A. Dorman. 1975. Diagnosis, systematics, and notes on *Grandidierella japonica* (Amphipoda: Gammaridea) and its introduction to the Pacific Coast of the United States. Bull. So. Calif. Acad. Sci. 74:104–108.
- Charter, S. R. and H. G. Moser. 1996. Albulidae: Bonefishes. Pages 79–81 in H. G. Moser, editor. The early stages of fishes in the California Current region. California Cooperative Oceanic Fisheries Investigations Atlas no. 33., Marine Life Research Program, Scripps Institution of Oceanography, La Jolla, California, xii + 1505 pp.
- Coan, E. V. 1997. Recent species of the genus *Petricola* in the Eastern Pacific (Bivalvia: Veneroidea). Veliger 40:298–340.
- Cowen, R. K. 1985. Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: Causes and implications. J. Mar. Res. 43:719–742.
- Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. Ecol. Applic. 8:309–322.
- Dean, T. A., and F. R. Jacobsen. 1986. Nutrient-limited growth of juvenile kelp, *Macrocystis pyrifera*, during the 1982–1984 'El Niño' in southern California. Mar. Biol. 90:597–601.
- De La Cruz-Aguero, J., and V. M. Cota-Gomez. 1998. Ictiofauna de la laguna de San Ignacio, Baja California Sur, Mexico: nuevos registros y ampliaciones de ambit. Ciencias Marinas 24:353–358.
- Desmond, J. S., D. H. Deutschman, and J. B. Zedler. In review. Fish and invertebrate community structure in three southern California estuaries: An 11-year study. Submitted to Estuaries.
- Desmond, J., M. Cordrey, J. Johnson, K. Ward, and J. Zedler. 2000. Tijuana River National Estuarine Research Reserve: Annual report on ecosystem monitoring. NOAA Technical Memorandum on the Tijuana River National Estuarine Research Reserve. NOAA National Ocean Service, Sanctuaries and Programs Division. Washington D.C., 60 pp.
- Desmond, J., G. Williams, M. James, J. Johnson, J. Callaway, and J. Zedler. 1999. Tijuana River

- National Estuarine Research Reserve: Annual report on ecosystem monitoring. NOAA Technical Memorandum on the Tijuana River National Estuarine Research Reserve. NOAA National Ocean Service, Sanctuaries and Programs Division, Washington D.C., 67 pp.
- Dore, I., and C. Frimodt. 1987. An illustrated guide to shrimp of the world. Van Nostrand Reinhold. New York, New York, 229 pp.
- Duggan, R. M. 1989. The bivalve community and role of *Laevicardium substriatum* in the Tijuana Estuary. M. S. Thesis, San Diego State University, San Diego, California, 131 pp.
- Emmett, R. L., S. L. Stone, S. A. Hinton, and M. E. Monaco. 1991. Distribution and abundance of fishes and invertebrates in west coast estuaries. Volume II: Species life history summaries. ELMR Rep. No. 8. NOAA/NOS Strategic Environmental Assessments Division, Rockville, Maryland, 329 pp.
- Follett, W. I. 1960. The fresh-water fishes—their origin and affinities. Symposium on the biogeography of Baja California and adjacent seas. Syst. Zool. 9(3–4):212–232.
- Garth, J. S., and W. Stephenson. 1966. Brachyura of the Pacific coast of America, Brachyrhyncha: Portunidae. Allan Hancock Monographs in Mar. Biol. 1:I–154.
- Greenstein, D. J., and L. L. Tiefenthaler. 1997. Reproduction and population dynamics of a population of *Grandidierella japonica* (Stephensen) (Crustacea: Amphipoda) in Upper Newport Bay, California. Bull. So. Calif. Acad. Sci. 96:34–42.
- Haston, L., and J. Michaelsen. 1994. Long-term central coastal California precipitation variability and relationships to El Niño-Southern oscillation. J. Climate 7:1373–1387.
- Hayward, T. L., T. R. Baumgartner, D. M. Checkley, R. Durazo, G. Gaxiola-Castro, K. D. Hyrenbach, & A. W. Mantyla, M. M. Mullin, T. Murphree, F. B. Schwing, P. E. Smith, and M. J. Tegner. 1999. The state of the California current in 1998–1999: Transition to cool-water conditions. Calif. Coop. Oceanic Fish. Invest. Rep. 40:29–62.
- Hendricks, L. J. 1961. The striped mullet, Mugil cephalus Linnaeus. Pp. 95–103 in The ecology of the Salton Sea, California, in relation to the sportfishery (B. W. Walker, ed.), California Dept. Fish and Game, Fish Bulletin 113, 204 pp.
- Horn, M. and L. Allen. 1985. Fish community ecology in southern California bays and estuaries. Pages 169–190 *in* Fish community ecology in estuaries and coastal lagoons: Toward an ecosystem integration (A. Yañez Arancibia, ed.), UNAM Press, México.
- Hubbs, C. L. 1948. Changes in the fish fauna of western North America correlated with changes in Science ocean temperature. J. Mar. Res. 7:459–482.
- Hubbs, C. L., and L. P. Schulz. 1929. The northward occurrence of southern forms of marine life along the Pacific Coast in 1926. Calif. Fish Game 15:234–241.
- along the Pacific Coast in 1926. Calif. Fish Game 15:234–241.

 Kahya, E., and J. A. Dracup. 1994. The influences of Type 1 El Niño and La Niña events on streamflows in the Pacific southwest of the United States. J. Climate 7:965–976.
- Karpov, K. A., D. P. Albin, and W. H. Van Buskirk. 1995. The marine recreational fishery in northern and central California: A historical comparison (1958–86), status of stocks (1980–86), and effects of changes in the California Current. California Dept. Fish and Game, Fish Bulletin 176, 192 pp.
- Ketchen, K. S. 1956. Climatic trends and fluctuations in yield of marine fisheries of the Northeast Pacific. Fish. Res. Board Canada 13:357–374.
- Lea, R. N., C. C. Swift, and R. J. Lavenberg. 1988. Records of *Mugil curema* Valenciennes, the white mullet, from southern California. Bulletin of the Southern California Academy of Sciences. 87(1):31–34.
- Levin, L. A., D. Talley, and G. Thayer. 1996. Succession of macrobenthos in a created salt marsh. Marine Ecology Progress Series 141:67–82.
- Los Peñasquitos Lagoon Foundation and State Coastal Conservancy. 1985. Los Penasquitos Lagoon Scheme enhancement plan and program. A California State Coastal Conservancy publication, 119 pp.
- Lynn, R. J., T. Baumgartner, J. Garcia, C. A. Collins, T. L. Hayward, K. D. Hyrenbach, A. W. Mantyla, T. Murphree, A. Shankle, F. B. Schwing, K. M. Sakuma, and M. J. Tegner. 1999. The state of the California current, 1997–1998: Transition to El Niño Conditions. Calif. Coop. Oceanic Fish. Invest. Rep. 39:25–49.
- Magallon-Barajas, F. J. 1987. The Pacific shrimp fishery of Mexico. Calif. Coop. Oceanic Fish. Invest. Rep. 28:43–52.
- Marcus, L. 1989. The coastal wetlands of San Diego County. California State Coastal Conservancy publication, 64 pp.

- Massey, B. W., D. W. Bradley, J. L. Atwood. 1992. Demography of a California least tern colony including effects of the 1982–1983 El Niño. Condor 94(4):976–983.
- McCall, P. L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. Mar. Res. 35:221–261.
- McGoodwin, J. R. 1979. The decline of Mexico's Pacific inshore fisheries. Oceanus 22(2):51-59.
- McLean, J. H. 1969. Marine shells of southern California. Los Angeles County Museum of Natural History Science Series 24, Zoology No. 11, 104 pp.
- Merino, J. 1981. A study of the temperature tolerances of adult *Solen rosaceus* and *Tagelus californianus* in south San Diego Bay: the effects of power plant cooling water discharge. Ph.D. Dissertation, San Diego State University, San Diego, California, 140 pp.
- Miller, D. J., and R. N. Lea. 1972. Guide to the coastal marine fishes of California. Fish Bulletin 157, 249 pp.
- Mojica, R., J. M. Shenker, C. W. Harnden, and D. E. Wagner. 1994. Recruitment of bonefish Albula vulpes, around Lee Stocking Island, Bahamas. Fish. Bull. 93:666–674.
- Morales-Bojorquez, E., and J. Lopez-Martinez. 1999. Brown shrimp fishery in the Gulf of California. Calif. Coop. Oceanic Fish. Invest. Rep. 40:28.
- Morris, R. H., D. P. Abbott, and E. C. Haderlie. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford, California, 690 pp.
- Moser, H. G., R. L. Charter, P. E. Smith, D. A. Ambrose, S. R. Charter, C. A. Meyer, E. M. Sandknop, and W. Watson. 1993. Distributional atlas of fish larvae in the California Current region: taxa with less than 1000 total larvae, 1951 through 1984. CalCOFI Atlas No. 31-32. Marine Life Research Program, Scripps Institution of Oceanography, La Jolla, California, xxix + 223 pp.
- Moyle, P. B. 1997. Fish invasions in California: Do abiotic factors determine success? Ecology 77: 1666–1670.
- Moyle, P. B., R. A. Daniels, B. Herbold and D. Baltz. 1986. Patterns in distribution and abundance of a noncoevolved assemblage of estuarine fishes in California. U.S. Fish. Bull. 84:105–117.
- Nordby C. S. and J. B. Zedler. 1991. Responses of fish and macrobenthic assemblages to hydrologic disturbances in Tijuana Estuary and Los Peñasquitos Lagoon, CA. Estuaries 14:80–93.
- Onuf, C. P. 1985. The ecology of Mugu Lagoon, California: An estuarine profile. U.S. Fish and Wildlife Service Biological Report 85. 122 pp.
- Onuf, C. P. and M. L. Quammen. 1983. Fishes in a California coastal lagoon: effects of major storms on distribution and abundance. Mar. Ecol. Prog. Ser. 12:1–14.
- Parrish, R. H., C. S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California current. Biol. Ocean. 1(2):175–203.
- Paul, R. K. G. 1981. Natural diet, feeding, and predatory activity of the crabs *Callinectes arcuatus* and *C. toxotes* (Decapoda, Brachyura, Portunidae). Mar. Ecol. Prog. Ser. 6:91–99.
- Paul, R. K. G. 1982a. Observations on the ecology and distribution of swimming crabs of the genus Callinectes (Decapoda, Brachyura, Portunidae) in the Gulf of California, Mexico. Crustaceana 42:96–100.
- Paul, R. K. G. 1982b. Abundance, breeding, and growth of *Callinectes arcuatus* Ordway and *Callinectes toxotes* Ordway (Decapoda, Brachyura, Portunidae) in a lagoon system on the Mexican Pacific coast. Estuar. Coast. Shelf Sci. 14:13–26.
- Peterson, C. H. 1985. Patterns of lagoonal bivalve mortality after heavy sedimentation and their paleoecological significance. Paleobiology 11:139–153.
- Pfeiler, E. 1981. Salinity tolerance of leptocephalous larvae and juveniles of the bonefish (Albulidae: *Albula*) from the Gulf of California. J. Exp. Mar. Biol. Ecol. 52:37–45.
- Pfeiler, E. 1984. Inshore migration, seasonal distribution and sizes of larval bonefish, *Albula*, in the Gulf of California. Environ. Biol. Fishes 10:117–122.
- Pfeiler, E., M. A. Mendoza, and F. A. Manrique. 1988. Premetamorphic bonefish (*Albula* sp.) leptocephali from the Gulf of California with comments on life history. Environ. Biol. Fishes 21: 241–249.
- Radovich, J. 1961. Relationships of some marine organisms of the Northeast Pacific to water temperatures, particularly during 1957 through 1959. Calif. Dept. Fish and Game, Fish Bull. No. 112, 62 pp.
- Rhoads, D. C., P. L. McCall, and J. Y. Yingst. 1978. Disturbance and production on the estuarine seafloor. Am. Scientist 578:577–586.

- Rosales-Casian, J. A. 1996. Ictiofauna de la Bahia San Quintin, Baja California, Mexico, y su costa adjacente. Ciencias Marinas 22:443-458.
- Ruiz-Campos, G., and J. L. Castro-Aguirre. 1999. First records of two tropical gobies, Awaous tajasica and Ctenogobius sagittula (Pisces: Gobiidae), in the continental waters of Baja California, Mexico. Bull. So. Calif. Acad. Sci. 98:131-136.
- Sandknop, E. M., and W. Watson. 1996. Mugilidae: Mullets. Pp. 1078-1081 in H. G. Moser, editor. The early stages of fishes in the California Current region. California Cooperative Oceanic Fisheries Investigations Atlas no. 33., Marine Life Research Program, Scripps Institution of Oceanography, La Jolla, California, xii + 1505 pp.
- Schonher, T. and S. E. Nicholson. 1989. The relationship between California rainfall and ENSO events. 8 J. Climate. 2:1258-1269.
- Simpson, J. J. 1984. El Niño-induced onshore transport in the California current during 1982-83. Geophys. Res. Let. 11(3):233-236.
- Snyder-Conn, E., and R. C. Brusca. 1975. Shrimp population dynamics and fishery impact in the northern Gulf of California. Ciencas Marinas 2(2):54-67.
- Squire, J. L. 1987. Relation of sea surface temperature changes during the 1983 El Niño to the geographical distribution of some important recreational pelagic species and their catch temperature parameters. Mar. Fish. Rev. 49(2):44-57.
- Stevenson, J. C., L. G. Ward, and M. S. Kearney. 1986. Vertical accretion in marshes with varying rates of sea level rise. Pp. 241–259 in Estuarine Variability (D. A. Wolfe, ed.), Academic Press, Inc., Orlando, Florida, 509 pp.
- Swift, C. C., T. R. Haglund, M. Ruiz, and R. N. Fisher. 1993. The status and distribution of the freshwater fishes of Southern California. Bull. So. Calif. Acad. Sci. 92:101-167.
- Talley, D. M. 2000. Ichthyofaunal utilization of newly-created versus natural salt-marsh creeks in Mission Bay, CA. Wetlands Ecol. Mgmt. 8:117-132.
- Tegner, M. J., and P. K. Dayton. 1987. El Niño effects on southern California kelp forest communities. Adv. Ecol. Res. 17:243-279.
- Usui, C. A. 1981. Behavioral, metabolic, and seasonal size comparisons of an introduced gobiid fish, *Acanthogobius flavimanus*, and a native cottid, *Leptocottus armatus*, from upper Newport Bay, California. M.S. Thesis, California State University Fullerton, California, ix + 52 pp.
- Veit, R. R., P. Pyle, and J. A. McGowan. 1996. Ocean warming and long-term change in the pelagic bird abundance within the California Current system. Mar. Ecol. Prog. Ser. 139:11–18.

 Walford, L. A. 1931. Northward occurrence of southern fish off San Pedro in 1931. Calif. Fish Game
- 17(4):401-405.
- Ward, K. M. 2000. Episodic colonization of an intertidal mudflat by cordgrass (*Spartina foliosa*) at Tijuana Estuary. M. S. Thesis, San Diego State University, San Diego, California, viii + No. 103 pp.
- Weis, D. A. 1999. Vertical accretion rates and heavy metal chronologies in wetland sediments of Tijuana Estuary. M. S. Thesis, San Diego State University, xi + 106 pp.
- Williams, A. B. 1974. The swimming crabs of the genus Callinectes. Fish. Bull. 72:685-798.
- Williams, G. D., J. Desmond, and J. Zedler. 1998a. Extension of two nonindigenous fishes, *Acanthogobius flavimanus* and *Poecilia latipinna*, in San Diego Bay marsh habitats. Calif. Fish Game 84:1-17.
- Williams, G. D., G. Noe, and J. Desmond. 1998b. The physical, chemical, and biological monitoring \(\mathbb{P} \) of Los Peñasquitos Lagoon. Annual report submitted to the Los Peñasquitos Lagoon Foundation. Pacific Estuarine Research Lab, San Diego State University, San Diego, California, 47 pp.
- Williams, G. D., J. West, M. Cordrey, and K. Ward. 1999a. The physical, chemical, and biological S. monitoring of Los Peñasquitos Lagoon. Annual report submitted to the Los Peñasquitos Lagoon Foundation. Pacific Estuarine Research Lab, San Diego State University, San Diego, California,
- Williams, G. D., J. Callaway, M. Wells, J. Jackson. 1999b. Monitoring and managing Los Peñasquitos Lagoon's biological resources: Effects of a rapidly changing watershed. in Coastal Zone 99: Abstracts of Presentations. July 27-29, 1999, San Diego, California, USA.
- Zajac, R. N., and R. B. Whitlatch. 1982. Responses of estuarine infauna to disturbance II. Spatial and temporal variation of succession. Marine Ecology Progress Series 10:15-27.
- Zedler, J. B., C. S. Nordby, and B. E. Kus. 1992. The ecology of Tijuana Estuary, California: A

National Estuarine Research Reserve. NOAA Office of Coastal Resource Management, Sanctuaries and Reserves Division, Washington, D. C. ii + 151 pp.

Zedler, J. B. Principal author. 1996. Tidal wetland restoration: A scientific perspective and southern California focus. California Sea Grant College System, University of California, La Jolla, California. Report No. T-038. vi + 129 pp.

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