Journal of Sea Research 171 (2021) 102021

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Sampling nearshore Infaunal ‘weeds’ rather than ‘trees’: Does this orthodoxy undervalue importance of sedimentary biomes?

Dennis Cody Lees [*]

Littoral Ecological & Environmental Services, Leucadia, CA, USA

ARTICLE INFO

Keywords:
Infaunal assemblages
Sedentary megafauna
Macrofauna
Species composition
Biomass
Secondary production
Sublethal predation
Ecosystem engineer
Life span

ABSTRACT

This study compares species composition, abundance, biomass, and several other factors by which sedentary megafaunal and macrofaunal assemblages at depths between 14 m and 55 m on the Hueneme Shelf in southern California, USA, can be characterized. It details fundamental differences between these assemblages in this study area and demonstrates how little we know about a diverse range of attributes that are important in describing and evaluating infaunal assemblages. It provides strong support for a recent claim that: “The soft-sediment seafloor of the open continental shelf is among the least-known biomes on Earth, despite its high diversity and importance to fisheries and biogeochemical cycling” (Tomašových and Kidwell, 2017).

Basic and applied research after the 1950s transformed infaunal ecology from a discipline focused primarily on long-lived sedentary megafauna (analogous to ‘trees’ on land) into a field concentrating on opportunistic or ephemeral macrofauna (analogous to ‘weeds’ on land). Based on findings of this study, macrofaunal assemblages play a subordinate role in ecosystem dynamics. Most research in recent decades has overlooked contributions by sedentary megafauna. This focus leads to a poor understanding of the dynamics of these widespread ecosystems, severely undervalues their ecological importance and production, underestimates impacts of anthropogenic activities on unconsolidated sediments as well as the duration of recovery trajectories following disturbances.

Sedentary megafaunal and macrofaunal assemblages were quite different in virtually all aspects assessed during this analysis. Although macrofauna in this study had far greater species richness and were far more abundant than sedentary megafauna, conservative estimates for megafaunal biomass and secondary production indicate these organisms contribute substantially more energy to higher trophic levels than macrofauna. In addition, the megafaunal assemblages are characterized by many influential ‘ecosystem engineers’. Consequently, the differences in numbers of species and individuals are irrelevant with regard to determining value to the ecosystem. Megafauna in this area also exhibited more sensitivity in environmental factors. They live substantially longer than macrofauna, likely leading to greater stability in megafaunal assemblages. These differences indicate that current approaches focusing on macrofauna severely undervalue infaunal resources and contributions to higher trophic levels. They imply that studies of megafaunal assemblages should provide considerably greater insight into ecosystem dynamics and secondary production than macrofaunal assemblages and would have greater power to predict or assess environmental degradation or change, and document or predict recovery trajectories.

1. Introduction

In describing a 19th century extinction of an important megafaunal ecosystem on the continental shelf in Santa Monica Bay, CA, USA, (Tomašových and Kidwell, 2017) claimed: “The soft-sediment seafloor of the open continental shelf is among the least-known biomes on Earth, despite its high diversity and importance to fisheries and biogeochemical cycling”. A major reason for this deficiency is that the majority of studies conducted to provide basic descriptions of infaunal assemblages on continental shelves (e.g., Sanders, 1956, 1958, 1960; Allan Hancock Foundation (AHF), 1965) or to assess effects of anthropogenic activities on infauna have focused on sampling macrofauna, i.e., the short-lived opportunistic ‘weeds’, rather than long-lived sedentary megafauna in these habitats, the ‘trees’. This includes programs sampling wastewater outfalls (e.g., Word, 1976; Bernstein and Dorsey, 1991; Bergen et al., 1998), dredging for aggregates, etc., (e.g., Newell et al., 1998; Seiderer

---

[*] Corresponding author at: 1075 Urania Ave., Leucadia, CA 92024, USA.
E-mail address: dennislees@cox.net.

https://doi.org/10.1016/j.seares.2021.102021
Received 2 November 2020; Received in revised form 3 February 2021; Accepted 20 February 2021

and Newell, 1999; Cooper et al., 2007), or petroleum-related activities and oil spills (e.g., Gray et al., 1990; Skalski et al., 2001; Fukuyama et al., 2014). The large sedentary megafaunal components of the infauna routinely have been ignored or avoided in these types of studies (e.g., Sanders, 1956, 1958, 1960; Young and Rhoads, 1971). This failure to accurately assess the value of infaunal assemblages by studying secondary productivity and recovery trajectories for sedentary megafaunal assemblages has undoubtedly led to long-term damage or destruction of large productive areas of sandy, silty, or heterogeneous gravel sediments in many areas around the world as a consequence of wastewater disposal or beach-replenishment or aggregate-dredging projects. This destruction was permitted because of a widespread lack of understanding of the value of these assemblages, how long it would take for the assemblages to recover, and their role in feeding many fisheries species. Some projects have dredged borrow pits to over 7 m below grade (Newell et al., 1998; Michel et al., 2013; U.S. Army Corps of Engineers, Los Angeles District 2015; unpublished data), leading to significant losses of productivity for hundreds of acres of rich habitat for many decades due to the loss of sedentary megafauna.

Soft-sediment ecosystems generally comprise four major types of assemblage. These include: 1) demersal fish and epifaunal invertebrate assemblages such as are sampled by trawling, dredging, etc.; 2) meiofauna, a varied group of tiny animals including nematodes, polychaetes, harpacticoid copepods, and ostracods that pass through a 0.5-mm mesh screen and generally live in porewater between the sand grains; 3) macrofauna, small, abundant, shorter-lived invertebrates including many kinds of small polychaetes and other worms, crustaceans, and bivalves retained on a 0.5- or 1.0-mm sieve that live within the sediment and are easily sampled with conventional grab or core samplers, i.e., the 'weeds'; and 4) sedentary, buried or burrowing perennial megafauna, which are much less abundant than macrofauna but much larger and longer-lived, e.g., tubicolous polychaetes, large bivalves, snails, and echinoderms generally with minimum dimensions of >1 cm (i.e., the 'trees'). The latter live at the surface of the sediments or buried or burrowing, often to a meter or more deep in the sediment. Megafaunal organisms are generally too uncommon or too deeply buried to be captured in statistically meaningful numbers in standard grab/core sampling programs with low sample replication.

The megafaunal and macrofaunal assemblages are components of the overall infaunal assemblage. However, in terms of their roles, they appear to be distinctly different. Both are linked to demersal and other predator assemblages primarily by benthic-pelagic coupling. In the case of macrofauna, this is mainly through lethal predation. Lethal predation is important for sedentary megafauna as well, but as is shown by a large body of autecological research summarized by Lawrence and Vasquez (1996), Lindsay (2010), and Lees (2021), sublethal predation is very important for megafaunal assemblages and higher trophic levels through secondary production from infaunal systems. Because both megafauna and sublethal predation have been largely ignored or overlooked in community analyses for infaunal ecosystems, the value of infaunal assemblages on continental shelves has been substantially underestimated and under-appreciated

These soft-sediment assemblages are found in varying degrees of development and richness in or on most unconsolidated sediments (Thorson, 1957). These include mud flats, sand beaches, sandy/silty plains on continental shelves, continental slopes, or abyssal plains. Biomass is generally greatest and biodiversity is substantial in intertidal and subtidal heterogeneous gravel sediments (Lees and Driskell, 1980).

C. G. J. Petersen was among the earliest scientists to attempt describing communities associated with marine sedimentary ecosystems (Petersen, 1913, 1915). The main objective of his pioneering studies of benthic assemblages was to quantify food resources available to support productive fisheries in the seas around Denmark. Toward this end, Petersen quantified principally large, persistent, mostly perennial megafaunal and epifaunal species living on or burrowing in seafloor sediments. His classic studies were subsequently followed up by several other investigators in the Atlantic Ocean (Ford, 1923; Buchanan, 1958, 1963). Thorson (1957) published a monograph that summarized a large number of infaunal studies from many areas in the world. Based on these, he identified ten general level-bottom communities from around the world that are characterized mostly by sedentary megafaunal taxa.

The initial studies of infauna living in sediments around North America were conducted on the Atlantic coast by Sanders (1956, 1958, 1960) and McNulty (1961). Nearly concurrently, the AHF conducted the first sampling of sedimentary biomes on the continental shelf off southern California (AHF, 1965). Data for these infaunal assemblages were analyzed by Barnard and Hartman (1959), Barnard and Ziesenhenne (1961), Barnard (1963), and Jones (1969).

Little research has focused on quantifying sedentary megafaunal assemblages living in estuarine or nearshore sediments. Most sampling of these assemblages was done in the 1960s and 1970s, by direct observation using SCUBA or submersible techniques, especially in southern California and France. Starting in 1960, Fager (1971) conducted studies on these assemblages and their effects on sediment stability at 12- to 14-m depths off La Jolla, CA. In 1965, Massé (1972) started conducting extensive air-lift excavation studies of macrofauna and megafauna combined in the upper 30–40 cm of sediment at depths between 1.5 m and 11 m off the Brittany coast of France. In 1970, Morin et al. (1985, 1988) started on a 5-year visual study to quantify biodiversity and stability for megafaunal assemblages living in nearshore sandy sediments at depths between 2.6 and 13.1 m off Zuma Beach, CA. A broad-scale study of Strangford Lough, Northern Ireland, included general observations of a variety of unconsolidated and rocky habitats in the lough (Erwin, 1977). These surveys were conducted by flying a sled over the seafloor, recording mainly epifaunal taxa but some readily identifiable infaunal taxa; the surveys were not quantitative. In 1974, Environmental Quality Analysts and Marine Biological Consultants studied co-occurring megafaunal and macrofaunal assemblages at five depth levels between 14 and 55 m on the Hueneme Shelf off Oxnard, CA (EQA and MBC, 1974a, 1974b). These latter studies provide the data that are the basis for the analyses in this paper. From 1974 to 1977, Davis et al. (1982) studied effects of man-made structures on megafaunal, macrofaunal, and demersal fish assemblages at depths ranging from 13 to 18 m near La Jolla, and at 18 to 34 m around offshore oil platforms in southern California. A study at the 18-m depth that incorporated all three benthic assemblages mentioned above showed very clearly the relationships and interactions between these components (VanBlaricom, 1982). This study demonstrated the importance of megafauna. None of these visual studies quantified abundance or biomass of buried or burrowing forms.

Two intertidal studies during this period examined biomass aspects. From 1969 to 1972, Peterson (1975, 1977) studied intertidal sedentary megafauna in two estuaries in southern California. An important element was his documentation of vertical distribution of species and biomass in the upper 56 cm of the sediments. Later, Lees et al. (1986) examined coexisting megafaunal and macrofaunal components in a mudflat in Cook Inlet, Alaska, in 1977/78. These studies demonstrated that sedentary megafauna can strongly dominate biomass for infaunal components to a depth of at least 50 cm into the sediment.

One study that involved sedentary megafauna on the Atlantic coast was a 1960 investigation to assess effects on the benthos of abating discharges of domestic sewage into Biscayne Bay, FL, USA (McNulty, 1970). In another, samples for a macrofaunal study in Cape Cod Bay included some sedentary megafauna (Young and Rhoads, 1971) but ultimately, these investigators mostly ignored these species because they caused undesirable anomalies in their biomass analyses.

Parry (2002) and Powell and Mann (2016) addressed the biomass issue that is discussed in detail below (Section 4.2). They noted the failure of most infaunal sampling programs to adequately collect megafauna and demonstrated how conventional sampling programs therefore "grievously underestimate" biomass in soft sediments where "large infauna are present even at moderate densities" (Powell and

Mann, 2016).

In contrast to the paucity of megafaunal studies, hundreds of studies focusing on macrofauna have been conducted around the world over this period (see Gray and Elliott, 2009). Consequently, current paradigms for sedimentary ecosystems have been driven by findings for macrofaunal assemblages, even though they probably comprise, on the whole, only a minor part of these systems overall. An important consequence of this is that sedimentary biomes are considered far less valuable than is warranted. Consequently, far less than adequate protection and research funding have been provided. Moreover, the level of injury to these assemblages due to anthropogenic activities is probably severely underestimated.

Besides providing descriptions of three sedentary megafaunal assemblages in southern California, an objective of this paper is to provide an opening discussion on some important aspects of these types of assemblage, compare these attributes between megafaunal and macrofaunal assemblages, and add context to Tomašových's and Kidwell's and Powell's and Mann's claims, which likely are applicable to nearshore areas over a vast portion of the world's continental shelves. Another purpose is to draw attention to the concept and importance of sublethal predation in infaunal ecosystems. Our lack of knowledge on the nature and dynamics of megafaunal assemblages in sedimentary ecosystems constitutes a major data gap in our understanding of what will likely be found to be highly productive nearshore systems and our ability to understand effects of anthropogenic activities and climate change.

2. Methods

2.1. Study site

The study, designed by the Los Angeles Regional Water Control Board, was designed to identify important natural resources and assess potential biological effects that might result from extending the existing wastewater outfall 1.6 km farther offshore. Approximately 12 million gallons per day of treated effluent were discharged through a diffuser section extending between depths of 15 and 18 m (EQA and MBC, 1975). Evaluation of the Organic Sediment Index (OSI; Ballinger and McKee, 1971) based on sediment organics (Total Organic Carbon [TOC] and Total Kjeldahl [TKN]) provides no indication of effluent effects on sediments anywhere in the study area. Ballinger and McKee (1971) categorized sediment with OSI values below 0.5 as clean sand or clay. Values for OSI ranged from 0.02 to 0.61. The highest value, an outlier, was located at the 55-m depth on Transect A on the edge of Hueneme Submarine Canyon (Fig. 1). OSI averaged 0.15 ± 0.12 overall; OSI values at the five stations closest to the OSD outfall averaged 0.07 ± 0.03.

Although significant deleterious environmental impacts have been reported within 400 m of much larger outfalls around the world (McNulty, 1961; Bellan-Santini, 1968; Borowitzka, 1972; SCCWRP, 1973; Burd et al., 2012), deleterious effects were not observed at the station nearest the diffuser (B18 $\approx$ 400 m distant). Consequently, I have assumed that effects of the outfall, if any, can be ignored for the descriptive purposes of these analyses.

In this moderately exposed nearshore area, we compared species composition, density, and biomass of macrofauna and species composition and density for sedentary megafauna living at five depth levels (14, 18, 27, 37, and 55 m) along four transects oriented perpendicularly to shore (Fig. 1). The supporting data are based on an intensive 1974 study for and funded by the Oxnard Sanitation District of sedentary megafauna and macrofauna living in nearshore sediments on the Hueneme Shelf, off Oxnard in southern California. The study area extended approximately 4.4 km along the shore and about 6.4 km offshore. The alignments of Transects A and C were about 0.8 km NW and SE of the Oxnard outfall line. Transect B was approximately aligned with the outfall line. The reference Transect OC was located approximately 3.6 km east of the outfall line. Sampling locations were determined through a combination of radar fixes, alignment of onshore landmarks, and tide-corrected depths.

2.2. Sample collection and data development

Very different approaches were employed to survey sedentary megafauna and macrofauna. Macrofauna comprised the small animals sampled by a 0.0413-m^2 Shipek grab sampler and retained on a 0.5-mm sieve. Based on sample volume data, we estimate that average depth sampled into sediments was $\approx$2 cm. Sedentary megafauna, sampled only during spring and fall surveys, included the larger, less numerous animals visually observed and counted in replicated ¼-m^2 quadrats by a diver/biologist using either SCUBA or submersible techniques to assess their abundance. These surveys enumerated only animals observed or producing identifiable surface features. Consequently, many large buried organisms were missed or undercounted. I acknowledge the approach taken is imperfect because it misses many of the buried components of the sedentary species but was the most widely employed and practicable approach at the time. Nonetheless, this approach does provide at least a limited perspective on the poorly described sedentary megafaunal assemblages.

Compared to current conventional macrofaunal sampling protocols, the Shipek grab sampler is inadequate. However, this program was conducted when marine scientists were struggling to determine the best ways to sample infauna. No standards (e.g., ISO 16665:2005) were available at the time. Although both techniques provide only limited accuracy on biodiversity and biomass, because of the dramatic contrasts between the two types of assemblages, the comparisons are considered highly defensible.

The approach for determining dominant taxa varied between megafauna and macrofauna. In both cases, the ten most abundant taxa at any depth level were considered dominants. The lists for Surveys I and II were then combined. In addition, megafaunal taxa estimated to contribute high biomass due to size and/or estimated biomass were added to the list of abundance-based megafaunal dominants if they were common but did not qualify as numerically dominant.

Macrofaunal biomass for each site was measured as blotted whole wet weight for 1) polychaetes and 2) all other taxa combined. For sedentary megafauna, biomass was conservatively estimated based on site density and likely whole wet tissue weight for specimens of average size for several dominant or larger taxa based on published literature cited below. The seven dominant species used were a large echiurid worm (*Listriolobus pelodes*), three large tubicolous polychaetes (*Diopatra ornata*, *D. tridentata*, and *Praxillura maculata*), a large bivalve (the geoduck clam, *Panopea abrupta*), an ophiurid (*Amphiura arcystata*), and a large holothurian (*Apostichopus californicus*). Secondary production for macrofauna range from 100 to 250%, based on turnover rates common in the literature (Boysen-Jensen, 1919; Cammen, 1979; Mistri et al., 2001; Nilsen et al., 2006; Gray and Elliott, 2009; Burd et al., 2013). The maximum rate was arbitrarily used for all calculations. For sedentary megafauna, secondary production was set at an average of 25% based on autecological literature for sublethal predation on several polychaetes, bivalves, echinoderms, and a crustacean, as described in Lees (2021). This conservative estimate does not account for production due to lethal predation, growth, respiration, excretion, and reproductive products.

Comparisons of life-span (longevity) estimates for megafaunal and macrofaunal species were based on literature records for minimum and maximum longevity for 17 megafaunal species common in the visual surveys and 33 macrofaunal species common in the grab samples. The literature sources for these longevity data are provided in Appendix F.

The discussion on geographic distribution was based on geographic ranges listed for species in EOL (Encyclopedia of Life), 2018 (http://www.eol.org).

2.3. Statistical analysis

Inferential statistical analyses were conducted primarily using

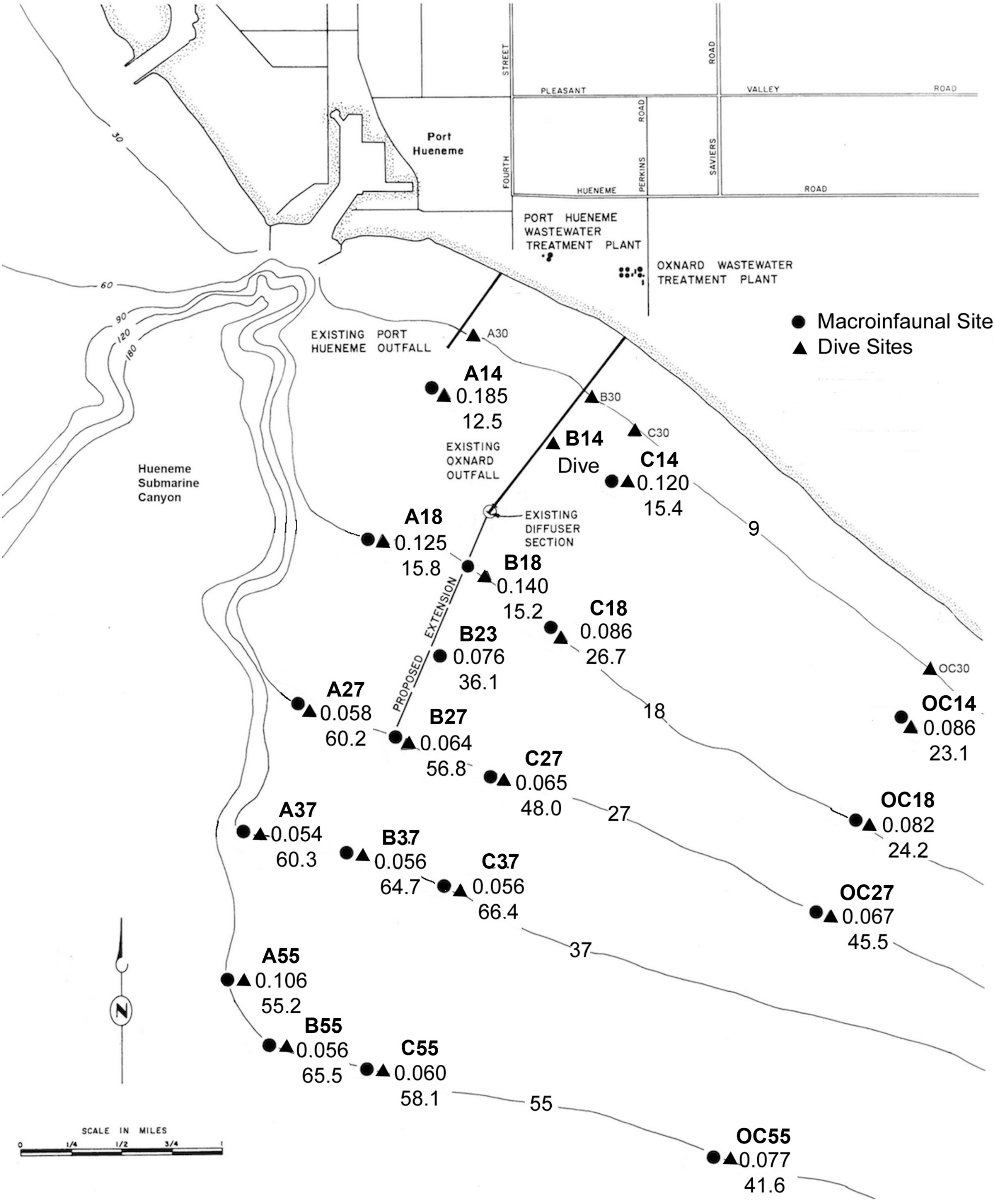


Fig. 1. Locations sampled in soft sediments on the Hueneme Shelf off Oxnard, California, USA, during the 1974 Oxnard Sanitation District pre-discharge receiving water monitoring program. Solid circles represent macrofaunal sampling sites, solid triangles represent direct-observation sampling sites. Upper numbers below site designations indicate median grain size (mm) and lower numbers indicate % silt/clay. Depth contours in meters.

resampling or randomization methodology, but standard parametric techniques were applied in some cases. The randomization approach approximates real probabilities based on the actual data and avoids transformations or assumptions required by parametric statistics that often are not applicable to biological field data. A Microsoft Excel add-in developed by Resampling Stats (Blank et al., 2001) was employed for resampling or randomization comparisons of means and ANOVA for sediment or biological variables. Relationships between variables were evaluated with linear regression analyses, often calculated using with logarithmic or power transformations for best fitted curves (Zar, 2010).

To assess statistical significance, an α value of 0.1 was adopted as the critical level of significance for all statistical testing. Values of p between 0.1 and 0.2 have been considered to represent trends. Except where indicated otherwise, variation around means is represented as standard error.

Several multivariate analyses were employed using PRIMER 6 (Clarke and Gorley, 2006). These examined relationships within macrofaunal and megafaunal assemblages. The analyses included cluster analysis using the Bray-Curtis similarity index. These indices were entered into non-metric multidimensional scaling (MDS) analyses for two-dimensional comparisons. The analyses were conducted based on relationships between species and depth or patterns among species assemblages at sites with regard to depth and TKN.

Since organic nitrogen and carbon have long been recognized an important sources of nutrition for suspension and deposit feeding infaunal invertebrates (e.g., Johannes and Satomi, 1966; Tyson, 1995), it is likely that these types of organisms demonstrate preference for specific levels of organics. The degree of eurytopy was analyzed for TKN and TOC by analyzing ranges exhibited by dominant species in the study area. The range for each organic within which each species was observed was calculated by determining differences between maximum and minimum values for TKN or TOC observed at the sites at which each species was observed.

To compare megafaunal and macrofaunal geographic distributions, slopes and separation on the number of taxa in geographical range categories of compared regressions were evaluated using the compared linear regression approach outlined in Zar (2010), as implemented in IGOR Pro version 6.22A (http://www.wavemetrics.com). As used in this discussion, 'elevation' refers to comparative position on the y-axis of the number of taxa for macrofauna and sedentary megafauna relative to the various geographic range categories, which are depicted on the x-axis of a graph.

For variables compared at multiple depth levels or for long-term studies addressed in the Discussion section, variability was evaluated using the Coefficient of Variation (CV) for a category or species (Krebs, 1998). For these long-term studies, CV was calculated for each species based on replicates within each survey during a study and averaged for the surveys comprising the study. These values were averaged for each species comprising macrofaunal (ephemeral) and megafaunal (perennial) assemblages under consideration. The premise was that, because they have greater longevity and therefore should be temporally more stable, CV values for megafaunal assemblages should be lower than for macrofaunal assemblages. The respective CV values thus were compared with 1-tailed paired resampling comparison of means.

3. Results

3.1. Measured environmental factors

Sedimentary environmental factors examined during this study that can influence infaunal organisms included median particle size (Md), silt/clay, TKN, and TOC. Sediments were predominantly fine sand but ranged from coarse silt to medium sand. Median grain size became significantly finer with increasing depth, from a mean of 0.13 mm at 14 m to 0.074 mm at 55 m (Fig. 1; $p < 0.0005$, power function regression). Silt/clay, TKN, and TOC increased directly with depth ($p < 0.0005$, power function regression; <0.0005, log function regression; and <0.0025, power function regression, respectively). These sediment variables were not autocorrelated with depth. Although TOC, silt/clay, and Md all exhibited significant correlations ($<0.05 < p < 0.0005$), TKN correlated significantly only with TOC ($p < 0.05$).

3.2. Species composition and abundance

Only three of ≈510 macrofaunal taxa identified during this study were classified as dominants among ≈100 sedentary megafaunal taxa identified in concurrent visual surveys (Table 1, Appendix A through Appendix D). These included an echiurid (*Listriolobus pelodes*), the long-lived geoduck clam (*Panopea abrupta*), and an ophiurid (*Amphiodia urtica*). For the echiurid and clam, only juveniles were observed in macrofaunal samples and only adults were observed in the megafaunal surveys. The macrofauna was dominated by small polychaete worms and several classes of microcrustaceans. In contrast, the sedentary megafauna was dominated by large tubicolous polychaetes, bivalves, and echinoderms.

Abundance of macrofaunal organisms in the grab samples was nearly 80 times greater than the numbers of the visually observed sedentary megafauna in many m^2 of area surveyed visually (Table 2). On average, values did not vary significantly by season or depth for either category (one-way resampling ANOVA). Nevertheless, because juvenile macrofaunal organisms were common during the spring survey, fall data mostly lacking seasonal juveniles were considered more representative and therefore were used for non-metric multidimensional scaling analyses.

3.3. Zonation by depth levels and distribution related to sediment properties

Zonation by depth was strong in both assemblages (Fig. 2). Megafauna segregated by depth into three visually distinctive and recognizable assemblages. The 14- and 18-m depth levels were dominated by large tubicolous suspension-feeding polychaetes, especially *Diopatra ornata* (Fig. 3) and *Diopatra splendidissima* (Table 1, Appendix A). The 27-m level was dominated by two bivalves (the very large geoduck clam, *Panopea abrupta*, and the large mahogany clam,?*Nuttallia nuttallii*; Fig. 4; Appendix B) and a large burrowing ophiurid (*Amphiura arcystata*). The 37- and 55-m levels were strongly dominated by a tubicolous suspension-feeding polychaete, the umbrella worm, *Praxillura maculata*, which appeared in dense meadow-like aggregations (Fig. 5; Appendices C and D). The large burrowing echiurid, *Listriolobus pelodes*, also was common at these depths.

In contrast, even though they had far greater numbers of individuals and taxa than the megafauna, the assemblages of small macrofaunal organisms mostly could not be perceived visually in the field because they comprised primarily small burrowing and tubicolous polychaetes and five higher taxa of microcrustaceans (Table 1; Appendices A through D). Abundance varied broadly by survey and depth level in both categories but substantially less so for macrofauna than for megafauna (Table 2a); coefficients of variation were substantially lower for macrofauna than for megafauna. Species richness was relatively stable by survey and depth level for both categories (Table 2b).

For both assemblages, stations in Survey II segregated very clearly on the basis of depth (Fig. 2). Except for Station 14A, all stations from the two shallower depth levels were loosely associated in groupings with greater than 60% similarity (Group A). For both assemblages, each of the three deeper depth levels and the 23-m station for macrofauna exhibited greater than 70% similarity (Group B). The taxa also segregated most strongly on the basis of depth.

The peculiarity of Station 14A is likely due to a decades-long biennial input of coarser sand resulting from a channel dredging/beach replenishment program by the U.S. Army Corps of Engineers (pers. obs. from 1972 to 1975). The dredged sand is discharged on the beach north of the station. Median grain size at this station is substantially coarser and % silt/clay is lower than other 14-m stations (Fig. 1).

Table 1

Comparison of mean density for most common species in macrofaunal samples and megafaunal surveys at the 14-m depth level on the Hueneme Shelf during Surveys I and II for the 1974 Oxnard Sanitation District studies. Underlined taxa are considered ephemeral organisms.

Macrofaunal samples			Megafaunal surveys		
	Survey I	Survey II		Survey I	Survey II
Taxon/Survey	Mean[a] ± SE	Mean ± SE	Taxon/Survey	Mean ± SE	Mean ± SE
Angulus modestus-B[b]	97.1 ± 59.0	81.1 ± 27.7	*Diopatra ornata*-P	5.2 ± 2.3	32.4 ± 31.1
Chaetozone setosa-P	77.5 ± 46.7	15.9 ± 9.2	*Astropecten verrilli*-E	2.0 ± 1.1	0.4 ± 0.3
Lumbrineris sp.-P	68.9 ± 29.2	25.0 ± 5.8	*Aglaophenia dispar*-E	1.9 ± 0.8	0.02 ± 0.02
Scoloplos armiger-P	45.1 ± 39.6	28.7 ± 5.2	*Onuphis elegans*-P	1.2 ± 1.0	14.3 ± 13.5
Anaitides sp.-P	42.7 ± 20.3	20.8 ± 7.3	*Diopatra splendidissima*-P	0.2 ± 0.1	0.5 ± 0.2
Armandia brevis-P	32.3 ± 16.7	12.2 ± 5.4	*Hydrallmania distans*-H	0.1 ± 0.1	0.4 ± 0.4
Magelona sacculata-P	30.5 ± 17.7	3.7 ± 2.1	*Spiochaetopterus costarum*-P	0.05 ± 0.03	0.2 ± 0.1
Prionospio pygmaeus-P	30.5 ± 16.8	144.1 ± 61.6	*Pisaster brevispinus*-E	0.02 ± 0.02	0.06 ± 0.03
Cumella sp. A-C	28.5 ± 11.7	53.1 ± 32.2			
Mediomastus ambiseta-P	26.2 ± 19.0	5.5 ± 1.8			
Micronephtys cornuta-P	26.2 ± 10.1	109.8 ± 86.6			
Erichthonius punctatus-C	9.8 ± 7.5	20.1 ± 20.1			
Dendraster excentricus-E	8.1 ± 3.5	317.1 ± 209.1			
Munna sp.-C	5.7 ± 1.9	20.1 ± 12.1			
Chaetozone corona-P	0.0 ± 0.0	34.8 ± 29.4			

[a] Mean of sum of three replicate grab samples for all sites at this level.

[b] Higher taxon abbreviations: B – Bivalve; C – Crustacean; E – Echinoderm; H – Hydroid; P - Polychaete.

Table 2

Comparison of density (individuals/m^2) and taxa for macrofauna and sedentary megafauna at depth of 14, 18, 27, 37, and 55 m on the Hueneme Shelf during Surveys I and II for the 1974 Oxnard Sanitation District studies.

Depth level	14 m	18 m	27 m	37 m	55 m	Overall mean ± SE	Coefficient of variation (%)
a. Number of Individuals							
Macrofauna							
Spring	2200	3585	2351	3069	3103	2862 ± 257	20.1
Fall	2381	2418	3215	2738	3158	2782 ± 177	14.2
Sedentary Megafauna							
Spring	12.0	51.9	12.5	52.3	30.7	31.9 ± 8.9	62.5
Fall	49.7	75.0	17.7	20.3	35.9	39.7 ± 10.5	59.3+
b. Number of Taxa							
Macrofauna							
Spring	141	201	200	179	210	186.2 ± 12.4	14.9
Fall	116	192	203	159	192	172.4 ± 15.9	20.6
Sedentary Megafauna							
Spring	20	26	32	36	38	30.4 ± 3.3	24.4
Fall	16	27	47	34	34	33.6 ± 5.7	37.7

Segregation of stations on the basis of TKN, TOC, and % silt/clay was somewhat similar to that observed for depth, but patterns within subgroups were varied and weaker. Segregation among these factors was strongest for TKN, slightly weaker for TOC, and weak for % silt/clay. Segregation by Md was poor.

3.4. Biomass

Even though macrofaunal organisms in this study area were ≈80 times more abundant than the sedentary megafaunal organisms (Table 2), conservative estimates for biomass indicated that megafaunal standing stocks were orders of magnitude greater than for macrofauna (Table 3d and e). Biomass for macrofauna, ranging from 2.8 to 12.8 g wet tissue weight/m^2 by depth level, averaged 6.7 ± 3.9 g wet tissue weight/m^2 across depths. It increased regularly with increasing depth. Conservative estimates for sedentary megafauna ranged from 25.3 to 1096.8 g wet tissue/m^2 by depth level and averaged 287.0 ± 455.7 g wet tissue weight/m^2 across depths. Megafaunal biomass peaked at the 27-m depth level, where two large clams and ophiurids were most abundant.

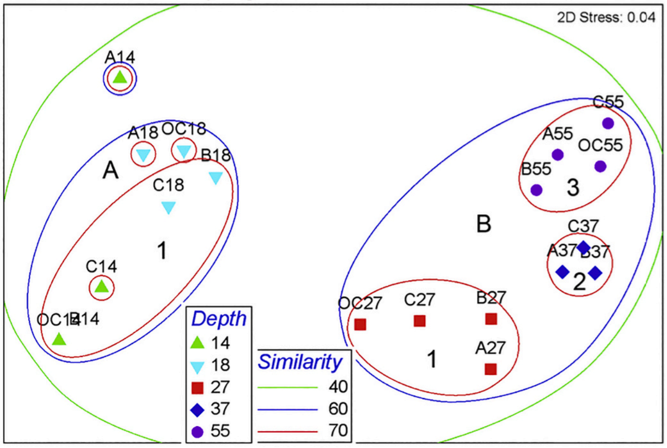
Estimates for megafaunal biomass are highly conservative for the five depth levels because they are based on only seven dominant megafaunal species. Estimated biomass at each depth level for the most important species from the three designated megafaunal assemblages is shown in Table 3. Geoduck clams (*P. abrupta*) were by far the most important contributor to biomass. Summed estimated biomass for the seven megafaunal organisms was 42.9 times greater than the measured weight for macrofauna in this study (Table 3). Likewise, estimates for macrofaunal biomass are conservative because of the small size of the sampler.

3.5. Geographic distribution and environmental sensitivity

Geographic distribution patterns for megafaunal taxa were generally more regional than for macrofaunal taxa, 44% of which appear to have cosmopolitan distributions (Fig. 6); 74% of the macrofaunal taxa had ranges exceeding 2500 km. In contrast, geographic distribution for dominant sedentary megafauna was significantly more constrained. Only 8% of megafaunal dominants (two species) have cosmopolitan distributions and only 44% have ranges greater than 2500 km. These differences in patterns for number of species within specific geographic ranges are significant, with megafaunal species declining but macrofauna increasing with increasing geographic range (slope, $p = 0.007$, and elevation, $p = 0.047$; compared linear regression analysis).

Dominant megafaunal species also exhibited greater specificity than macrofaunal species to three important environmental attributes. On average, megafaunal taxa were significantly more depth-specific than macrofauna (Fig. 7, Table 4; 1-tailed resampling comparison of means). The majority of megafauna occurred at two or three levels (71%). In contrast, the majority of macrofaunal taxa (58%), but only12.5% of

a. Dominant sedentary megafaunal taxa.



b. Dominant macrofaunal taxa.

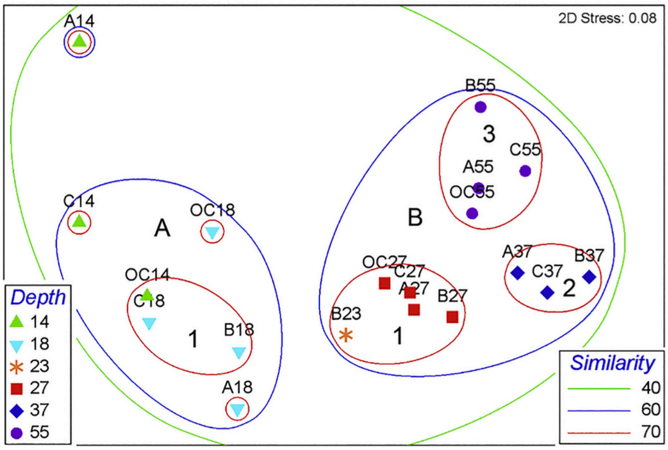


Fig. 2. Multidimensional scaling plots showing strong depth distribution patterns among stations based on dominant taxa for: a) sedentary megafauna; and b) macrofauna on the Hueneme Shelf during Survey II for the 1974 survey for Oxnard Sanitation District. Letters in station names represent transect designation and numbers represent station depth (m).

Fig. 3. Appearance of habitat in the shallow depth range on the Hueneme Shelf was characterized by moderately dense beds of the tubicolous parchment worm, *Diopatra ornata*, whose tubes are hidden here under attached red algae.

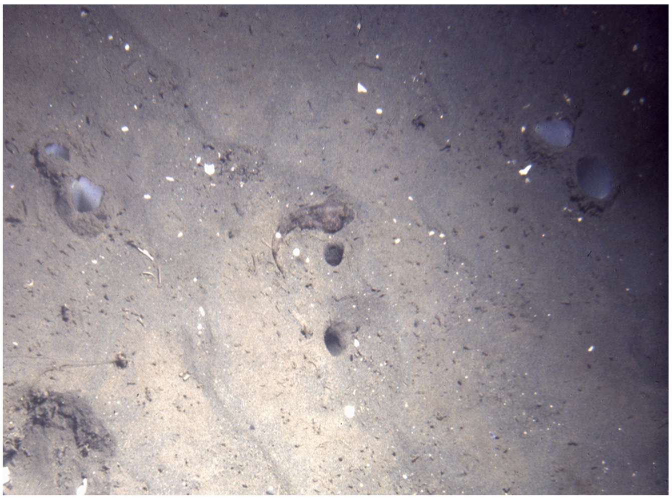


Fig. 4. Appearance of habitat in the middle depths on the Hueneme Shelf was characterized by beds of the geoduck clam, *Panopea abrupta*, and a large clam with separate siphons (?*Nuttallia nuttallii*). Siphon openings for both species span ≈8 cm.

megafaunal taxa, occurred at all five depth levels.

Organic nitrogen and carbon are important as nutrients for suspension- and deposit-feeding infaunal organisms and could influence their distribution. TKN ranged from 150 to 870 mg/Kg; TOC ranged from 0.11 to 0.89%. Based on the mean of differences between highest and lowest concentrations for TKN and TOC in sediments at stations at which each taxon was observed, the range of concentrations for these organics was significantly more specific (narrower) for sedentary megafaunal species than for macrofauna (Table 4; 1-tailed resampling comparison of means). The ranges in median particle size (coarsest minus finest) did not differ significantly between megafaunal and macrofaunal taxa (0.11 ± 0.01 mm vs. 0.10 ± 0.01 mm; $p = 0.49$; 2-tailed resampling comparison of means).

4. Discussion

4.1. Species composition and abundance

Types of dominant sedentary megafauna differed markedly from macrofaunal dominants. The megafauna included easily visible, large, relatively long-lived species of tubicolous polychaetes, bivalves, and a variety of echinoderms (a sea cucumber, ophiurids, and sea stars; Figs. 2, 3, and 4), many of which are important ecosystem engineers that also contribute substantial biomass and secondary productivity to associated systems. In contrast, macrofaunal samples were dominated by small

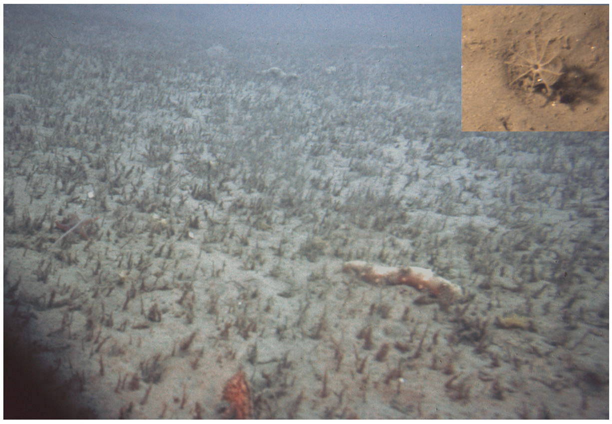


Fig. 5. Appearance of deeper depths on the Hueneme Shelf was characterized by beds of a moderate-sized tubicolous Umbrella worm, *Praxillura maculata*. The large sea cucumber, *Apostichopus californicus*, (right center) was also a dominant species. Note the tessellated structure of the worm tube and the numerous burrows of unidentified burrowing organisms in the insert.

Table 3

Biomass and secondary production estimates (g wet tissue/m^2) for sedentary megafauna and macrofauna based on density at specific depth levels on the Hueneme Shelf during Surveys I and II for1974 Oxnard Sanitation District studies. a, b, c. Values for sedentary megafaunal species that dominate in one of the three identified megafaunal assemblages. d. Estimates for seven dominant megafaunal species based on observed mean density and estimated mean wet tissue weights. e. Mean measured biomass and estimated secondary production for macrofauna.

Depth level	14 m	18 m	27 m	37 m	55 m
Estimates for three dominant sedentary megafaunal organisms on Hueneme Shelf					
a. *Diopatra ornata* (tubicolous polychaete worm)					
Observed Mean Density at Level (no./m^2)	18.81	31.24	0.45	0	0
Est. Mean Biomass (g/m^2)[a]	78.3	129.9	1.87	0	0
Est. Sublethal Predation Loss (g/m^2/year)[b]	19.6	32.5	0.47	0	0
b. Geoduck clam (*Panopea abrupta*)					
Observed Mean Density at Level (no./m^2)	0	0.1	2.94	0.1	0
Est. Mean Biomass (g/m^2)[c, d, g, h]	0	35.7	1089.0	34.0	0
Est. Sublethal Predation Loss (g/m^2/year)[d]	0	8.9	272.2	8.5	0
c. Umbrella worm (*Praxillura maculata*)					
Observed Mean Density at Level (no./m^2)	0	0	0	21.68	17.18
Est. Mean Biomass (g/m^2)[e]	0	0	0	22.55	17.86
Est. Sublethal Predation Loss (g/m^2/year)[d]	0	0	0	5.64	4.47
d. Conservative estimates for biomass and secondary production for sedentary megafauna					
Estimated Wet Tissue Weight (g/m^2)[e]	78.3	167.2	1096.8	67.5	25.3
Est. Secondary Production (g/m^2/year)[f]	19.6	41.8	274.2	16.9	6.3
e. Mean measured biomass and estimated secondary production for macrofauna					
Observed Wet Tissue Weight (g/m^2)	2.76	5.97	4.42	7.50	12.81
Est. Range of Secondary Production (g/m^2/year)[g]	2.76–6.90	5.97-14.92	4.42–11.05	7.50–18.75	12.81–32.02

[a] Mean individual weight used = 4.16 g/worm. Based on 3.3 g from Berke et al. (2009) and 5.0 g from Morin et al. (1985).

short-lived polychaetes and microcrustaceans, mostly nearly invisible during visual surveys. Macrofaunal biomass and secondary production are significantly less important. While species richness and abundance differ dramatically between these assemblages, because of the greater importance of biomass, secondary production, and the influences of ecosystem engineers on the ecology and geochemistry of the ecosystems, these differences become irrelevant to the discussion.

Data from studies by Petersen (1913, 1915) and several others included megafauna and macrofauna, but they did not make the types of ecological distinctions that are covered in this paper. Based on work by Spärck (1935), Jones (1950), and others, Thorson (1957) described 10 level-bottom infaunal communities that he characterized using mainly sedentary megafaunal genera or, in some cases, higher taxa. The communities were characterized and depicted in figures by several different clams (*Macoma*, *Tellina*, *Venus*, and *Syndosmya* [=*Abra*]), some ophiurids (*Amphiura*, *Amphiodia*, *Amphioplus*, and *Ophiura*), two snails (*Turritella* and *Cerithium*), and a tubicolous polychaete, *Maldane*. Foraminifera or an amphipod characterized two other communities. The important point is that most of these communities were characterized by megafaunal rather than macrofaunal organisms and most subordinate species listed were also megafauna. This was mostly true in the descriptions of infaunal assemblages off southern California by Barnard and Hartman (1959), Barnard and Ziesenhenne (1961), and Jones (1969).

4.2. Biomass and secondary production

Biomass was an important criterion in these decisions by Petersen (1913, 1915) and his approach was followed by most infaunal investigators until Sanders (1956), who was unable to apply it because his sampling equipment was designed to sample only the upper 7.6 cm of sediment. The sampling design, i.e., a single shallow sample collected at each site during each survey, was inadequate for collecting most sedentary megafauna. Consequently, biomass of the rarely collected megafauna produced what was deemed unacceptably high variability for biomass analyses. Later, Sanders (1960) concluded: “Numbers are considered more valid than biomass in quantitative benthic studies, since only 0.15% of the fauna [individuals] constitute 55.17% of the entire [sample] weight.” Based on a conservative estimate for sedentary megafaunal biomass in this study (only seven species), ≈1% of the fauna comprised ≈98% of the biomass. Nonetheless, Sanders’ approach for sampling infauna, i.e., relatively small shallow samples and low replication, has been adopted as the model for infaunal sampling by the generations that followed.

Estimates for megafaunal biomass and secondary production in this

[b] Based on estimated mean loss of 30 mg dry weight/worm from head and chaetigers for *Diopatra cuprea* Berke et al. (2009) and reconstitution to wet weight using wet to dry weight conversion factor of 0.1725 (Thorson, 1957).

[c] Mean individual whole weights estimated as 872 g (Goodwin and Pease, 1989); conversion factor to wet tissue weight = 0.425 (Andersen Jr., 1971).

[d] Turnover rates estimated as roughly 25% based on literature cited below for polychaetes, bivalves. and ophiurids in Section 4.6 on sublethal predation.

[e] Mean individual weight estimated at 25% of *Diopatra cuprea* wet weight; used = 1.04 g/worm.

[f] Based on sum of *D. ornata*, *P. abrupta*, and *P. maculata* above plus contributions from *A. arcystata*, *D. tridentata*, *Listriolobus pelodes*, and *Apostichopus californicus*.

[g] Megafaunal turnover rates estimated as roughly 25%/year based on literature cited below for polychaetes, bivalves, and ophiurids in Section 4.6 below on sublethal predation.

[h] Macrofaunal turnover rates estimated as 100 to 250% based on Burd et al. (2013).

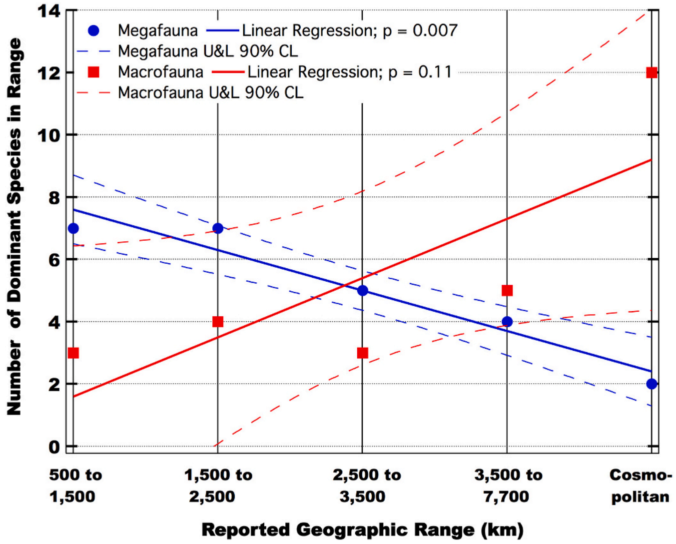


Fig. 6. Number of dominant sedentary megafaunal and macrofaunal species comprising infaunal assemblages on the Hueneme Shelf during Oxnard Sanitation District studies in 1974 with distributions limited to specified geographic ranges. The geographic range assigned to most species is based on reports in the Encyclopedia of Life website (http://www.eol.org). Ranges for others are based on other widely researched reference documents (Coan et al., 2000; Morris et al., 1980). U&L 90% CL means upper and lower 90% confidence limits.

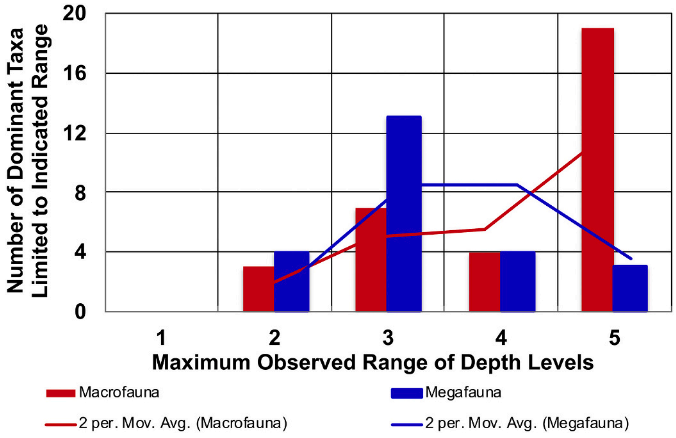


Fig. 7. Numbers of taxa in dominant higher taxonomic groups in megafaunal and macrofaunal assemblages at five depth levels in Surveys I and II on the Hueneme Shelf during the Oxnard Sanitation District studies in 1974. Moving average is for two depth levels.

Table 4

Comparison of ranges in mean number of depth levels and mean breadth of range of variation for TKN (mg/Kg) and TOC (%) concentrations occupied by dominant sedentary megafaunal and macrofaunal taxa observed on the Hueneme Shelf during Surveys I and II for the 1974 OSD studies.

	Macrofauna (n = 33)	Sedentary megafauna[a]	p[b]
Mean Depth Levels ± SE	4.18 ± 0.19	3.25 ± 0.18 (n = 24)	0.0015
Mean TKN Breadth ± SE	582.4 ± 26.4	482.5 ± 33.7 (n = 20)	0.013
Mean TOC Breadth ± SE	0.51 ± 0.03	0.43 ± 0.04 (n = 20)	0.070

[a] Several megafaunal species evaluated for depth levels live independently of and were not evaluated for sediment organics, accounting for differences in n.

[b] 1-tailed resampling comparison of means.

study area are very conservative but clearly indicate dominance by megafauna. Megafaunal estimates are based on only seven of 31 dominant species megafaunal taxa. Notably, they do not include any large buried taxa that could not be identified by surficial clues during the visual surveys. Macrofaunal estimates based on lab measurements of the small animals living in the upper few centimeters of sediment are also conservative. Nevertheless, conservative estimates for megafauna were substantially higher than for macrofauna at all depth levels (Table 3; Fig. 8). Estimates for macrofaunal biomass comprised only ≈2.3% of the estimated total infaunal biomass per unit area in the OSD study area. This pattern is repeated in other studies described below.

Estimates of mean secondary production for the abbreviated megafauna at 14-, 18-, and 27-m levels were an order of magnitude higher than for macrofaunal assemblages because of large contributions through sublethal predation on tubicolous polychaetes and the geoduck clam (*P. abrupta*; Table 3; Fig. 8). Although secondary production at the 37- and 55-m levels appeared lower for megafauna than for macrofauna, adding biomass and secondary production for several other megafaunal dominants observed at those levels (e.g.,? *Nuttallia nuttallii* and a sea pen; see Appendices C and D) would substantially raise estimates for biomass and secondary production.

The average annual turnover rate applied for megafauna, approximated at 25%, is quite conservative as it was based solely on rates of sublethal predation for polychaetes, clams, and ophiurids (see Section 4.6). It does not

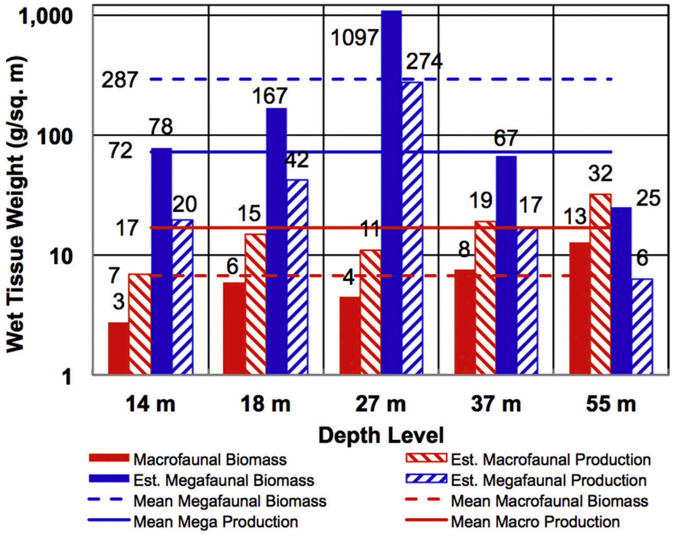


Fig. 8. Comparison of 1) observed biomass and estimates for secondary production for macrofaunal assemblages and 2) estimated conservative biomass and secondary production based on estimated sublethal predation for megafaunal assemblages at five depth levels on the Hueneme Shelf during 1974 Oxnard Sanitation District studies.

account for several other major processes related to secondary production, e.g., lethal predation, growth, respiration, excretion, and reproductive products. The maximal annual turnover rate used for the macrofaunal assemblages, where published rates range from 100 to 250% (Burd et al., 2013), was 250%. Conservative biomass and secondary production for these seven megafaunal organisms were 42.9 and 4.3 times greater, respectively, than those for the macrofauna sampled (Table 3).

Similar relationships between megafaunal and macrofaunal biomass have been reported in other areas. For example, five surveys were conducted over 18 months at four intertidal elevations (+1.1, +0.8, +0.3, and – 0.4 m) on a mudflat on the west side of Cook Inlet, Alaska (Lees et al., 1986). Forty 0.009-m^2 core samples 15 cm deep were collected in each survey, providing a good representation of both sedentary megafauna and macrofauna. Mean whole wet weight for the sedentary megafaunal assemblage dominated by bivalves (*Macoma balthica* (n = 5439) and three species of *Mya* (n = 104)) was 2455 ± 406 g whole wet weight/m^2/survey. In contrast, whole wet weight for the macrofaunal component averaged 42.6 ± 7.7 g whole wet weight/m^2/survey ($p = 0.0003$; 1-tailed resampling comparison of means). Macrofauna contributed only ≈1.7% of total whole wet weight in these core samples over the 18-month period of the study.

Comparably high levels for megafaunal biomass have been reported elsewhere in intertidal and subtidal sediments. In one example, a mactrid clam (*Lutraria lutraria*) contributed over 90% of the total biomass of 157.7 g ash-free dry weight/m^2 (≈2.3 Kg/m^2 whole wet weight) for the infaunal assemblage at 10-15 m depths in Plymouth Sound, England (Parry, 2002). The investigator stated: “Results indicate that the assessment of benthic biomass and respiration by consideration of macrofaunal samples alone will underestimate severely the biomass and respiration of the entire endobenthic [infaunal] assemblage”.

Populations of deep-burrowing ghost shrimp (*Callianassa* [now *Neotrypaea*] *californiensis*) in intertidal sand habitats in Puget Sound were sufficiently dense to constitute an “energetically valuable prey” for migrating gray whales (Weitkamp et al., 1992). Estimated consumption by the whales was 3–6 Kg of shrimp per foraging pit (nearly 1.5 Kg whole wet weight/m^2). Since sampled biomass inside the pits was 2–5 times lower than in surrounding sediments, it is clear that shrimp biomass must have exceeded 3 Kg whole wet weight/m^2 in the surrounding area.

Powell and Mann (2016) lamented that because of limitations in sampling gear and sampling design, large infaunal taxa are recorded only infrequently in community surveys of continental shelf benthos. They implied that, because megafauna are less abundant but much larger, this leads to poor estimates of biomass. They commented on the effects of patchy distribution and concluded: “Without recourse to modern high-volume sampling gear capable of sampling many meters at a swath, such as hydraulic dredges, biomass of the continental shelf will be grievously underestimated if large infauna are present even at moderate densities.”

This is clearly demonstrated in the OSD study, especially when its results are compared to other studies in southern California. Sedentary megafaunal biomass conservatively estimated in the OSD study was substantially higher than infaunal biomass measured in two major infaunal studies reporting for continental shelf depths within southern California based on conventional sampling methods. As part of its major study of the continental shelf off southern California in 1956/59, the Allan Hancock Foundation conducted complete taxonomic analysis on seven 0.25-m^2 orange-peel grab samples collected from within the relevant depth range in the OSD study area (AHF, 1965). Mean whole wet tissue weight in the AHF samples in this area (153.8 ± 121.4 g whole wet weight/m^2; Appendix E) averaged substantially lower than the conservative estimate for combined infauna in this study (293.7 g whole wet weight/m^2; Table 3). Notably, the AHF samples collected with a ¼-m^2 grab sampler lacked most of the species that dominated in the OSD visual megafaunal surveys.

Many species that dominated macrofaunal samples in the OSD study also were sampled by 0.1-m^2 van Veen grab samplers in a bight-wide study off southern California at depths between 10 and 200 m (Bergen et al., 1998). However, as in the AHF samples, many sedentary megafaunal taxa abundant in the OSD visual study (e.g., *Diopatra* spp., *L. pelodes*, *A. arcystata*, and *P. abrupta*) were uncommon or absent in these samples. They reported a mean wet weight of 58 g/m^2. This was substantially less than the biomass reported by AHF in this study area but far more than the measured mean OSD macrofaunal biomass (≈6.7 g/m^2). However, it was only one-fifth of the conservative estimate for mean whole wet weight for infauna in the OSD study (Table 3). Neither of these macrofaunal studies appears to adequately represent biomass or species composition for the complete infaunal assemblages on the continental shelf off southern California.

4.3. Zonation by depth levels and in the sediment column

Zonation by depth was clearly observable in terms of the distribution of sedentary megafauna to field observers in this study (Figs. 3, 4 and 5). Moreover, the major groupings for both megafauna and macrofauna determined by MDS analyses (Fig. 2) appear to correspond with the depth levels described for the three recognizable megafaunal assemblages identified above, suggesting that distribution of the macrofaunal assemblages may be influenced by the visually dominant megafauna, most of which are important ecosystem engineers.

Except for Station A14, zonation was strong throughout the study area in both the dominant sedentary megafauna (Fig. 2a) and the macrofauna (Fig. 2b). Stations at these depth levels were clearly strongly and distinctively associated, especially at the three deeper depth levels. The peculiarity of Station A14 was likely due to an historic beach replenishment program.

Similar findings of megafaunal zonation by depth have been reported for megafauna in sediments at Zuma Beach, ≈30 km east of the OSD study site (Morin et al., 1985, 1988). In their 5-year study at depths shallower than the OSD study area, they observed three distinct suspension-feeder assemblages. Pismo clams (*Tivela stultorum*) and a sea pansy (*Renilla kollikeri*) dominated the shallowest zone (2.6–6.4 m). Very dense aggregations of a sand dollar (*D. excentricus*) formed beds and dominated between 6.4 and 9.1 m, where the species exerted strong stabilizing and destabilizing ecological engineering effects on sediments, depending on season. The deeper zone (9.1–13.1 m) was dominated by the sea pansy, a sea pen (*Stylatula elongata*), the large tubicolous polychaete, *D. ornata*, and a sea star (*A. verrilli*). This zone appears to be an inshore extension of the 14-m and 18-m depth levels described in the present study.

Peterson’s studies (1977) in two southern California estuaries demonstrated that sampling to greater depth in the sediment column contributes greatly to understanding the complexities of the overall infaunal assemblage. Core tubes were hand-excavated to a depth of 56 cm in intertidal sand, muddy sand, and mud habitats in two lagoons in southern California. In ten sampling events over 37 months, Peterson focused on vertical distribution of each of ten dominant megafaunal species to determine their specific depth ranges in the sediment column (Table 5). In sandy or mud sediments, between 67% and 90% of the estimated volume of the species living in nearby Mugu Lagoon, California, (≈7 km east of the OSD study area) was found deeper than the 10-cm depth recommended by several investigators as adequate for sampling infauna (e.g., (Jones, 1969, Word, 1976, Quintana et al., 2010). Estimated averages for total volume for these species in the three sediment types ranged from 5644 to 7167 cm^3/m^2. Based on a rough equivalence of 1 g of whole wet weight per cm^3, these volumes constitute considerable biomass (5–7 Kg whole wet weight/m^2).

4.4. Longevity and assemblage stability

Longevity or life span estimates for dominant organisms are important considerations because of their implications related to faunal stability and recovery trajectories. Assemblages dominated by long-lived species are likely more stable than those dominated by ephemeral taxa.

Table 5
Vertical distribution of estimated volume (cm^3/m^2) occupied by dominant megafaunal organisms in sand, muddy sand, and mud sediments in Mugu Lagoon, California, U.S.A., from July 1969 through July 1972. Based on Peterson (1977). Percentages total less than 100% because values for non-dominant taxa were not provided.

	Sediment Depth Inhabited (cm)	Volume Occupied (cm^3/m^2)		
		Sand	Muddy sand	Mud
Dendraster excentricus	0–2	324	234	
Protothaca staminea	2–5	726	371	1383
Apolymetis biangulata	5–15		138	161
Macoma nasuta	5–15			1774
Cryptomya californica	10–50	484		
Callianassa californiensis	10–50	1218		
Sanguinolaria nuttallii	20–50	2754		
Saxidomus nuttalli	25–52		2470	3744
Tresus nuttalli	35–60		3850	
Tagelus californianus	32–55	138		105
Tabulated Volume Occupied (cm^3/m^2)		5644	7063	7167
Volume Deeper Than 10 cm (cm^3/m^2)		4594	6389	4817
% Volume Deeper Than 10 cm[a]		81	90	67

[a] Percentages would not total 100% because values for non-dominant taxa were not provided.

Moreover, they will require longer to re-establish mature age or size structure than assemblages dominated by short-lived species. Mean longevity for the 17 dominant megafaunal organisms in this study area, when calculated by the range for longevity estimates available in the literature, was significantly greater (14.4 to 18.8 years) than for 34 dominant macrofaunal taxa (1.6 to 2.1 years; Appendix F). The deep-burrowing geoduck clam, *P. abrupta*, has the greatest reported longevity for megafauna in the OSD study area (146 years; Goodwin and Pease, 1989). For macrofauna, a burrowing polychaete (*Micronephtys cornuta*) is reported to live up to 10 years (MarLIN, 2021) but most other species live less than 2 years.

Greater longevity in the megafauna likely leads to substantially greater stability and homogeneity in assemblage dominants. The tubicolous polychaete, *D. ornata*, a megafaunal species living up to five years (Emerson, 1975), was surveyed monthly for 18 months in twelve fixed 0.25-m^2 quadrats at Santa Catalina Island, CA, USA. Mean density increased steadily from 58 worms/m^2 in May 1972 to over 74 worms/m^2 in August 1973 before declining to 64/m^2 in December 1973. Density, averaging 64.9 ± 1.1 worms/m^2, was extremely stable over that period, varying by only 25%. The coefficient of variation (CV) for this study was 8.8%.

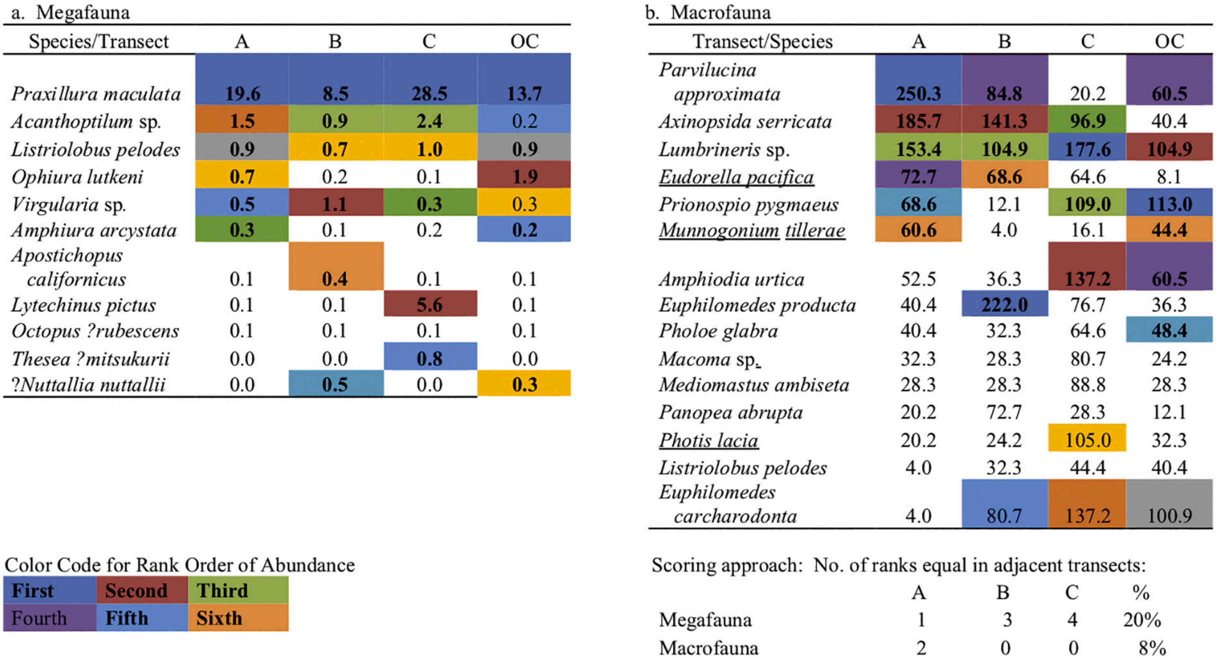
In nearby Mugu Lagoon, long-lived suspension-feeding bivalves were relatively stable during a 37-month study, even though they were recovering from major freshwater flooding at the beginning of the study (Peterson, 1975). By the end of the study, the major perennial species, including bivalves, burrowing shrimp, and sand dollars, had densities as high as, or higher than, those observed in the first survey. As an indication they were more stable, mean CVs for the perennial species (e.g., *P. staminea*, *Saxidomus nuttalli*, and *Sanguinolaria nuttallii*) were about half those observed over the period of the study for the more short-lived species (e.g., snails (*Acteocina inculta* and *Bulla gouldiana*), bivalves (*Donax californica* and *Tellina carpenteri*), and crabs (*Hemigrapsus oregonensis* and *Scleroplax granulata* (CV = 73 ± 9% vs.142 ± 21%, respectively; $p < 0.008$; 1-tailed resampling comparison of means). In another example of extreme stability, a dense population of the long-lived ophiurid *Amphiura filiformis*, comprising mainly “one functional adult group”, is reported to have survived for at least 17 years in Galway Bay, Ireland, with no significant changes in density (O’Connor et al., 1986).

Within the OSD study, sedentary megafaunal dominants exhibited significantly greater homogeneity within depth levels than macrofauna. Equal rank-order-of-abundance in adjacent transects (indicated by same colors in adjacent transects) occurred significantly more frequently in megafauna than in macrofauna. At the 55-m depth level, equal ranks occurred in 20% of the megafaunal species in contrast to only 8% for the macrofauna (Fig. 9). Across all five depth levels, the comparison for mean occurrence in adjacent transects was 22.5% ± 3.0 for megafauna vs. 6.2% ± 0.9 ($p = 0.0004$; 1-tailed resampling comparison of means), strongly suggesting greater heterogeneity in macrofaunal assemblages at all depth levels.

Because sedentary megafauna live longer, studies of those assemblages should be better predictors of the time that would be required for an ecosystem to recover or reach stability following disturbance. A comparison of studies of infaunal assemblages exposed to high-pressure hot-water washing on heterogeneous gravel beaches in Prince William Sound following the 1989 *Exxon Valdez* oil spill provides an example of differing predictions provided by these different assemblages. Based on studies of macrofaunal assemblages living in these beaches, Fukuyama et al. (2014) reported, “By 1992, abundances of major taxonomic categories at [three] disturbed sites had either converged or paralleled populations at [three] Unoiled sites”, implying macrofaunal assemblages had recovered. This may be a somewhat accurate interpretation for the short-lived macrofauna, the ‘weeds’, but does not appear to represent an accurate interpretation for the megafauna, the ‘trees’ (Houghton et al., 1997). While they further stated that “abundances of littleneck clams, *Leukoma* (*Protothaca*) *staminea*, slowly increased at Treated sites and converged with Unoiled sites by 2000”, their Fig. 9 data do not support convergence of the long-lived clams. Densities in eight designated size classes for this clam in the three Treated sites averaged 85% less than densities observed in the three Unoiled sites in 1991. Differences had improved to only about 50% less by 1999. Moreover, comparison of linear regression analysis for the 1999 curves indicates the slopes of change were significantly different ($p < 0.1$) and means for size-class frequency for the Treated sites trended lower ($p < 0.2$). While these statistics suggest that populations of *Leukoma* were improving, they did not appear recovered, as claimed, 10 years after the cleanup.

In contrast, based on an extensive study of sedentary megafauna on 18 oiled but unwashed and 22 washed similar beaches in the sound, Lees and Driskell (2007) predicted that recovery to pre-cleanup conditions for large bivalves like *Leukoma* and *Saxidomus* would require in excess of five decades. The credibility of this prediction is supported by a recent study on similar heterogeneous gravel beaches near San Onofre, in southern California. Before being decimated by 1982/83 El Niño storms, rich bivalve assemblages in these beaches, dominated by *L. staminea* and *Saxidomus nuttalli*, were considered by California Dept. of Fish and Wildlife to be the richest littleneck clam harvest areas in the state (Reilly, 2001). 2012/2013 studies found that, 30 years after the storms, while populations of those species appeared to be recovering, they were still decades away from achieving the high pre-storm stocks reported by CDF&W (unpublished results). Littleneck clams were among the least abundant of the eight large clam species sampled. Pre-storm data that would permit a more precise evaluation of clam recovery are not available from CDF&W.

A possible way to resolve these apparently contradictory conclusions regarding recovery of megafauna (Lees and Driskell, 2007) and macrofaunal assemblages (Fukuyama et al., 2014) in Prince William Sound is to assume that each type of assemblage has a different climax successional stage. Norkko et al. (2006) noted “seemingly random patterns” in response of macrofauna to disturbance. They commented these could be due to scale, i.e., size of the patch disturbed, or alterations in availability of space or food resources. The scales relevant to megafaunal and macrofaunal assemblages are very different and could lead to differences in climax communities. Another possible cause for randomness in recovery, especially for short-lived species, is timing of a disturbance relative to reproductive patterns of potential colonists, i.e., larval availability at the time of a disturbance. This concept may explain the great variance in recovery times of 2 months to >10 years for macrofaunal assemblages, as summarized by Wilber and Clarke (2007), or of



a. Megafauna

Species/Transect	A	B	C	OC
Praxillura maculata	19.6	8.5	28.5	13.7
Acanthoptilum sp.	1.5	0.9	2.4	0.2
Listriolobus pelodes	0.9	0.7	1.0	0.9
Ophiura lutkeni	0.7	0.2	0.1	1.9
Virgularia sp.	0.5	1.1	0.3	0.3
Amphiura arcystata	0.3	0.1	0.2	0.2
Apostichopus californicus	0.1	0.4	0.1	0.1
Lytechinus pictus	0.1	0.1	5.6	0.1
Octopus ?rubescens	0.1	0.1	0.1	0.1
Thesea ?mitsukurii	0.0	0.0	0.8	0.0
?Nuttallia nuttallii	0.0	0.5	0.0	0.3

b. Macrofauna

Transect/Species	A	B	C	OC
Parvilucina approximata	250.3	84.8	20.2	60.5
Axinopsida serricata	185.7	141.3	96.9	40.4
Lumbrineris sp.	153.4	104.9	177.6	104.9
Eudorella pacifica	72.7	68.6	64.6	8.1
Prionospio pygmaeus	68.6	12.1	109.0	113.0
Munnogonium tillerae	60.6	4.0	16.1	44.4
Amphiodia urtica	52.5	36.3	137.2	60.5
Euphilomedes producta	40.4	222.0	76.7	36.3
Pholoe glabra	40.4	32.3	64.6	48.4
Macoma sp.	32.3	28.3	80.7	24.2
Mediomastus ambiseta	28.3	28.3	88.8	28.3
Panopea abrupta	20.2	72.7	28.3	12.1
Photis lacia	20.2	24.2	105.0	32.3
Listriolobus pelodes	4.0	32.3	44.4	40.4
Euphilomedes carcharodonta	4.0	80.7	137.2	100.9

Color Code for Rank Order of Abundance

First	Second	Third
Fourth	Fifth	Sixth

Scoring approach: No. of ranks equal in adjacent transects:

	A	B	C	%
Megafauna	1	3	4	20%
Macrofauna	2	0	0	8%

Fig. 9. Comparison of mean and rank order of density for sedentary megafaunal and macrofaunal dominants at 55-m depth level on the Hueneme Shelf during Surveys I and II for the 1974 Oxnard Sanitation District surveys.

≈50 years for sedentary megafaunal assemblages, as in the case of Prince William Sound (Lees and Driskell, 2007) or San Onofre (unpublished results).

4.5. Geographic distribution and environmental sensitivity

As demonstrated in Fig. 6, geographic distributions for dominant megafauna appear to be significantly more limited than those for macrofauna. A large fraction of dominant macrofaunal species have cosmopolitan distributions. Those macrofaunal species must be able to tolerate a much wider range of environmental and ecological conditions than would be experienced across narrower geographic ranges by more regional megafaunal species. This is an important consideration when studying effects of environmental insults such as wastewater discharges or when monitoring responses to climate change. Sedentary megafauna also appeared to be significantly more sensitive to differences in depth than macrofauna in the OSD study area (Table 4).

Based on microbial and macrofaunal studies, Watling (1991) claimed that measures such as TKN and TOC have been shown to be nearly meaningless. Nevertheless, dominant sedentary megafauna in the OSD study area appeared to respond with greater sensitivity than macrofauna to TKN and TOC (Table 4). One explanation for this apparent difference from Watling's, 1991 findings relates to differences in the scales that apply to megafauna and macrofauna. Scales described by Watling are in terms of micro- or millimeters, which relates nicely to the size of microbial or macrofaunal organisms he studied. In addition, species that concerned Watling were mostly deposit feeders. In contrast, scales more applicable to the much larger megafauna in this study are more on the order of centimeters or decimeters. Furthermore, it is likely many of these taxa respond to different nutritional factors because many are suspension feeders. Johannes and Satomi (1966) described dependence of the shrimp, *Palaemonetes pugio*, on nitrogen-rich bacteria. This suggests that organic nitrogen may be a useful measure for many megafaunal taxa and that megafaunal assemblages could provide better insights to changes or differences in sediment organics or microbial biomass than macrofauna.

4.6. Sublethal predation

Based on reviews by Lawrence and Vasquez (1996) and Lindsay (2010), it is clear that sublethal predation is an important interaction that has been mostly overlooked in discussions of infaunal community dynamics. In a comprehensive review of for echinoderms, Lawrence and Vasquez (1996) reported on sublethal predation for several genera of echinoderms that were observed in the OSD study area. Subsequently, Lindsay (2010) summarized regeneration resulting from sublethal predation for a wide variety of invertebrates, including polychaetes, bivalves, and ophiurids. Most relevant to this study is a review that focuses on sublethal predation in sedentary megafaunal assemblages (Lees, 2021). Many of the genera discussed in that review relate to local prey species abundant in this study area. They include the polychaete *Diopatra*, the bivalves *Leukoma*, *Macoma*, *Nuttallia*, *Panopea*, and *Saxidomus*, the ophiurids *Amphiura*, *Amphiodia*, and *Ophiura*, the sea stars *Astropecten* and *Luidia*, and the sand dollar *Dendraster*.

This interaction was not observed directly during the OSD studies, but it is likely the interaction was a common occurrence in this area and led to a considerable transfer of energy from sedentary megafaunal assemblages to higher trophic levels. It was quantified in nearby Mugu Lagoon for bivalve species that actually or probably occurred in the OSD study area (e.g., *Leukoma staminea*, *Sanguinolaria* [now *Nuttallia*] *nuttallii*, and *Saxidomus nuttalli*; Peterson and Quammen, 1982). Three fish species consistently common in monthly beach seine hauls in Mugu Lagoon were also common in trawls in the OSD study area (EQA and MBC, 1974a and b, Morin et al., 1985, 1988). These included staghorn sculpin (*Leptocottus armatus*), diamond turbot (*Hypsopsetta guttulata*), and California halibut (*Paralichthys californicus*), which were observed to have consumed siphons of L. *staminea* and *Macoma* spp. The interaction was also reported by Lane (1975) for Anaheim Bay, CA, USA, where the diamond turbot (*Hypsopsetta guttulata*) population was observed to consume ≈0.5 Kg of siphons/fish/year of the razor clam *Tagelus californianus*.

Few investigators have provided sufficient details for estimating mean annual rates for sublethal predation. Based on nine studies, a preliminary estimate for the rate of tissue transferred to higher trophic levels is 23.8 ± 17.7% of the biomass for three major sedentary megafaunal taxa

(Table 6). The mean contributions by the major taxa were polychaetes (20% [n = 1]), bivalves (25% [n = 4]), and ophiurids (22%, [n = 4]). Since this mean only covers sublethal predation and excludes lethal predation and reproduction, is seems reasonable to apply a rate of 25% of standing stocks annually in calculating the sublethal predation component for the secondary production contribution from sedentary megafaunal.

4.7. Ecosystem engineers

Sedentary megafaunal species have far greater influences on the physical and biogeochemical environment than macrofaunal assemblages due to their ecosystem engineering activities. These influences add another reason why investigators would benefit from studying megafaunal assemblages. Lindsay et al. (2008) noted that sublethal predation can affect bioturbation, recruitment, and competition. The importance of these effects is pointed out by Bouma et al. (2009) and Braeckman et al. (2014). The former indicated that many coastal sediments are 'strongly modified' by ecosystem engineers and that different 'engineers' have dramatic and often divergent effects on biodiversity of the systems. The latter commented that a top priority for conservation should be identification and preservation of ecological engineers.

Effects of ecosystem engineering by dominant sedentary megafaunal assemblages were widespread in the study area and historically have appeared throughout southern California. Bioturbation, considered "an archetypal example of 'ecosystem engineering' and…among the most important 'engineering' mechanisms", is a critical factor in geochemical interactions (Meysman et al., 2007). Its importance to these interactions is demonstrated in studies showing that 'faunal-mediated oxygen uptake' accounted for between 33% and 89% of total oxygen uptake in sediments in the Seine River estuary (Janson et al., 2012). Burrows of geoduck clams and thalassinid shrimp extend at least a half-meter into the sediment, thus oxygenating sediments and affecting geochemical characteristics. Pemberton et al. (1976) showed that burrowing shrimp can burrow up to 3 m into the sediment, likely accompanied by oxygenation and other geochemical effects.

Megafaunal 'engineers' in the OSD study area included several tubicolous polychaetes which increased sediment stability in the same manner as *Diopatra cuprea* (Thomsen and McGlathery, 2005; Berke, 2012) and *Lanice conchilega* (Alves et al., 2017). The structures created by these worms undoubtedly positively influenced infaunal biodiversity, density, and community composition where they were common. Most important of these in this study area were *D. ornata* and *P. maculata* but numerous other tubicolous polychaetes were common. Surficial feeding by echiurans (Pilger, 1977a), polychaetes (Brey, 1991), bivalves (Trevallion, 1971; Skilleter, 1992; Ahn et al., 1993), and ophiurids (Feder, 1981; Ambrose, 1993) can clear or encourage recruiting juveniles of other megafaunal and macrofaunal taxa over large areas. The effects of predation on recruiting macrofauna by the sea star, *Astropecten verrilli*, were demonstrated by VanBlaricom (1982) in southern California. Discharge of fecal material by the echiurid, *L. pelodes*, caused destabilization of sediments and macrofaunal assemblages (Pilger, 1977a). Burrowing and discharge of burrow ejecta and fecal masses by burrowing shrimp (*Alpheus mackayi* [Gust and Harrison, 1981]; *Neotrypaea* spp. [Posey, 1985]; *Alpheus californiensis* [unpublished results] and burrowing holothurians (Rhoads and Young, 1970) act to greatly destabilize sediments and/or increase concentrations of suspended solids in the water column. Volkenborn et al. (2007) showed that activities of burrowing lugworms significantly influence sediment permeability, depth of oxygen penetration, nutrient concentrations, and macrofaunal species composition to at least 20 cm deep into the sediment.

Table 6
Percentage of population biomass lost annually to sublethal predation for three higher taxa of sedentary megafauna.

Species	Higher taxon	Annual biomass loss (%)	Structure lost	Reference
Acrocnida brachiata Intertidal	Ophiurid	11	Arm	Bourgoin and Guillou (1994)
Acrocnida brachiata Subtidal	Ophiurid	6	Arm	Bourgoin and Guillou (1994)
Amphiura filiformis	Ophiurid	22	Arm	Sköld et al. (1994)
Arenicola marina	Polychaete	20	Tail segment	De Vlas (1979)
Donax spp.	Bivalve	20	Foot	Salas et al. (2001)
Macoma balthica	Bivalve	Ca. 50	Siphon	De Vlas (1985)
Nuttallia olivacea	Bivalve	6	Siphon	Sasaki et al. (2008)
Protothaca staminea	Bivalve	25	Siphon	Peterson and Quammen (1982)
Microphiopholis gracillima	Ophiurid	50	Arm	Stancyk et al. (1994)
Mean ± SD		23.8 ± 17.7		

Many ecological engineers can assume more than one role (Needham et al., 2011) or act cooperatively (Passarelli et al., 2014). Depending on season, sand dollars (*D. excentricus*) can either stabilized or destabilized upper layers of sediment depending on season (Merrill and Hobson, 1970; unpublished results). In addition to destabilizing sediments, burrowing and feeding activities by *L. pelodes*, deep-burrowing clams, shrimp, holothurians, heart urchins, and enteropneusts exert important geochemical effects in sediment by reducing organic matter either at or below the sediment surface and by entraining oxygenated water to deeper layers of sediment, thereby reducing sulfides (e.g., Dornhoffer et al., 2012). Many burrowing shrimp fill multiple roles (e.g., Gust and Harrison, 1981). Cooperation was very clear in sediments in San Diego Bay where surface area and volume of complex interconnected burrows created by a community of five burrowing shrimp species contributed $\approx$1.6 m^2 surface area and 9 l/m^2 of burrow volume in the bay floor, based on resin casts of burrows (unpublished results). Thus, these shrimp had expelled this volume of sediment, some of it badly contaminated with PCBs and trace metals, onto the sediment surface or into the water column while creating considerable surface area to a depth of at least 30 cm in the sediment to accomplish a variety of geochemical actions.

Burrowing, respiratory, and feeding activities and consumption of sediment organics by *L. pelodes* "aerated and reworked sediments, and thus reduced wastewater impacts on the ocean bottom, enabling a diverse fauna to develop in the outfall region" in southern California (Stull et al., 1986). From 1972 until mid-year 1975, organic nitrogen (ON) concentrations were greater than 0.5% for up to 15 miles along the 60-m depth contour in the vicinity of the White's Point wastewater outfalls off Palos Verdes Peninsula. In mid-1973, *Listriolobus* concentrations greater than 200/m^2 were noted extending over 3 miles of that contour within that area. The extent of these densities increased to 8 miles by 1975 and then declined to 2 miles by 1978. During the period of elevated *Listriolobus* densities, the miles of elevated ON concentrations declined to 5 miles, suggesting that activities of the echiurid were related to the decline of organic nitrogen. Apparently, ecosystem effects by macrofauna, limited to bioturbation [sensu (Kristensen et al., 2012) in the upper few centimeters of sediment (Solan et al., 2003) were unable to accomplish this effect.

4.8. Trophic fate and roles

Trophic fate and roles of sedentary megafauna and macrofauna differ substantially. A large proportion of the trophic fate for sedentary megafaunal assemblages is likely characterized by sublethal predation, where it is likely many individuals contribute more than their body weight over their lifetime through the sublethal process as well as their body weight to lethal predation ultimately. In addition, they contribute substantially with reproductive products. In contrast, macrofaunal assemblages are mostly subject to lethal predation; their contribution through sublethal predation and reproductive products are comparatively minimal.

Trophic roles varied widely among the 17 dominant megafaunal taxa (Table 7). The sedentary megafaunal assemblages in this study area were strongly dominated by large suspension feeders such as tubicolous polychaetes (*Diopatra* spp. and *P. maculata*) and bivalves (*P. abrupta*, *?N. nuttallii*) and predators such as sea stars (*A. verrilli*) and large ophiurids (*A. arcystata* and *Ophiura lutkeni*; Table 7; Appendix G). Deposit feeders and herbivore/scavengers were of lesser importance in assemblages observed during these surveys. However, many large burrowing deposit-feeders (e.g., large polychaetes, sipunculids, bivalves, shrimp, sea cucumbers, heart urchins, and enteropneusts) that likely constitute a significant part of sedentary megafaunal assemblages were not sampled. Consequently, importance of deposit-feeding sedentary megafauna is undervalued.

In contrast, the 31 taxa dominating the macrofauna were strongly dominated by small burrowing deposit feeders (errant, tubicolous, and burrowing polychaetes, tanaids, small bivalves, and ophiurids) and less strongly by small suspension feeders such as microcrustacean taxa (ostracods, isopods, and caprellid and gammarid amphipods. Planktivores and herbivore/scavengers were of lesser importance (<15%). Cumaceans and ostracods are reported to be bentho-hyponeustonic planktivores (Macquart-Moulin, 1999), i.e., they reside on or in sediment during daytime, sometimes deposit-feeding, but migrate toward the surface of the water at night to feed on phyto- or zooplankton and breed (Appendix G).

Macrofaunal trophic roles are relatively poorly documented; roles of 57% of the local dominants are based on assumptions from research on similar taxa, i.e., the trophic role is only presumed based on structure or similar species (Appendix G). Detailed analyses indicate that considerable trophic diversity is exhibited within major macrofaunal groups (Fauchald and Jumars, 1979, Chapman, 2007), suggesting that assigning a trophic role on the basis of taxonomic analogy is risky. Pearson (2001) points out: "…critics of the [feeding guild] concept suggest that such analyses are both superficial and misleading without a much better knowledge of the life histories and behaviour of benthic organisms than is available at present." In contrast, solid research has been conducted on trophic roles for 79% of dominant sedentary megafauna. As differences in trophic roles indicate (Table 7), trophic structure varies substantially between sedentary megafauna and macrofauna but trophic roles of macrofauna are more questionable. Finally, megafauna are likely by far the more important consumers based on biomass.

4.9. General remarks

Macrofaunal assemblages in this region, the 'weeds', have been well described in multiple papers. However, since descriptions of sedentary megafaunal assemblages are based primarily on visual observations by only a few investigators, it is clear they remain poorly described in this region. The differences between the descriptions of the megafaunal assemblages by Fager (1971) for the La Jolla area and those described by Davis et al. (1982) 6 Km N and Morin et al. (1985, 1988) ca. 160 Km NW of Fager's sampling location in the 10-m depth range demonstrate clearly the paucity of observations. Very little research has been conducted on sedentary megafaunal assemblages. The first attempts to describe infaunal assemblages for this region were made in papers by Barnard and Hartman (1959), Barnard and Ziesenhenne (1961), Barnard (1963), and finally in a detailed summary by Jones (1969). All papers were describing results of 1956–59 surveys by the Allan Hancock Foundation (1965). These papers did not distinguish between macrofauna and megafauna although they did identify several assemblages using names of taxa that are considered megafaunal in this paper. As the OSD study shows, the interesting megafauna hinted at in these papers is incomplete because, as pointed out by Powell and Mann (2016), limited sample penetration and area sampled in a single sample collected by a 0.25-m^2 orange-peel grab sampler per site did not capture representative numbers or biomass for many major megafaunal taxon, especially deep-burrowing species like large tubicolous polychaetes, *P. abrupta*, *?N. nuttallii*, or burrowing shrimp. Moreover, subsequent visual surveys of the megafauna such as this study have provided only a partial description of these complex and productive assemblages.

Table 7
Summary of trophic roles for dominant sedentary megafaunal and macrofaunal taxa at 14-, 18-, 27-, 37-, and 55-m depth levels on the Hueneme Shelf during Surveys I and II for the 1974 Oxnard Sanitation District studies.

Trophic role	Assemblage	No. of taxa	% of Megafauna taxa
Deposit Feeder	Sedentary Megafauna	3	18%
	Macrofauna	14	45%
Suspension Feeder	Sedentary Megafauna	8	47%
	Macrofauna	10	32%
Planktivore	Sedentary Megafauna	0	0%
	Macrofauna	3	10%
Herbivore/ Scavenger	Sedentary Megafauna	1	6%
	Macrofauna	1	3%
Predator	Sedentary Megafauna	5	29%
	Macrofauna	3	10%

Some may comment that quantitative visual surveys are insufficient for the purposes of this analysis because they do not measure abundance and species diversity of buried species. However, that argument applies at least equally to results of conventional sampling studies that infaunal investigators have relied on since the mid-1950s since those methods do not measure abundance or biomass of macrofauna deeper than sampler penetration, generally cover only a very limited surface area, and do not reliably sample sedentary megafauna. They miss the 'trees'.

Similarly, while it is clear that visual surveys described above (e.g., Fager, 1964, 1968; Davis et al., 1982; Davis and vanBlaricom, 1978; Morin et al., 1985; VanBlaricom, 1982) and herein do not provide a complete picture of the megafauna, they do provide valuable insights into different and, as this analysis demonstrates, a more important component of the infauna. So, while results of visual surveys may be imperfect, they provide great insight into many very important ecosystem engineers and central aspects of ecosystem dynamics that are missing in conventional sampling programs. Critical investigators should be cautious about letting perfection be the enemy of the good.

It is clear that a full account of these megafaunal assemblages must await surveys that employ large samplers that can provide well-replicated samples to a depth of at least 30 cm and collections of samples covering several square meters of seafloor to obtain a reasonable representation of species, abundance, and biomass of the sedentary megafauna in any specific area. As Peterson (1977) demonstrated, the preponderance of megafaunal, and therefore infaunal, biomass resides more than 10 cm deep in the sediment in estuaries in southern California. We can assume this probably holds true in sediments on many continental shelves. Powell et al. (2017) show the daunting magnitude of effort that is necessary to get representative results, especially on target species. Where possible, these studies also should quantify sublethal predation. Until biomass and secondary production of sedentary megafauna assemblages can be reasonably estimated, we will have only a very poor understanding of the value and contributions of these extensive ecosystems. However, since the taxonomy of target megafaunal species is generally well known, samples can be screened on coarse sieves and analyzed rapidly, mostly in the field, much in the same manner as is employed in trawling surveys. Thus, surveys of these assemblages could likely be conducted rapidly and comparatively inexpensively.

5. Conclusions

Sedentary megafaunal and macrofaunal assemblages are different components of infaunal assemblages that differ dramatically across a wide variety of attributes and provide widely different insights into the value and condition of infaunal assemblages and the sediments in which they live. Some of these attributes include: 1) species composition; 2) abundance; 3) biomass; 4) secondary production; zonation by 5) depth levels and 6) burial depth in sediment; 7) susceptibility to and importance of sublethal predation; 8) geographic distribution; 9) environmental sensitivity; 10) longevity and stability; 11) importance as ecological engineers; and 12) trophic fates and roles. In many cases, these differences demonstrate that sedentary megafaunal assemblages provide more sensitive insights into long-term conditions, functioning, and value of infaunal assemblages, and are substantially more important to sedimentary ecosystems than macrofaunal assemblages. It should be noted that sedentary megafaunal assemblages are quite distinct from motile demersal megafaunal assemblages that can be collected in the area by trawling or dredging and are quite often seasonally highly variable.

In terms of importance, this study demonstrates clearly that biomass provides far more insight into importance of these assemblages to ecosystem dynamics and secondary production than any other attribute, even in light of the weaknesses of biomass estimates in this study. Ecosystem engineering roles and sublethal predation rates are of considerable importance. Differences in biomass appear to reflect effectively the differences in influence on the environment of the two types of assemblage as driven largely through the effects of ecosystem engineers. Differences in megafaunal and macrofaunal abundance are meaningless for the most part, except in highly polluted situations where megafaunal organisms have been seriously injured or lost whereas highly tolerant macrofaunal species are favored.

The near absolute difference in species composition, with only three species occurring as dominants in the megafaunal and macrofaunal assemblages, suggests they are hardly related. They live in the same medium and appear to respond to many of the same environmental factors, but where they interact (e.g., predation or competition for space), megafaunal organisms likely drive the dynamics. Moreover, many megafaunal organisms penetrate deeper into the sediment and therefore likely exert far greater biogeochemical influence on the sediment than macrofauna. Differences in secondary production indicate that sedentary megafaunal assemblages contribute substantially more energy to higher trophic levels and are therefore substantially more important to the ecosystem. Major trophic roles differ considerably. Megafauna in this area are represented strongly by large suspension feeders, even at the 55-m depth level, but small deposit feeders predominate in the macrofauna. Sedentary megafaunal organisms appear to provide more sensitive responses to environmental attributes than macrofauna in terms of geographic and depth ranges and to sediment organics. Because they are longer lived and more stable, megafauna appear to provide better insight into long-term conditions at a site, the magnitude of injury a site might experience as a consequence of disturbance, and the likely time required for recovery.

These differences amplify findings by others that infaunal resources and dynamics are poorly described and are undervalued, especially when studies are limited to macrofauna. Studies of sedentary megafaunal assemblages would provide far greater insights into ecosystem dynamics and environmental conditions and have greater power to assess or predict responses to anthropogenic activities or long-term environmental change or degradation. Finally, they would provide far more insight into the high value of infaunal ecosystem on continental shelves and in estuaries around the world.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2021.102021.

Declaration of Competing Interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

I wish to acknowledge the Oxnard Sanitation District for funding these studies on the Hueneme Shelf in 1974-75. I am grateful to Charles 'Chuck' Mitchell at MBC Applied Environmental Sciences for retaining the reports for these studies, without which this comparison would not have been possible. In addition, I wish to thank the 1974-75 staff at MBC that participated in the field studies and laboratory analyses and assisted in obtaining records. I thank the late Don Sieverts, designer, builder, and pilot of the two-man submersible, SNOOPER, who designed special sampling equipment that enabled identification of many megafaunal species and contributed substantially to the field efforts.

I am sincerely grateful to the late Dr. Robert R. 'Bob' Given, who, in the '60s, cautioned me about missing the perennial 'trees' by relying on the 'weeds' in grab samples. He inspired me to pay attention to the 'trees' and 'walk in the woods'.

Other colleagues that contributed through discussion and/or review of early drafts include: Arny Blanchard, the late Howard Feder, Jonathan Houghton, James Klick, Alan Mearns, Marion Patton, Jason Stutes, and Howard Teas. Their valuable comments and critiques were extremely helpful. The paper benefited greatly from the critiques of several anonymous reviewers. Finally, I offer heartfelt thanks to my wife, Kathleen, for encouraging and supporting me in the extended effort to complete this manuscript, for careful editorial critique, and for tolerating my obsessive attention to this issue.

Appendix A. Mean density (number/m^2) for dominant macrofaunal and megafaunal taxa at the 18-m depth level on the Hueneme Shelf during Surveys I and II for the 1974 OSD study. Underlined taxa are considered ephemeral organisms

Macrofaunal samples			Megafaunal surveys		
Taxon/survey	Survey I	Survey II	Taxon/survey	Survey I	Survey II
	Mean[a] ± SE	Mean ± SE		Mean ± SE	Mean ± SE
All Caprellidae-C[b]	617.7 ± 197.3	89.2 ± 73.9	*Diopatra ornata*-P	22.4 ± 12.2	40.1 ± 7.8
Ericthonius punctatus-C	325.7 ± 325.7	13.0 ± 5.7	*Aglaophenia dlspar*-H	17.7 ± 9.1	0.05 ± 0.05
Angulus modestus-B	163.8 ± 59.7	151.8 ± 32.6	*Onuphis elegans*-P	4.5 ± 0.6	22.9 ± 12.7
Mediomastus ambiseta-P	115.9 ± 46.3	6.1 ± 4.1	*Astropecten verrilli*-E	2.4 ± 0.5	1.4 ± 0.3
Aoroides spinosus-C	108.0 ± 60.1	32.5 ± 20.5	*Loimia* sp. A-P	0.7 ± 0.4	0.07 ± 0.03
Munna sp.-C	82.9 ± 48.5	4.9 ± 2.4	*Diopatra tridentata*-P	0.4 ± 0.2	0.3 ± 0.3
Euphilomedes carcharodonta-C	70.7 ± 60.4	38.2 ± 17.6	*Scrupocellaria ?diegensis*-BR	0.3 ± 0.3	3.9 ± 1.9
Exogone naidina-P	61.0 ± 18.3	4.3 ± 4.3	*Plumularia ?alicia*-H	0.3 ± 0.1	0.7 ± 0.6

(*continued on next page*)

(*continued*)

Macrofaunal samples			Megafaunal surveys		
Taxon/survey	Survey I	Survey II	Taxon/survey	Survey I	Survey II
	Mean[a] ± SE	Mean ± SE		Mean ± SE	Mean ± SE
Anaitides sp.-P	58.6 ± 16.3	26.2 ± 10.6	*Panopea abrupta*-B	0.05 ± 0.05	0.1 ± 0.05
Microjassa litotes-C	52.5 ± 34.1	0.0 ± 0.0	*Luidia foliolata*-E	0.03 ± 0.02	0.0 ± 0.0
Macoma sp.-B	50.3 ± 11.9	40.3 ± 30.1	*Cellaria diffusa*-BR	0.02 ± 0.02	3.7 ± 3.7
Cumella sp. A-C	47.0 ± 11.9	56.9 ± 30.6			
Prionospio pygmaeus-P	44.5 ± 9.6	258.1 ± 60.9			
Rutiderma rostratum- C	40.1 ± 7.5	41.5 ± 14.1			
Micronephtys cornuta-P	30.0 ± 14.5	95.8 ± 34.3			
Acuminodeutopus periculosus-C	7.9 ± 5.8	43.1 ± 7.1			

[a] Mean of densities for all sites at this level based on three replicate grab samples at each site.

[b] Higher taxon abbreviations: B – Bivalve; BR – Bryozoan; C – Crustacean; E – Echinoderm; H - Hydroid; P – Polychaete.

Appendix B. Mean density (number/m^2) for dominant macrofaunal and megafaunal taxa at the 27-m depth level on the Hueneme Shelf during Surveys I and II for the 1974 OSD study. Underlined taxa are considered ephemeral organisms

Macrofaunal samples			Megafaunal Surveys		
Taxon/survey	Survey I	Survey II	Taxon/Survey	Survey I	Survey II
	Mean[a] ± SE	Mean ± SE		Mean ± SE	Mean ± SE
Munnogonium tillerae-C[b]	174.4 ± 72.8	59.2 ± 27.9	*Panopea abrupta*-B	3.2 ± 1.5	2.7 ± 1.1
Euphilomedes carcharodonta-C	112.2 ± 2.4	197.2 ± 27.6	*Amphiura arcystata*-E	1.8 ± 0.7	2.1 ± 0.7
Liralucina approximata-P	81.1 ± 24.2	83.0 ± 9.8	?*Nuttallia nuttallii*-B	1.4 ± 0.3	1.9 ± 0.5
Listriolobus pelodes-EC	73.3 ± 28.4	0.0 ± 0.0	*Aglaophenia dispar*-H	1.2 ± 0.7	0.6 ± 0.3
Mediomastus ambiseta-P	67.1 ± 15.6	25.0 ± 5.8	*Diopatra tridentata*-P	1.0 ± 0.4	1.6 ± 0.3
Amphideutopus oculatus-C	57.7 ± 26.5	64.1 ± 17.9	*Diopatra ornata*-P	0.8 ± 0.7	0.2 ± 0.2
Pholoe glabra-P	48.8 ± 19.4	15.9 ± 5.8	*Astropecten verrilli*-E	0.5 ± 0.3	1.6 ± 0.9
Anaitides sp.-P	46.9 ± 9.9	22.6 ± 7.2	*Virgularia ?agassizi*-SP	0.4 ± 0.1	0.3 ± 0.2
Tharyx sp.-P	40.3 ± 13.1	73.2 ± 46.4	*Tubularia* sp. A-H	0.2 ± 0.1	0.9 ± 0.6
Macoma sp.-B	36.6 ± 14.4	20.1 ± 4.3	*Amphiodia urtica*-E	0.0 ± 0.0	3.0 ± 0.3
Micronephtys cornuta-P	36.6 ± 5.4	166.5 ± 9.8			
Angulus modestus-B	32.3 ± 14.2	62.8 ± 38.5			
Prionospio pygmaeus-P	30.5 ± 28.1	70.8 ± 14.0			
Asterope mariae-C	28.7 ± 5.2	79.9 ± 19.4			
Ampelisciphotis podophthalma-C	17.7 ± 6.2	77.5 ± 15.0			

[a] Mean of densities for all sites at this level based on three replicate grab samples at each site.

[b] Higher taxon abbreviations: B – Bivalve; C – Crustacean; E – Echinoderm; EC – Echiurid; H – Hydroid; P – Polychaete; SP – Sea Pen.

Appendix C. Mean density (number/m^2) for dominant macrofaunal and megafaunal taxa at the 37-m depth level on the Hueneme Shelf during Surveys I and II for the 1974 OSD study. Underlined taxa are considered ephemeral organisms

Macrofaunal samples			Megafaunal surveys		
Taxon/survey	Survey I	Survey II	Taxon/survey	Survey I	Survey II
	Mean[a] ± SE	Mean ± SE		Mean ± SE	Mean ± SE
Munnogonium tillerae-C[b]	184.6 ± 92.8	18.7 ± 7.1	*Praxillura maculata*-P	41.6 ± 21.1	1.7 ± 0.4
Listriolobus pelodes-EC	100.0 ± 58.4	8.1 ± 5.0	*Listriolobus pelodes*-EC	1.0 ± 0.3	0.7 ± 0.1
All Caprellidae-C	78.1 ± 53.8	108.7 ± 100.3	*Diopatra tridentata*-P	1.0 ± 0.1	0.7 ± 0.3
Euphilomedes carcharodonta-C	67.5 ± 5.7	146.3 ± 9.8	*Thesea ?mitsukurii*-G	0.8 ± 0.7	0.7 ± 0.2
Panopea abrupta-B	65.0 ± 52.9	20.8 ± 3.7	*Acanthoptilum ?gracile*-SP	0.6 ± 0.2	0.12 ± 0.04
Amphiodia urtica-E	56.9 ± 44.8	15.9 ± 8.6	*Apostichopus californicus*-E	0.5 ± 0.3	0.07 ± 0.02
Pholoe glabra-P	52.0 ± 19.7	25.2 ± 8.1	?*Nuttallia nuttallii*-B	0.4 ± 0.4	0.2 ± 0.1
Mediomastus ambiseta-P	51.2 ± 36.6	32.5 ± 16.8	*Tubularia* sp. A-H	0.2 ± 0.2	0.4 ± 0.1
Leptognathia sp.-C	51.2 ± 16.2	61.0 ± 12.2	*Amphiodia urtica*-E	0.2 ± 0.1	8.5 ± 4.5
Liralucina approximata-B	48.0 ± 8.1	93.9 ± 52.4	*Panopea abrupta*-B	0.1 ± 0.1	0.05 ± 0.03
Amphideutopus oculatus-C	43.9 ± 2.4	87.0 ± 14.4	*Luidia foliolata*-E	0.03 ± 0.03	0.03 ± 0.02
Micronephtys cornuta-P	24.4 ± 9.9	57.4 ± 33.1	*Amphiura arcystata*-E	0.0 ± 0.0	1.9 ± 0.9
Ampelisciphotis podophthalma-C	24.4 ± 4.2	57.4 ± 8.6	*Kylix halocydne*-S	0.0 ± 0.0	1.4 ± 1.2
Leptostylis sp. A-C	24.4 ± 4.2	48.8 ± 17.1	*Ophiura lutkeni*-E	0.0 ± 0.0	0.7 ± 0.3
Cooperella subdiaphana-B	13.0 ± 9.6	125.6 ± 52.4			
Prionospio pygmaeus-P	13.0 ± 9.6	95.1 ± 26.1			

[a] Mean of densities for all sites at this level based on three replicate grab samples at each site.

[b] Higher taxon abbreviations: B – Bivalve; C – Crustacean; E – Echinoderm; EC – Echiurid; G – Gorgonian; H – Hydroid; P – Polychaete; S – Snail; SP – Sea Pen.

Appendix D. Mean density (number/m^2) for dominant macrofaunal and megafaunal taxa at the 55-m depth level on the Hueneme Shelf during Surveys I and II for the 1974 OSD study. Underlined taxa are considered ephemeral organisms

Macrofaunal samples			Megafaunal surveys		
Taxon/survey	Survey I	Survey II	Taxon/survey	Survey I	Survey II
	Mean[a] ± SE	Mean ± SE		Mean ± SE	Mean ± SE
Euphilomedes producta-C[b]	129.9 ± 68.9	83.8 ± 22.9	*Praxillura maculata*-P	18.3 ± 6.8	16.9 ± 13.2
Lumbrineris sp.-P	107.9 ± 13.3	164.7 ± 24.7	*Lytechinus pictus*-E	2.8 ± 2.7	0.1 ± 0.1
Amphiodia urtica-E	69.5 ± 28.4	81.3 ± 41.8	*Cellaria diffusa*-BR	1.2 ± 0.5	1.5 ± 0.6
Pholoe glabra-P	56.7 ± 10.1	30.5 ± 6.8	*Listriolobus pelodes*-EC	1.0 ± 0.4	0.7 ± 0.2
Axinopsida serricata-B	56.7 ± 12.7	217.3 ± 60.8	*Acanthoptilum ?gracile*-SP	1.0 ± 0.4	1.5 ± 0.8
Listriolobus pelodes-EC	54.9 ± 10.8	18.9 ± 8.5	*Thuiaria ?alba*-H	0.9 ± 0.6	0.7 ± 0.2
Mediomastus ambiseta-P	54.9 ± 14.7	14.0 ± 6.9	*Virgularia ?agassizi*-SP	0.5 ± 0.2	0.5 ± 0.3
Munnigonium tillerae-C	53.1 ± 17.5	7.9 ± 5.8	*Ophiura lutkeni*-E	0.5 ± 0.4	0.9 ± 0.4
Euphilomedes carcharodonta-C	53.1 ± 17.5	138.2 ± 43.0	*Thesea ?mitsukurii*-G	0.4 ± 0.4	0.0 ± 0.0
Macoma sp.-B	49.4 ± 29.9	38.2 ± 7.2	?*Nuttallia nuttallii*-B	0.4 ± 0.2	0.01 ± 0.01
Eudorella pacifica-C	40.8 ± 15.1	86.2 ± 19.2	*Apostichopus californicus*-E	0.2 ± 0.1	0.2 ± 0.1
Prionospio pygmaeus-P	36.6 ± 31.2	116.5 ± 39.6	*Amphiura arcystata*-E	0.2 ± 0.1	0.3 ± 0.1
Liralucina approximata-B	34.2 ± 24.1	173.7 ± 61.2	*Octopus ?rubescens*-O	0.09 ± 0.04	0.04 ± 0.01
Panopea abrupta-B	10.4 ± 10.4	59.3 ± 44.4			
Photis lacia-C	6.1 ± 4.1	91.9 ± 55.3			

[a] Mean of densities for all sites at this level based on three replicate grab samples at each site.

[b] Higher taxon abbreviations: B – Bivalve; BR – Bryozoan; C – Crustacean; E – Echinoderm; EC- Echiurid; G – Gorgonian; H – Hydroid; O – Octopus; P – Polychaete; SP – Sea Pen.

Appendix E. Station characteristics and numbers of taxa and individuals for higher taxa in 0.25-m^2 orange-peel grab samples at locations sampled on the Hueneme Shelf. Based on: Allan Hancock Foundation (1965) An Oceanographic and Biological Survey of the Southern California Mainland Shelf. Sacramento, California. California State Water Quality Control Board, Publ. 27. pp. 232, 215 appendix tables

Station	4836–57	4852–57	5535–57	4847–57	5111–57	5533–57	4850–57	Mean
Station characteristics								
Water Depth (m)	23.2	15.2	17.1	18.3	31.4	38.7	55	
Whole Wet Weight of Organisms (g/m^2)	54.8	358.4	30.4	317.6	72.4	101.6	141.6	153.8
Sediment Volume (l)	19.5	24.9	12.5	26.9	7.1	14.2	14.2	17.0
Est. Area Sampled (m^2)	0.165	0.184	0.140	0.192	0.120	0.146	0.146	0.156
Est. Depth of Penetration (cm)	11.34	13.21	8.58	13.87	6.02	9.29	9.29	10.2
Number of Taxa and Individuals for Higher Taxa at Stations								
ANNELIDA								Totals
No. of Taxa	43	60	27	26	32	37	49	122
No. of Individuals	156	417	128	98	99	174	230	1,302
CRUSTACEA								
No. of Taxa	34	39	14	21	22	25	37	96
No. of Individuals	642	812	67	102	201	244	602	2,670
MOLLUSCA								
No. of Taxa	5	11	3	12	18	15	17	55
No. of Individuals	6	34	8	22	27	16	26	139
ECHINODERATA								
No. of Taxa	3	6	6	8	4	5	6	10
No. of Individuals	13	22	13	64	15	70	45	242

Appendix F. Observed life stage, estimated longevity, and higher taxon of dominant macrofaunal, megafaunal, and attached epifaunal taxa on soft sediments at 14-, 18-, 27-, 37-, and 55-m depths on the Hueneme Shelf during the 1974 OSD study

Macrofaunal species					Megafaunal species				
Species	Life stage[a]	Estimated longevity (years)	Source	Taxon	Species	Life stage[1]	Estimated longevity (years)	Source	Taxon
Acuminodeutopus periculosus	AD	≈0.5	Grosse and Pauley (1989)	Gammarid	*Acanthoptilum* sp.	AD	10–15	Inferred from Hill and Wilson (2000)	Sea Pen
All Caprellidae	JUV & AD	0.25–0.75	Takeuchi et al. (2001), Prato et al. (2012)	Caprellid	*Aglaophenia dlspar*	AD	0.5	Inferred from OSD study	Attached Hydroid
Ampelisciphotis podophthalma	AD	≈0.5	Grosse and Pauley (1989)	Gammarid	*Amphiodia urtica*	AD	5	Lie (1968)	Burrowing Ophiuroid
	AD	≈0.5		Gammarid		AD	11–20	MarLIN[b]	

(continued on next page)

(*continued*)

Macrofaunal species					Megafaunal species				
Species	Life stage[a]	Estimated longevity (years)	Source	Taxon	Species	Life stage[1]	Estimated longevity (years)	Source	Taxon
Amphideutopus oculatus			Grosse and Pauley (1989)		*Amphiura arcystata*				Burrowing Ophiuroid
Amphiodia urtica	JUV & AD	5	Lie (1968)	Brittlestar	*Apostichopus californicus*	AD	10–14	Woodby et al. (1993)	Sea Cucumber
Aoroides spinosus	JUV & AD	≈0.5	Grosse and Pauley (1989)	Gammarid	*Astropecten verrilli*	AD	≈5	MacGinitie and MacGinitie (1968)	Asteroid
Armandia brevis	AD	0.11	Hermans (1966); Fernald et al. (1987)	Polychaete	*Cellaria diffusa*	AD	0.5	Inferred from OSD study	Attached Bryozoan
Asterope mariae	AD	<3	Fenwick (1983)	Ostracod	*Diopatra ornata*	AD	5–6	Emerson (1975)	Tubicolous Polychaete
Axinopsida serricata	JUV & AD	2	Lie (1968)	Bivalve	*Diopatra splendidissima*	AD	5–6	Inferred from Emerson (1975)	Tubicolous Polychaete
Chaetozone corona	AD	1–2	MarLIN	Polychaete	*Diopatra tridentata*	AD	5–6	Inferred from Emerson (1975)	Tubicolous Polychaete
Chaetozone setosa	AD	1–2	MarLIN	Polychaete	*Hydrallmania distans*	AD	0.5	Inferred from OSD study	Attached Hydroid
Cumella sp. A	AD	1	Univ. Oregon Scholars Bank (1988)[c]	Cumacean	*Listriolobus pelodes*	AD	≈3–4	Inferred from Stull et al. (1986)	Echiurid
Ericthonius punctatus	JUV & AD	≈0.5	Grosse and Pauley (1989)	Gammarid	*Lytechinus pictus*	AD	7	Detwiler (1996)	Echinoid
Eudorella pacifica	AD	≈1.5	Watling (1979)	Cumacean	*Octopus ? rubescens*	AD	1–2	Wood and O'Dor (2000)	Octopod
Euphilomedes carcharodonta	JUV & AD	<3	Fenwick (1983)	Ostracod	*Ophiura lutkeni*	AD	5–10	Fell (1966)	Brittlestar
Euphilomedes producta	JUV & AD	<3	Fenwick (1983)	Ostracod	*Panopea abrupta*	AD	146	Goodwin and Pease (1989)	Bivalve
Exogone niadina	AD	1–2	MarLIN	Polychaete	*Pisaster brevispinus*	AD	>30	Inferred from Ruppert et al. (2004)	Asteroid
Leptognathia sp.	JUV & AD	1	Leite et al. (2003)	Tanaid	*Plumularia ? alicia*	AD	0.5	Inferred from OSD study	Attached Hydroid
Leptostylis sp. A	AD	2–3	Akiyama and Yamamoto (2004)	Cumacean	*Praxillura maculata*	AD	3–5	MarLIN	Tubicolous Polychaete
Listriolobus pelodes	JUV & AD	≈3–4	Inferred from Stull et al. (1986)	Echiurid	*Scrupocellaria ? diegensis*	AD	0.5	Inferred from OSD study	Attached Bryozoan
Magelona sacculata	JUV & AD	≈3	MarLIN	Polychaete	*Thesea ? mitsukurii*	AD	Species in family ≈42	Chadwick-Furman et al. (2000)	Reptant Gorgonian
Mediomastus ambiseta	AD	≈1–1.5	MarLIN	Polychaete	*Thuiaria ?alba*	AD	1–5	MarLIN	Attached Hydroid
Micronepthys cornuta	JUV & AD	3–10	MarLIN	Polychaete	*Tubularia* sp. A	AD	0.5	Inferred from OSD study	Free-living Hydroid
Microjassa litotes	AD	≈0.5	Grosse and Pauley (1989)	Polychaete	*Virgularia* sp.	AD	10–15	Inferred from Hill and Wilson (2000)	Sea Pen
Munna sp.	AD	2–3	Ruppert et al. (2004)	Isopod					
Munnogonium tillerae	AD	≈0.5	Grosse and Pauley (1989)	Gammarid					
Parvilucina approximata	JUV & AD	≈3?[d]	Based on figure in Coan et al. (2000)	Bivalve					
Pholoe glabra	AD	≈4	MarLIN	Polychaete					
Photis lacia	AD	≈0.5	Grosse and Pauley (1989)	Gammarid					
Prionospio pygmaeus	JUV & AD	1–2	Anger et al. (1986)	Polychaete					
Rutiderma rostratum	JUV & AD	≈<1	Fenwick (1983)	Ostracod					
Scoloplos armiger	AD	≈4	MarLIN	Polychaete					
Tharyx sp.	AD	2–3	Caracciolo and Steimle (1983)	Polychaete					

---

[a] AD = adults; JUV = juveniles; JUV & AD = juveniles and adults

[b] MarLIN - Marine Macrofauna Genus Trait Handbook - http://www.marlin.ac.uk/searchindex.php?searchType=general.

[c] https://scholarsbank.uoregon.edu/xmlui/bitstream/handle/1794/12703/C_vulgaris%20FINAL.pdf?sequence=1.

[d] Based on apparent annular rings on figure.

Appendix G. Likely trophic role for dominant macrofauna and megafaunal on soft sediments at 14-, 18-, 27-, 37-, and 55-m depths on the Hueneme Shelf during the 1974 OSD study. When ‘?’ precedes trophic role, no direct report has been found; feeding type is inferred from reference.

Macrofaunal species				Megafaunal species			
Species	Taxon	Likely trophic role	Source	Species	Taxon	Likely trophic role	Source
Acuminodeutopus periculosus	Aorid gammarid	? Suspension feeder, tube-building	Chapman (2007)	*Acanthoptilum* sp.	Sea pen	Suspension feeder, water-column	Macdonald et al. (2010)
All Caprellidae	Caprellid amphipod	Suspension feeder or diatom grazer	Ruppert et al. (2004)	*Amphiodia urtica*	Burrowing ophiurid	Suspension & surficial deposit feeder	Dailey et al. (1994)
Ampelisciphotis podophthalma	Isaeid gammarid	?Suspension feeder, tube-building	Chapman (2007)	*Amphiura arcystata*	Burrowing ophiurid	Predator, surficial/ deposit feeder	EQA and MBC, 1974a
Amphideutopus oculatus	Aorid gammarid	?Suspension feeder, tube-building	Chapman (2007)	*Apostichopus californicus*	Sea cucumber	Deposit feeder, surficial	Yingst (1974), Muscat (1983)
Amphiodia urtica	Burrowing ophiurid	Suspension & surficial deposit feeder	Dailey et al. (1994)	*Astropecten verrilli*	Sea star	Predator, mega	VanBlaricom (1982); Kraeuter and Castagna (2001)
Aoroides spinosus	Aorid gammarid	?Suspension feeder, tube-building	Cadien (2015)	*Diopatra ornata*	Tubicolous polychaete	Suspension feeder, omnivorous	Fauchald and Jumars (1979)
Armandia brevis	Burrowing polychaete	Deposit feeder, non-selective	Fauchald and Jumars (1979)	*Diopatra splendidissima*	Tubicolous polychaete	Suspension feeder, omnivorous	Fauchald and Jumars (1979)
Asterope mariae	Ostracod	?Planktivore, bentho-hyponeustonic	Macquart-Moulin (1999)	*Diopatra tridentata*	Tubicolous polychaete	? Detritivore, surficial	Unpubl. data
Axinopsida serricata	Shallow-burrowing bivalve	?Deposit feeder, detrital	Burd et al. (2013) Zanzerl et al. (2019)	*Listriolobus pelodes*	Echiurid	Deposit feeder, surficial, major	Pilger (1977a, 1977b)
Chaetozone corona	Burrowing polychaete	Deposit feeder, selective surficial	Fauchald and Jumars (1979)	*Lytechinus pictus*	Sea urchin	Herbivore/ Scavenger/ Omnivore	Brusca (1980); Unpubl. data
Chaetozone setosa	Burrowing polychaete	Deposit feeder, selective surficial	Fauchald and Jumars (1979)	*Octopus ? rubescens*	Cephalopod	Predator, crustacean	Lamb and Hanby (2005)
Cumella sp. A	Cumacean	?Suspension feeder or microdeposit feeder	Ruppert et al. (2004)	*Ophiura lutkeni*	Surficial ophiurid	?Predator, surficial meio/macro-	Feder (1981)Ambrose (1993)
Erichthonius punctatus	Ischyrocerid gammarid	?Suspension feeder, tube-building	Chapman (2007)	*Panopea abrupta*	Deep burrowing bivalve	Suspension feeder on phyto- and zooplankton	Goodwin and Pease (1989)McDonald et al. (2015)
Eudorella pacifica	Cumacean	?Deposit feeder, micro, bentho-hyponeustonic	Cadien (2011)	*Pisaster brevispinus*	Sea star	Predator, bivalve	Lambert (2000)
Euphilomedes carcharodonta	Ostracod	?Planktivore, bentho-hyponeustonic	Macquart-Moulin (1999)	*Praxillura maculata*	Tubicolous polychaete	Suspension feeder, water column	McDaniel and Banse (1979)
Euphilomedes producta	Ostracod	?Planktivore, bentho-hyponeustonic	Macquart-Moulin (1999)	*Thesea ? mitsukurii*	Reptant gorgonian	?Suspension feeder, surficial	
Exogone niadina	Errant polychaete	Predator, micro	Fauchald and Jumars (1979)	*Virgularia* sp.	Sea pen	Suspension feeder, water column	Macdonald et al. (2010)
Leptognathia sp.	Tanaid	Deposit feeder, burrow-dwelling	Reidenauer and Thistle (1985)				
Leptostylis sp. A	Cumacean	?Deposit feeder, micro, bentho-hyponeustonic	Cadien (2011)				
Listriolobus pelodes	Echiurid	Surfical deposit feeder	Pilger (1977a, 1977b)				
Magelona sacculata	Burrowing polychaete	Deposit feeder, detrital	EOL				
Mediomastus ambiseta	Burrowing polychaete	Deposit feeder, non-selective	Fauchald and Jumars (1979)				
Microjassa litotes	Ischyrocerid gammarid	?Suspension feeder, tube-building	Chapman (2007)				
Micronephtys cornuta	Burrowing polychaete	Deposit feeder, non-selective	Dailey et al. (1994)				
Munna sp.	Isopod	?Scavenger, omnivorous	Ruppert et al. (2004)				
Munnogonium tillerae	Isopod	?Omnivorous scavenger	Ruppert et al. (2004)				
Parvilucina approximata	Shallow burrowing bivalve	Deposit feeder, non-selective and chemoautroph	Duplessis et al. (2004)				
Pholoe glabra	Errant polychaete	?Predator, micro	Fauchald and Jumars (1979)				
Photis lacia	Isaeid gammarid	?Suspension feeder, tube-building	Chapman (2007)	1			
Prionospio pygmaeus	Tubicolous polychaete	?Deposit feeder, selective surficial	Fauchald and Jumars (1979)				
Rutiderma rostratum	Ostracod	?Predator female or detritivore male, bentho-hyponeustonic	Kornicker (1985)				
Scoloplos armiger							

(continued on next page)

(*continued*)

Macrofaunal species				Megafaunal species			
Species	Taxon	Likely trophic role	Source	Species	Taxon	Likely trophic role	Source
	Burrowing polychaete	Deposit feeder, non-selective	Fauchald and Jumars (1979)				
Tharyx sp.	Burrowing polychaete	?Deposit feeder, non-selective	Fauchald and Jumars (1979)				

References

Ahn, I.Y., Malouf, R., Lopez, G., 1993. Enhanced larval settlement of the hard clam *Mercenaria mercenaria* by the gem clam *Gemma gemma*. Mar. Ecol. Prog. Ser. 99, 51–59.

Akiyama, T., Yamamoto, M., 2004. Life history of *Nippoleucon hinumensis* (Crustacea: Cumacea: Leuconidae) in Seto Inland Sea of Japan. I. Summer diapause and molt cycle. Mar. Ecol. Prog. Ser. 284, 211–225.

Allan Hancock Foundation (AHF), 1965. An Oceanographic and Biological Survey of the Southern California Mainland Shelf. Sacramento, California, vol. 27. California State Water Quality Control Board, Publ. (232 pp; 215 appendix tables). Available from: http://nmbl.org/cgi-bin/koha/opac-detail.pl?biblionumber=9194

Alves, R.M.S., Van Colen, C., Vincx, M., Vanaverbeke, J., De Smet, B., Rabaut, M., Bouma, T.J., 2017. A case study on the growth of *Lanice conchilega* (Pallas, 1766) aggregations and their ecosystem engineering impact on sedimentary processes. J. Exp. Mar. Biol. Ecol. 489, 15–26.

Ambrose, W.G., 1993. Effects of predation and disturbance by ophiuroids on soft-bottom community structure in Oslofjord - results of a mesocosm study. Mar. Ecol. Prog. Ser. 97, 225–236.

Andersen Jr., A.M., 1971. Spawning, Growth, and Spatial Distribution of the Geoduck Clam, *Panope generosa* Gould, in Hood Canal, Washington. Ph.D. Dissertation. University of Washington, Seattle, WA (132 pp).

Anger, K., Anger, V., Hagmeier, E., 1986. Laboratory studies on the larval growth of *Polydora ligni*, *Polydora ciliata* and *Pygospio elegans* (Polychaeta, Spionidae). Helgoländer Meeresun. 40, 377–395.

Ballinger, D.G., McKee, G.D., 1971. Chemical characterization of bottom sediments. J. Water Pollut. Control Fed. 43, 216–227.

Barnard, J.L., 1963. Relationship of benthic Amphipoda to invertebrate communities of inshore sublittoral sands of southern California. Pac. Nat. 3, 439–467.

Barnard, J.L., Hartman, O., 1959. The sea bottom off Santa Barbara, California: biomass and community structure. Pac. Nat. 1, 1–16.

Barnard, J.L., Ziesenhenne, F.C., 1961. Ophiuroid communities of southern California coastal bottoms. Pac. Nat. 2, 131–152.

Bellan-Santini, D., 1968. Contribution a l'étude des milieux portuaires (le Vieux Port de Marseille). Rapports,P.-v. Réun. Commn int. Explor. scientifique Mer Méditeranee, vol. 18, pp. 93–95.

Bergen, M., Weisberg, S.B., Cadien, D., Dalkey, A., Montagne, D., Smith, R.W., Stull, J.K., Velarde, R.G., 1998. Southern California Bight 1994 Pilot Project: IV. Benthic Infauna. Southern California Coastal Water Research Project, Westminster, CA (260 pp). ftp.sccwrp.org/pub/download/DOCUMENTS/AnnualReports/1997AnnualReport/ar12.pdf.

Berke, S.K., 2012. Biogeographic variability in ecosystem engineering: patterns in the abundance and behavior of the tube-building polychaete *Diopatra cuprea*. Mar. Ecol. Prog. Ser. 447, 1–13.

Berke, S.K., Cruz, V., Osman, R.W., 2009. Sublethal predation and regeneration in two onuphid polychaetes: patterns and implications. Biol. Bull. 217, 242–252.

Bernstein, B.B., Dorsey, J., 1991. Marine monitoring in heterogeneous environments. J. Environ. Manag. 32, 227–240.

Blank, S., Seiter, C., Bruce, P., 2001. Resampling Stats in Excel, Version 2. Resampling Stats, Inc., Arlington, Virginia (172 pp).

Borowitzka, M.A., 1972. Intertidal algal species diversity and the effect of pollution. Aust. J. Mar. Freshwat. Res. 23, 73–84.

Bouma, T., Olenin, S., Reise, K., Ysebaert, T., 2009. Ecosystem engineering and biodiversity in coastal sediments: posing hypotheses. Helgol. Mar. Res. 63, 95–106.

Bourgoin, A., Guillou, M., 1994. Arm regeneration in two populations of *Acrocnida brachiata* (Montagu) (Echinodermata: Ophiuroidea) in Douarnenez Bay, (Brittany: France): an ecological significance. J. Exp. Mar. Biol. Ecol. 184, 123–139.

Boysen-Jensen, P., 1919. Valuation of the Limfjord. 1. Reports of the Danish Biological Station, vol. 26, pp. 3–44.

Braeckman, U., Rabaut, M., Vanaverbeke, J., Degraer, S., Vincx, M., 2014. Protecting the commons: the use of subtidal ecosystem engineers in marine management. Aquat. Conserv. Mar. Freshwat. Ecosyst. 24 (2), 1–10.

Brey, T., 1991. Interactions in soft bottom benthic communities - quantitative aspects of behaviour in the surface deposit feeders *Pygospio elegans* (Polychaeta) and *Macoma balthica* (Bivalvia). Helgoländer Meeresun. 45, 301–316.

Brusca, R.C., 1980. Common Intertidal Invertebrates of the Gulf of California, 2nd ed. University of Arizona Press, Tucson, Arizona.

Buchanan, J.B., 1958. The bottom fauna communities across the continental shelf off Accra, Ghana (Gold Coast). Proc. Zool. Soc. London 130, 1–56.

Buchanan, J.B., 1963. The bottom fauna communities and their sediment relationships off the coast of Northumberland. Oikos 14, 152–175.

Burd, B., Bertold, S., Macdonald, T., 2012. Responses of infaunal composition, biomass and production to discharges from a marine outfall over the past decade. Mar. Pollut. Bull. 64, 1837–1852.

Burd, B., Macdonald, T., Bertold, S., 2013. The effects of wastewater effluent and river discharge on benthic heterotrophic production, organic biomass and respiration in marine coastal sediments. Mar. Pollut. Bull. 74, 351–363.

Cadien, D.B., 2011. Cumacea of the Northeastern Pacific: Equator to Aleutians and intertidal to the abyss Part 1. Introduction and General Comments. Southern California Association for Marine Invertebrate Taxonomy.

Cadien, D.B., 2015. Amphipoda of the Northeast Pacific Equator to Aleutians, intertidal to abyss: III. Aoroidea - a review.

Cammen, L., 1979. The macro-infauna of a North Carolina salt marsh. Am. Midl. Nat. 102, 244–253.

Caracciolo, J.V., Steimle, F.W., 1983. An Atlas of the Distribution and Abundance of Dominant Benthic Invertebrates in the New York Bight Apex with Reviews of Their Life Histories. NOAA Technical Report NMFS SSRF-766. U.S. Dep't of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

Chadwick-Furman, N.E., Goffredo, S., Loya, Y., 2000. Growth and population dynamic model of the reef coral *Fungia granulosa* Klunzinger, 1879 at Eilat, northern Red Sea. J. Exp. Mar. Biol. Ecol. 249, 199–218.

Chapman, J.W., 2007. Amphipoda. In: Carlton, J. (Ed.), The Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon. Completely Revised and Expanded. University of California Press, Berkeley CA, pp. 545–611.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth (190 pp).

Coan, E.V., Scott, P.V., Bernard, F.R., 2000. Bivalve Seashells of Western North America. Santa Barbara Museum of Natural History, Santa Barbara, California (764 pp).

Cooper, K., Boyd, S., Aldridge, J., Rees, H.L., 2007. Cumulative impacts of aggregate extraction on seabed macro-invertebrate communnities in an area off the east coast of the United Kingdom. J. Sea Res. 57, 288–302.

Dailey, M., Reish, D.J., Anderson, J.W. Editors, 1994. Ecology of the Southern California Bight: A Synthesis and Interpretation. University of California Press.

Davis, N., VanBlaricom, G., 1978. Spatial and temporal heterogeneity in sand-bottom epifaunal community of invertebrates in shallow water. Limnol. Oceanogr. 23, 417–427.

Davis, N., VanBlaricom, G.R., Dayton, P.K., 1982. Man-made structures on marine sediments: effects on adjacent benthic communities. Mar. Biol. 70, 295–303.

Detwiler, P.M., 1996. Demography, Growth, Mortality and Resource Allocation in the White Sea Urchin *Lytechinus pictus*. Master's Thesis. San Diego State University, San Diego, California (133 pp).

De Vlas, J., 1979. Secondary production by tail regeneration in a tidal flat population of lugworms (*Arenicola marina*), cropped by flatfish. Neth. J. Sea Res. 13, 362–393.

De Vlas, J., 1985. Secondary production by siphon regeneration in a tidal flat population of *Macoma balthica*. Neth. J. Sea Res. 19, 147–164.

Dornhoffer, T., Waldbusser, G., Meile, C., 2012. Burrow patchiness and oxygen fluxes in bioirrigated sediments. J. Exp. Mar. Biol. Ecol. 412, 81–86.

Duplessis, M.R., Dufour, S.C., Blankenship, L.E., Felbeck, H., Yayanos, A.A., 2004. Anatomical and experimental evidence for particulate feeding in Lucinoma aequizonata and Parvilucina tenuisculpta Bivalvia: Lucinidae from the Santa Barbara Basin. Mar. Biol. 145, 551–561. https://doi.org/10.1007/s00227-004-1350-6.

Emerson, R.R., 1975. The Biology of a Population of *Diopatra ornata* at Santa Catalina Island, California. Ph. D. Dissertation. University of Southern California, Los Angeles, CA (325 pp). http://digitallibrary.usc.edu/cdm/ref/collection/p15799coll3/id/497614.

Environmental Quality Analysts, Marine Biological Consultants, 1974a. City of Oxnard Pre-Discharge Receiving Water Monitoring Study-2nd Quarterly Report. May 1974. Prepared for the City of Oxnard (47 pp,18 appendices).

Environmental Quality Analysts, Marine Biological Consultants, 1974b. City of Oxnard Pre-Discharge Receiving Water Monitoring Study-4th Quarterly Report. January 1975. Prepared for the City of Oxnard (36 pp, 18 appendices).

Environmental Quality Analysts, Marine Biological Consultants, 1975. City of Oxnard predischarge receiving water monitoring study-results of biological studies. Infaunal findings. Final report. Prepared for the City of Oxnard, pp. 45–138.

EOL (Encyclopedia of Life) 2018 Available from http://eol.org. (Accessed 15 July 2018).

Erwin, D.G., 1977. A diving survey of Strangford Lough: the benthic communities and their relation to substrate. Pages 215-224. In: 11th European Symposium on Marine Biology, 1976. Pergamon Press, Galway, Irreland.

Fager, E.W., 1964. Marine sediments: effects of a tube-building polychaete. Science 145, 356–359.

Fager, E.W., 1968. A sand-bottom epifaunal community of invertebrates in shallow water. Limnol. Oceanogr. 13, 448–464.

Fager, E.W., 1971. Pattern in the development of a marine community. Limnol. Oceanogr. 16, 241–253.

Fauchald, K., Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Annu. Rev. 17, 193–284.

Feder, H.M., 1981. Aspects of the feeding biology of the brittle star *Ophiura texturata*. Ophelia 20, 215–235.

Fell, H.B., 1966. The ecology of ophiuroids. In: Boolootian, R.A. (Ed.), Physiology of Echinodermata. Interscience Publishers, New York, pp. 129–144.

Fenwick, G.D., 1983. Population Ecology and Life-History Tactics of Shallow, Sand-Bottom Crustaceans at Kaikoura. Ph.D Dissertation. University of Canterbury, Canterbury, NZ (305 pp).

Fernald, R.L., Hermans, C.O., Lacalls, T.C., Wilson Jr., W.H., Woodin, S.A., 1987. Phylum Annelida, Class Polychaeta. In: Strathmann, M.F. (Ed.), Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast. University of Washington Press, Seattle, WA, pp. 138–195.

Ford, E., 1923. Animal communities of the level sea bottom in the waters adjacent to Plymouth. J. Mar. Biol. Assoc. U. K. 13, 164–224.

Fukuyama, A.K., Shigenaka, G., Coats, D.A., 2014. Status of intertidal infaunal communities following the *Exxon Valdez* oil spill in Prince William sound, Alaska. Mar. Pollut. Bull. 84, 56–69.

Goodwin, C.L., Pease, B., 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest)–Pacific geoduck clam. U.S. Fish. Wildl. Serv. Biol. Rep. 82 (11), 120.

Gray, J.S., Elliott, M., 2009. The Ecology of Marine Sediments: From Science to Management, 2nd ed. Oxford University Press. (225 pp).

Gray, J.S., Clarke, K.R., Warwick, R.M., Hobbs, G., 1990. Detection of initial effects of pollution on marine benthos: an example from the Ekofisk and Eldfisk oilfields, North Sea. Mar. Ecol. Prog. Ser. 66, 285–299.

Grosse, D.J., Pauley, G.B., 1989. Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Pacific Southwest), 82. Coastal Ecology Group, Waterways Experiment Station, U. S. Army Corps of Engineers and U. S. Department of the Interior, Fish and Wildlife Service, Research and Development, National Wetlands Research Center, Vicksburg, MS, and Washington, DC. Biological Report. (11.92). TR EL-82-4. (27 pp). (Available from Coastal Ecology Group, Waterways Experiment Station, U. S. Army Corps of Engineers, Vicksburg, MS, and U. S. Department of the Interior, Fish and Wildlife Service, Research and Development, National Wetlands Research Center, Washington, DC).

Gust, G., Harrison, J.T., 1981. Biological pumps at the sediment-water interface: mechanistic evaluation of the alpheid shrimp *Alpheus mackayi* and its irrigation pattern. Mar. Biol. 64, 71–78.

Hermans, C.O., 1966. The Natural History and Larval Anatomy of *Armandia brevis* (Polychaeta: Opheliidae). Ph.D. Dissertation. University of Washington, Seattle, WA (175 pp).

Hill, J.M., Wilson, E., 2000. *Virgularia mirabilis*. Slender sea pen. *Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme* [on-line]. Marine Biological Association of the United Kingdom, Plymouth [cited 25/03/2008]. http://www.marlin.ac.uk/species/Virgulariamirabilis.htm.

Houghton, J.P., Gilmour, R., Lees, D.C., Driskell, W.B., Lindstrom, S.C., 1997. Long-term recovery (1989-1996) of Prince William sound littoral biota following the *Exxon Valdez* oil spill and subsequent shoreline treatment. In: NOAA Tech Memo NOS ORCA 119. National Oceanic and Atmospheric Administration, Ocean Assessment Division, Seattle, WA.

ISO 16665., 2005. Guidelines for Quantitative Sampling and Sample Processing of Marine Soft- Bottom Macrofauna (UNE-EN).

Janson, A.-L., Denis, L., Rauch, M., Desroy, N., 2012. Macrobenthic biodiversity and oxygen uptake in estuarine systems: the example of the seine estuary. J. Soils Sediments 12.

Johannes, R.E., Satomi, M., 1966. Composition and nutritive value of fecal pellets of a marine crustacean. Limnol. Oceanogr. 11, 191–197.

Jones, G.F., 1969. The benthic macrofauna of the mainland shelf of Southern California. In: Allan Hancock Monographs in Marine Biology. Allan Hancock Foundation, University of Southern California, Los Angeles (219 pp).

Jones, N.S., 1950. Marine bottom communities. Biol. Rev. 25, 283–313.

Kornicker, L.S., 1985. Sexual dimorphism, ontogeny, and functional morphology of *Rutiderma hartmanni* Poulsen, 1965 Crustacea: Ostracoda (32 pp). In: Smithsonian Contributions to Zoology. https://doi.org/10.5479/si.00810282.408.

Kraeuter, J.N., Castagna, M. (Eds.), 2001. Biology of the Hard Clam. Elsevier Science, Amsterdam, The Netherlands.

Krebs, C.J., 1998. Ecological Methodology, 2nd ed. Addison-Welsey Educational Publishers, Inc., Menlo Park, CA.

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C.O., Banta, G. T., 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar. Ecol. Prog. Ser. 446, 285–302.

Lamb, A., Hanby, B., 2005. Marine Life of the Pacific Northwest. Harbour Publishing, Madeira Park, BC, Canada.

Lambert, P., 2000. Sea Stars of British Columbia, Southeast Alaska and Puget Sound. UBC Press, Vancouver, BC.

Lane, E.D., 1975. Quantitative aspects of the life history of the diamond turbot, *Hypsopsetta guttulata* (Girard). Fish. Bull. U.S. 165, 153–173.

Lawrence, J.M., Vasquez, J., 1996. The effect of sublethal predation on the biology of echinoderms. Oceanol. Acta 19, 431–440.

Lees, D.C., 2021. MS. Importance of Sublethal Predation in Sedentary Megafaunal Assemblages in Soft Sediments.

Lees, D.C., Driskell, W.B., 1980. Investigations on shallow subtidal habitats and assemblages in lower Cook Inlet. 115 pp + Appendices A - P. In: Feder, H.M., Paul, A.J., Hoberg, M., Jewett, S. (Eds.), 1981. Distribution, Abundance, Community Structure and Trophic Relationships of the Nearshore Benthos of Cook Inlet. Final Report, Environmental Assessment of the Alaskan Continental Shelf, Biological Studies, vol. 14. NOAA OCSEAP, Juneau, AK, pp. 45–676. http://www.arlis.org/docs/vol1/N/55997671.pdf. Prepared for Institute of Marine Sciences, Fairbanks, editor.

Lees, D.C., Driskell, W.B., 2007. Assessment of Bivalve Recovery on Treated Mixed-Soft Beaches in Prince William Sound. Dept. of Commerce, National Oceanic & Atmospheric Administration, National Marine Fisheries Service, Office of Oil Spill Damage & Restoration and *Exxon Valdez* Oil Spill Trustee Council, Anchorage, AK. Restoration Project 040574, Final Report. (121 pp). Available from: http://www.arlis.org/docs/vol1/180774340.pdf.

Lees, D.C., Houghton, J.P., Erikson, D.E., Driskell, W.B., Boettcher, D.E., 1986. Ecological Studies of Intertidal and Shallow Subtidal Habitats in Lower Cook Inlet, vol. 44. U.S. Dept. of Commerce, NOAA OCSEAP Final Reports, Alaska, pp. 1437–1646. Available from: https://www.data.boem.gov/PI/PDFImages/ESPIS/0/161.pdf.

Leite, F.P.P., Turra, A., Souza, E.C.F., 2003. Population biology and distribution of the tanaid *Kalliapseudes schubarti* Mañé-Garzon, 1949, in an intertidal flat in southeastern Brazil. Braz. J. Biol. 63, 469–479.

Lie, U., 1968. A quantitative study in Puget Sound, Washington, USA, in 1963-1964. FiskeriDirektoratets Skrifter Serie Havundersokekelserlser 14, 229–556.

Lindsay, S.M., 2010. Frequency of injury and the ecology of regeneration in marine benthic invertebrates. Integr. Comp. Biol. 50, 479–493.

Lindsay, S.M., Jackson, J.L., Forrest, D.L., 2008. Morphology of anterior regeneration in two spionid polychaete species: implications for feeding efficiency. Invertebr. Biol. 127, 65–79.

Macdonald, T.A., Burd, B.J., Macdonald, V.I., van Roodselaar, A., 2010. Taxonomic and feeding guild classification for the marine benthic macroinvertebrates of the Strait of Georgia. Canadian Technical Report of Fisheries and Aquatic Sciences, British Columbia.

MacGinitie, G.E., MacGinitie, N., 1968. Natural History of Marine Animals, 2nd ed. McGraw-Hill, New York. (523 pp).

Macquart-Moulin, C., 1999. Diel vertical migration and endogenous swimming rhythm in *Asterope* mariae (Baird) and *Philomedes interpuncta* (Baird) (Crustacea Ostracoda Cypridinidae). J. Plankton Res. 21, 1891–1910.

MarLIN, 2021. Marine Macrofauna Genus Trait Handbook.

Massé, H., 1972. Quantitative investigations of sand-bottom macrofauna along the Mediterranean north-west coast. Mar. Biol. 15, 209–220.

McDaniel, N., Banse, K., 1979. A novel method of suspension feeding by the maldanid polychaete *Praxillura maculata*. Mar. Biol. 55, 129–132.

McDonald, P.S., Essington, T., Davis, J.P., Galloway, A., Stevick, B.C., Jensen, G., Vanblaricom, G.R., Armstrong, D.A., 2015. Distribution, abundance, and habitat associations of a large bivalve *Panopea generosa* in a eutrophic fjord estuary. J. Shellfish Res. 34, 137–145.

McNulty, J.K., 1961. Ecological effects of sewage pollution in Biscayne Bay, Florida: sediments and the distribution of benthic and fouling macro-organisms. Bull. Mar. Sci. Gulf Caribb. 11, 394–447.

McNulty, J.K., 1970. Effects of Abatement of Domestic Sewage Pollution on the Benthos, Volumes of Zooplankton, and the Fouling Organisms of Biscayne Bay, Florida. Inst. of Marine and Atmospheric Sciences, University of Miami, Univ. of Miami Press.

Merrill, R.L., Hobson, E.S., 1970. Field observations of *Dendraster excentricus*, a sand dollar of western North America. Am. Midl. Nat. 83, 595–624.

Meysman, F., Middelburg, J., Heip, C., 2007. Bioturbation: a fresh look at Darwin's last idea. Trends Ecol. Evol. 21, 688–695.

Michel, J., Bejarano, A.C., Peterson, C.H., Voss, C., 2013. Review of Biological and Biophysical Impacts from Dredging and Handling of Offshore Sand. OCS Study BOEM 2013-0119. Bureau of Oceanic Energy Management, Herndon, VA.

Mistri, M., Rossi, R., Fano, E.A., 2001. Structure and secondary production of a soft bottom macrobenthic community in a brackish lagoon (Sacca di Goro, North-Eastern Italy). Estuar. Coast. Shelf Sci. 52, 605–616.

Morin, J.G., Kastendiek, J.E., Harrington, A., Davis, N., 1985. Organization and patterns of interactions in a subtidal sand community on an exposed coast. Mar. Ecol. Prog. Ser. 27, 163–185.

Morin, J.G., Kastendiek, J.E., Harrington, A., Davis, N., 1988. Organisms of a subtidal sand community in southern California. Bull. South. Calif. Acad. Sci. 87, 1–11.

Morris, H.M., Abbott, D.P., Haderlie, E.C., 1980. Macrura and Anomura: The Ghost Shrimps, Hermit Crabs, and Allies. Intertidal Invertebrates of California. Stanford University Press, Stanford, California, pp. 579–593.

Muscat, A.M., 1983. Population dynamics and the effect on the infauna of the deposit-feeding holothurian *Parastichopus parvimensis* Clark. University of Southern California, Los Angeles, CA.

Needham, H.R., Pilditch, C.A., Lohrer, A.M., Thrush, S.F., 2011. Context-specific bioturbation mediates changes to ecosystem functioning. Ecosystems 14, 1096–1109.

Newell, R.C., Seiderer, L.J., Hitchcock, D.R., 1998. The impact of dredging works in coastal waters: a review of the sensitivity to disturbance and subsequent recovery of biological resources on the sea bed. Oceanogr. Mar. Biol. Annu. Rev. 36, 127–178.

Nilsen, M., Pedersen, T., Nilssen, E., 2006. Macrobenthic biomass, productivity (P/B) and production in a high-latitude ecosystem, North Norway. Mar. Ecol. Prog. Ser. 321, 67–77.

Norkko, A., Rosenberg, R., Thrush, S., Whitlatch, R., 2006. Scale- and intensity-dependent disturbance determines the magnitude of opportunistic response. J. Exp. Mar. Biol. Ecol. 330, 195–207.

O'Connor, B., Bowmer, T., McGrath, D., Raine, R., 1986. Energy flow through an *Amphiura filiformis* (Ophiuroidea: Echinodermata) population in Galway Bay, west coast of Ireland: a preliminary investigation. Ophelia 26, 351–357.

Parry, D.M., 2002. Quantification of Marine Megafaunal Distribution Patterns Using a Remotely Operated Vehicle. Ph.D Dissertation. University of Plymouth, Plymouth, U.K.

Passarelli, C., Olivier, F., Paterson, D., Meziane, T., Hubas, C., 2014. Organisms as cooperative ecosystem engineers in intertidal flats. J. Sea Res. 92, 92–101.

Pearson, T.H., 2001. Functional group ecology in soft-sediment marine benthos: the role of bioturbation. Oceanogr. Mar. Biol. Annu. Rev. 39, 233–267.

Pemberton, G.S., Risk, M.J., Buckley, D.E., 1976. Supershrimp: deep bioturbation in the strait of Canso, Nova Scotia. Science 192, 790–791.

Petersen, C.G.J., 1913. Valuation of the sea. II. The animal communities of the sea bottom and their importance for marine zoogeography. In: Report of Danish Biological Station, vol. 21 (44 pp).

Petersen, C.G.J., 1915. On the animals communities of the sea bottom in the Skagerak, the Christiana Fjord, and the Danish waters. In: Dansk Biol. Stat., Beretning (Reports), vol. 23, pp. 3–28.

Peterson, C.H., 1975. Stability of species and of community for the benthos of two lagoons. Ecology 56, 958–965.

Peterson, C.H., 1977. Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. Mar. Biol. 43, 343–359.

Peterson, C.H., Quammen, M.L., 1982. Siphon nipping its importance to small fishes and its impact on growth of the bivalve *Protothaca staminea* Conrad. J. Exp. Mar. Biol. Ecol. 63, 249–268.

Pilger, J.F., 1977a. Listriolobus pelodes (Echiura). Ph.D. Dissertation. Univ. of Southern California, Los Angeles (221 pp). http://digitallibrary.usc.edu/cdm/ref/collection/p15799coll30/id/224182.

Pilger, J.F., 1977b. Biology and gametogenesis of *Listriolobus pelodes* Echiura. Univ. of So, California, Los Angeles.

Posey, M.H., 1985. The Effects upon the Macrofaunal Community of a Dominant Burrowing Deposit Feeder, *Callianassa californiensis*, and the Role of Predation in Determining its Intertidal Distribution. Univ. of Oregon, Eugene, OR.

Powell, E., Mann, R., Ashton-Alcox, K., Kuykendall, K., Long, M., 2017. Can we estimate molluscan abundance and biomass on the continental shelf? Estuar. Coast. Shelf Sci. 198A, 213–224.

Powell, E.N., Mann, R., 2016. How well do we know the infaunal biomass of the continental shelf? Cont. Shelf Res. 115, 27–32.

Prato, E., Parlapiano, I., Biandolino, F., 2012. Population dynamics of the amphipod *Caprella scaura* in the Mar Piccolo of Taranto. Biol. Mar. Mediterr. 19, 190–191.

Quintana, C.O., Yoshinaga, M.Y., Sumida, P.Y.G., 2010. Benthic responses to organic matter variation in a subtropical coastal area off SE Brazil. Mar. Ecol. 31, 457–472.

Reidenauer, J.A., Thistle, D., 1985. The tanaid fauna from a region of the deep North Atlantic where near-bottom current velocities are high. Oceanol. Acta 8, 355–360.

Reilly, P.N., 2001. Littleneck clams. In: Leet, W.S., Dewees, C.M., Klingbeil, R., Larson, E.J. (Eds.), California's Living Marine Resources: A Status Report. The Resources Agency, The California Department of Fish and Game, pp. 448–452.

Rhoads, D.C., Young, D.K., 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28, 150–178.

Ruppert, E., Fox, R., Barnes, R., 2004. Invertebrate Zoology: A Functional Evolutionary Approach, 7th ed. Brooks/Cole, Toronto, Canada. (1056 pp).

Salas, C., Tirado, C., Manjon-Cabeza, M.E., 2001. Sublethal foot-predation on Donacidae (Mollusca: Bivalvia). J. Sea Res. 46, 43–56.

Sanders, H.L., 1956. Biology of marine bottom communities. In: Bull. Bingham Oceanographic Collection, vol. 15, pp. 345–414. Oceanography of Long Island Sound, 1952–1954.

Sanders, H.L., 1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. Limnol. Oceanogr. 3, 245–258.

Sanders, H.L., 1960. Benthic studies in Buzzards Bay. III. The structure of the soft-bottom community. Limnol. Oceanogr. 5, 138–153.

Sasaki, K., Kudo, M., Tomiyama, T., Ito, K., Omori, M., 2008. Predation pressure on the siphons of the bivalve *Nuttallia olivacea* by the juvenile stone flounder *Platichthys bicoloratus* in the Natori River estuary, North-Eastern Japan. Fish. Sci. 68, 104–116.

Seiderer, L.J., Newell, R.C., 1999. Analysis of the relationship between sediment composition and benthic community structure in coastal deposits: implications for marine aggregate dredging. ICES J. Mar. Sci. 56, 757–765.

Skalski, J.R., Coats, D.A., Fukuyama, A.K., 2001. Criteria for oil spill recovery: a case study of the intertidal community of Prince William sound, Alaska, following the Exxon Valdez oil spill. Environ. Manag. 28, 9–18.

Skilleter, G.A., 1992. Recruitment of Cerithiid gastropods (*Rhinoclavis* spp) in sediments at one tree reef, great barrier reef. J. Exp. Mar. Biol. Ecol. 156, 1–21.

Sköld, M., Loo, L.O., Rosenberg, R., 1994. Production, dynamics and demography of an *Amphiura filiformis* population. Mar. Ecol. Prog. Ser. 103, 81–90.

Solan, M., Germano, J.D., Rhoads, D.C., Smith, C., Michaud, E., Parry, D., Wenzhöfer, F., Kennedy, B., Henriques, C., Battle, E., Carey, D., Iocco, L., Valente, R., Watson, J., Rosenberg, R., 2003. Towards a greater understanding of pattern, scale and process in marine benthic systems: a picture is worth a thousand worms. J. Exp. Mar. Biol. Ecol. 285–286, 313–338.

Southern California Coastal Water Research Project (SCCWRP), 1973. The Ecology of the Southern California Bight: Implications for Water Quality Management: Three-Year Report. El Segundo, CA.

Spärck, R., 1935. On the importance of quantitative investigations of the bottom fauna in marine biology. J. Conseil. 10, 3–19.

Stancyk, S., Golde, H., Pape-Lindstrom, P., Dobson, W., 1994. Born to lose. I. Measures of tissue loss and regeneration by the brittlestar *Microphiopholis gracillima*. (Echinodermata: Ophiuroidea). Mar. Biol. 118, 451–462.

Stull, J.K., Haydock, C.I., Montagne, D.E., 1986. Effects of *Listriolobus pelodes* (Echiura) on coastal shelf benthic communities and sediments modified by a major California wastewater discharge. Estuar. Coast. Shelf Sci. 22, 1–17.

Takeuchi, I., Takahashi, S., Tanabe, S., Miyazaki, N., 2001. *Caprella* watch: a new approach for monitoring butyltin residues in the ocean. Mar. Environ. Res. 52, 97–113.

Thomsen, M.S., McGlathery, K., 2005. Facilitation of macroalgae by the sedimentary tube forming polychaete *Diopatra cuprea*. Estuar. Coast. Mar. Sci. 62, 63–73.

Thorson, G., 1957. Bottom communities (sublittoral or shallow shelf). In: Hedgpeth, J.W. (Ed.), Treatise on Marine Ecology and Paleoecology. Geological Society of America, Washington, D.C., pp. 461–534

Tomašových, A., Kidwell, S.M., 2017. Nineteenth-century collapse of a benthic marine ecosystem on the open continental shelf. Proc. R. Soc. B Biol. Sci. 284, 10.

Trevallion, A., 1971. Studies on *Tellina tenuis* Da Costa. III. Aspects of general biology and energy flow. J. Exp. Mar. Biol. Ecol. 7, 95–122.

Tyson, R.V., 1995. Sedimentary Organic Matter: Organic Facies and Palynofacies. Chapman & Hall, London.

Univ. Oregon Scholars Bank, 1988. https://scholarsbank.uoregon.edu/xmlui/bitstream/handle/1794/12703/C_vulgaris%20FINAL.pdf?sequence=1.

U.S. Army Corps of Engineers, 2015. Encinitas-Solana Beach Coastal Storm Damage Reduction Project Integrated Feasibility Report & Environmental Impact Statement/Environmental Impact Report (EIS/EIR). San Diego County. Los Angeles, CA (574 pp, Appendices A to N).

VanBlaricom, G.R., 1982. Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. Ecol. Monogr. 52, 283–305.

Volkenborn, N., Polerecky, L., Hedtkamp, S., van Beusekom, J., 2007. Bioturbation and bioirrigation extend the open exchange regions in permeable sediments. Limnol. Oceanogr. 52, 1898–1909.

Watling, L., 1979. Marine flora and fauna of the Northeastern United States. Crustacea: Cumacea. National Marine Fisheries Service Technical Report NMFS Circ, p. 423 (23 p). Available from: https://archive.org/details/marineflorafauna00watl.

Watling, L., 1991. The sedimentary milieu and its consequences for resident organisms. Am. Zool. 31, 789–796.

Weitkamp, L.A., Wissmar, R.C., Simenstad, C.A., Fresh, K.L., Odell, J.G., 1992. Gray whale foraging on ghost shrimp (*Callianassa californiensis*) in littoral sand flats of Puget Sound, USA. Can. J. Zool. 70, 2275–2280.

Wilber, D., Clarke, D., 2007. Defining and assessing benthic recovery following dredging and dredged material disposal. In: Proceedings of World Dredging Congress. WODCON XVIII Conference, Lake Buena Vista, FL, pp. 603–618.

Wood, J.B., O'Dor, R.K., 2000. Do larger cephalopods live longer? Effects of temperature and phylogeny on interspecific comparisons of age and size at maturity. Mar. Biol. 136, 91–99.

Woodby, D.A., Kruse, G.H., Larson, R.C., 1993. A conservative application of a surplus production model to the sea cucumber fishery in Southeast Alaska. Proc. Int'l Symp. Management Strategies for Exploited Fish Populations. University of Alaska Fairbanks: Alaska Sea Grant Program. Available from: http://nsgl.gso.uri.edu/aku/akuw92001/akuw92001_part-2c.pdf.

Word, J.Q., 1976. Biological comparison of grab sampling devices. In: Southern California Coastal Water Research Project, El Segundo, CA, pp. 189–194. Available from: http://ftp.sccwrp.org/pub/download/DOCUMENTS/AnnualReports/1976AnnualReport/ar27.pdf.

Yingst, J.Y., 1974. The utilization of organic detritus and associated microorganisms by *Parastichopus parvimensis*, a benthic deposit-feeding holothurian. University of Southern California, Los Angeles, CA.

Young, D.K., Rhoads, D.C., 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. I. a transect study. Mar. Biol. 11, 242–254.

Zanzerl, H., Salvo, F., Jones, S.W., Dufour, S.C., 2019. Feeding strategies in symbiotic and asymbiotic thyasirid bivalves. J. Sea Res. 145, 16–23.

Zar, J.H., 2010. Biostatistical Analysis, 5th ed. Prentice Hall, Inc, Englewood Cliffs, New Jersey.