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Historical Comment

Revisiting Paine's 1966 Sea Star Removal Experiment, the Most-Cited Empirical Article in the *American Naturalist*

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ABSTRACT: "Food Web Complexity and Species Diversity" (Paine 1966) is the most-cited empirical article published in the *American Naturalist*. In short, Paine removed predatory sea stars (*Pisaster ochraceus*) from the rocky intertidal and watched the key prey species, mussels (*Mytilus californianus*), crowd out seven subordinate primary space-holding species. However, because these mussels are a foundational species, they provide three-dimensional habitat for over 300 associated species inhabiting the mussel beds; thus, removing sea stars significantly increases community-wide diversity. In any case, most ecologists cite Paine (1966) to support a statement that predators increase diversity by interfering with competition. Although detractors remained skeptical of top-down effects and keystone concepts, the paradigm that predation increases diversity spread. By 1991, "Food Web Complexity and Species Diversity" was considered a classic ecological paper, and after 50 years it continues to influence ecological theory and conservation biology.

Keywords: predator, diversity, *Pisaster*, competitive exclusion, rocky intertidal, trophic cascade.

Introduction

What is the most influential ecological paper ever? One candidate has recently had its fiftieth anniversary: "Food Web Complexity and Species Diversity" (Paine 1966). The influence of Paine (1966)—in terms of relative citation rates—peaked in the early 1970s and declined through the 1980s but has held relatively steady for the last several decades. Specifically, for every five articles on rocky intertidal ecosystems, two articles (on any topic) cite Paine (1966). As a result, "Food Web Complexity and Species Diversity" is the most-cited empirical article in the *American Naturalist*'s history, with over 2,900 citations in the Web of Science at the time of Bob Paine's death (June 13, 2016). In memory of Bob and his larger-than-life personality and contributions to ecology, we look at the article's historical context, consider how it was cited in the literature, and discuss its effects on ecological theory and conservation biology. We conclude that most authors cite Paine (1966) to support the paradigm that predators maintain diversity, when, ironically, by some measures, sea stars have the opposite effect on rocky intertidal diversity.

Before Paine's time, generations of ecologists had pondered coexistence among similar competitors. For instance, Grinnell (1904) had observed that species could not coexist on a shared resource, a premise backed by Lotka's (1925) and Volterra's (1926) competition models and Park's (1948) laboratory experiments with two *Tribolium* beetle species. If similar species were to coexist in the same niche, something needed to interfere with the successional process. That something was sometimes humans. For example, Darwin (1859) noted that mowing or grazing increased coexistence among grassland plants, and Slobodkin (1964) interrupted competitive exclusion between cultured hydra species through periodic culling. In nature, Elton (1958, p. 148–149) intuited that "there are many species of enemies and parasites ready to turn on any species that starts being unusually numerous, and by a complex system of checks and buffers, keep them down." Connell (1961) had used field experiments to show that predatory whelks reduced competition between barnacles in the lower intertidal zone. The similar view that predators might keep herbivores in check (the green world hypothesis) had been argued by Paine's advisor, Fred Smith, and two other University of Michigan faculty, Nelson Hairston and Lawrence Slobodkin (oddly, Paine [1966] does not cite Hairston et al. [1960]). However, it was Paine who pushed the concept that predation could increase diversity. Paine's intertidal work remains relevant because today's ecologists

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are still pondering the mechanisms that maintain diversity, especially with respect to predators.

Marine ecology was primarily an observational science until Connell showed that the intertidal zone was a tractable system for conducting experiments to test basic ecological questions. For instance, ecologists had been interested in how wolves affected moose on Isle Royale since 1949 (Peterson 1995), but wolves were not amenable to controlled experiments that could determine cause and effect. Whelks are like little wolves in slow motion, and Connell manipulated them as a model system with cages. Like Connell's whelks, sea stars could be manipulated by Paine. Moreover, the results could be seen in a few months.

Paine's study began just after he was hired at the University of Washington. He traveled to Mukkaw (now Makah) Bay in spring 1963 to lead the rocky intertidal field trip for a course he had inherited on the natural history of marine invertebrates. He pointed out the sea stars (*Pisaster ochraceus*) that were abundant in a band below the *Mytilus californianus* mussel beds. In Paine's mind, this band was evidence that "local species diversity is directly related to the efficiency with which predators like sea stars prevent the monopolization of the major environmental requisites by one species" (p. 65), a hypothesis that derives from the works of Gause, Lack, Slobodkin, and Connell. Whereas most ecological thought about diversity had focused on latitudinal gradients, predation was a local effect. To test this hypothesis, Paine (1966) compared the rocky intertidal food webs he observed at Mukkaw Bay, the Sea of Cortez, and Costa Rica. Because Costa Rica lacks a sea star and also has the simplest food web, Paine credits sea stars for the high diversity of space holders in Washington and Mexico. This multiweb comparison that dominates the paper is almost never cited. Instead, most authors cite Paine (1966) for a single-page description of a preliminary field experiment at Mukkaw Bay. After using a crowbar to pry sea stars from an 8-m-wide by 2-m-high stretch of Mukkaw Bay, Paine observed a massive juvenile acorn barnacle settlement followed by mussels on the primary substratum (i.e., bare rock). Later, the mussels replaced the barnacles, algae, and other primary space holders (i.e., species attached to rocks). As the mussel bed expanded, Paine noted that "the area has become trophically simpler" (p. 70), from 15 to eight primary space-holding species. He surmised that sea stars interrupted succession and fostered coexistence among these space-holding species. Paine contrasts this with earlier assertions in the literature that succession moves systems to increased complexity. Paine ends by noting that he has not quantified changes in the species associated with the shift in microhabitat from algal mats to mussel byssal threads—a caveat we will address later. "Diversity, thanks to MacArthur, was in the air," says Paine. The *American Naturalist*, with its penchant for big ideas, was Paine's first and only choice for his results.

How and Why Has Paine (1966) Been Cited?

To gauge the influence of "Food Web Complexity and Species Diversity," we used the Web of Science to gather data on who cites Paine (1966) and for what reason. Most ecologists remember Paine (1966) for the sea star removal experiment. The clarity and simplicity of the experimental results combined with keen natural history observation resulted in its extensive citation in ecology journals, lectures, and texts. The article's broad reach is evidenced by the 900 different authors that have cited it. The authors that cite Paine (1966) the most have, not surprisingly, been West Coast marine ecologists and Paine's prolific students and their students. Pick up an article in *Ecology* about the rocky intertidal or from a member of the Paine family tree and odds are high that it will cite Paine (1966). The most typical Paine (1966) citation (~30%) is a generic reference to the role that predators play in reducing competition and promoting diversity. Only 10% specify that Paine's predators were sea stars, and 5% specify that the prey were mussels. Oddly, 22% cite Paine (1966) for the keystone species concept, even though the word "keystone" was coined in his subsequent *American Naturalist* note (Paine 1969). Surprisingly few (2%) authors cite Paine (1966) for a trophic cascade. Overall, most authors cite Paine (1966) to support a brief statement that predators increase diversity by interfering with competition, leaving out what Paine did, where he did it, and what increased.

The Caveat

When Paine looks back on how people have cited "Food Web Complexity and Species Diversity," he emphasizes that readers often miss that he was talking about the response of primary space holders to sea star removal (to his chagrin, only 1% of papers that cite Paine [1966] specify primary space holders). To clarify this point, Paine later emphasized,

> I apply the term "primary space" or "primary substratum" to surfaces that either appear barren or are encrusted with coralline algae such as *Lithothamnium* and *Lithophyllum*. All other substrata, such as barnacle valves, mussel shells or benthic algae are considered to provide secondary substratum, and have not been considered. The epifaunal community on such secondary substrata as well as the infaunal community associated with mussels is almost certainly characterized by its own organization and has not yet been studied adequately. (Paine 1974, p. 94)

This caveat is key to applying the rocky intertidal as a model system to study how predation interferes with competition. In other words, to generalize from Paine (1966) to other systems requires the assumption that either the competitive dominant is not also a foundational species or species facilitated by the dominant are not counted in the tally of biodiversity.

Suchanek (1979, 1985) and Lohse (1993*a*, 1993*b*) took Paine's suggestion to study the community associated with mussels, showing that mussel shells increase the surface area of hard substrate and create three-dimensional matrices of stable microhabitats that support diverse species assemblages (Hewatt 1935; Kanter 1978; Suchanek 1979, 1985, 1992; Seed and Suchanek 1992), including most primary space holders. Yet only 0.5% of the papers citing Paine (1966) mention that mussel shells or mussel beds are habitat for other species. These other species add up, even where sea stars are present. At Tatoosh Island, in the presence of *Pisaster*, the biodiversity on intertidal primary substratum (rock without mussels) is low (ca. 15–18 spp.) but increases to ~45 species when secondary space occupiers (those species that attach to the primary space occupiers) are taken into account. Though low in biomass, such secondary space occupiers dominate the intertidal species list at control plots. When *Pisaster* is removed, things get even more interesting (fig. 1; table A1). As described by Paine (1966), the primary substratum becomes covered with mussels and then supports only about eight primary space-holding species. However, the community-wide diversity (including all those associated organisms within the mussel bed) increases to over 300 species (Suchanek 1979, 1985, 1992; Seed and Suchanek 1992), attached to the mussels and hard surfaces as epizoans (17%–33%), living within the organic detrital mud or silt layer beneath the mussels as infauna (5%–21%), and moving over and throughout the interstices of the mussel matrix as mobile fauna (58%–74%). Therefore, because the competitive dominant (*Mytilus*) also happens to be a habitat-forming foundational species, removing *Pisaster* reduces the diversity of primary space occupiers, but it increases community-wide diversity.

Legacy

The paradigm that predation increases diversity spread among marine, aquatic, and terrestrial scientists. Paine's success with the elegant simplicity of the far-reaching keystone predator, keystone species, and trophic cascade concepts attracted many bright students and collaborators. As a result, his academic dynasty is well respected and has fostered a dense web of influential ecologists, many of whom have developed high-profile careers of their own, both within academia and in environmental activism and national policy arenas (Yong 2013). Paine's students worked on other aspects of the rocky intertidal, building on and informing each other's work. For instance, Paul Dayton's (1971, 1975) experiments showed the relative roles of predation and disturbance for both exposed and more protected West Coast rocky intertidal communities in Washington State. Another early student, Bruce Menge, expanded studies on the keystone species concept at exposed sites in both Washington and Oregon (Menge et al. 1994). In addition, Menge and former Paine master's student Jane Lubchenco evaluated competition and predation along the rocky coastlines of New England (Lubchenco and Menge 1978). It was Paine who critiqued Jim Estes's initial plan to study how the ecosystem affected sea otters, convincing him that it was more interesting to ask how sea otters affected the ecosystem (Estes 2016). Estes found that sea otters, like sea stars, had cascading effects on food webs. In particular, kelp forests (and their associated species) increased on reefs after sea otters preyed on sea urchins that otherwise overgrazed the giant kelp (Estes and Palmisano 1974). One could fill several volumes with the work published by the students Paine mentored.

Paine's experimental manipulation at Mukkaw Bay influenced the course of ecological theory and conservation practices. Not only did "Food Web Complexity and Species Diversity" expand field experimentation in marine ecology, it also popularized the idea that predators are influential players. Paine was pleased to see that workers in other systems, such as Hall et al. (1970), "ate it up" and that MacArthur was "a big fan." Connell (1971) cites "Food Web Complexity and Species Diversity" as a key rationale for the influential Janzen-Connell hypothesis stating that herbivores help maintain tropical tree diversity. By 1991, "Food Web Complexity and Species Diversity" was considered a classic ecological paper (Real and Brown 2012).

As with any high-profile paper, Paine's work has had detractors, especially those skeptical of top-down effects. Intertidal biologists such as Underwood and Denley (1984) argued that food-web interactions in intertidal communities were dependent on patterns of recruitment, whereas Foster (1991) pointed out exceptions to the strong zonation patterns in Washington. Martinez and Dunne (1998) have, on theoretical grounds, questioned whether particular species are more or less important in food webs, suggesting that such observations could be artifacts of the spatial and temporal scale of observation. Paine has not been shy to respond by questioning the value of the "opaque" computer models and "glitzy graphics" favored by such food web theoreticians (Paine 2004).

Paine's broader legacy is hard to estimate, but after "Food Web Complexity and Species Diversity," and perhaps not coincidentally, the media started to depict predators as noble rather than villainous (Dunlap 1991). By the early 1970s, public perspective had changed enough that the US Endangered Species Act protected wolves and brown bears for their intrinsic value. However, the intrinsic value of predators remained a tough sell to the rural public, so conservationists pointed to utilitarian reasons, such as increased forest production, ecotourism, and road safety (Bath 1991). Eventually, Paine's argument that predators maintain biodiversity began to hold broad appeal among conservation biologists. Although

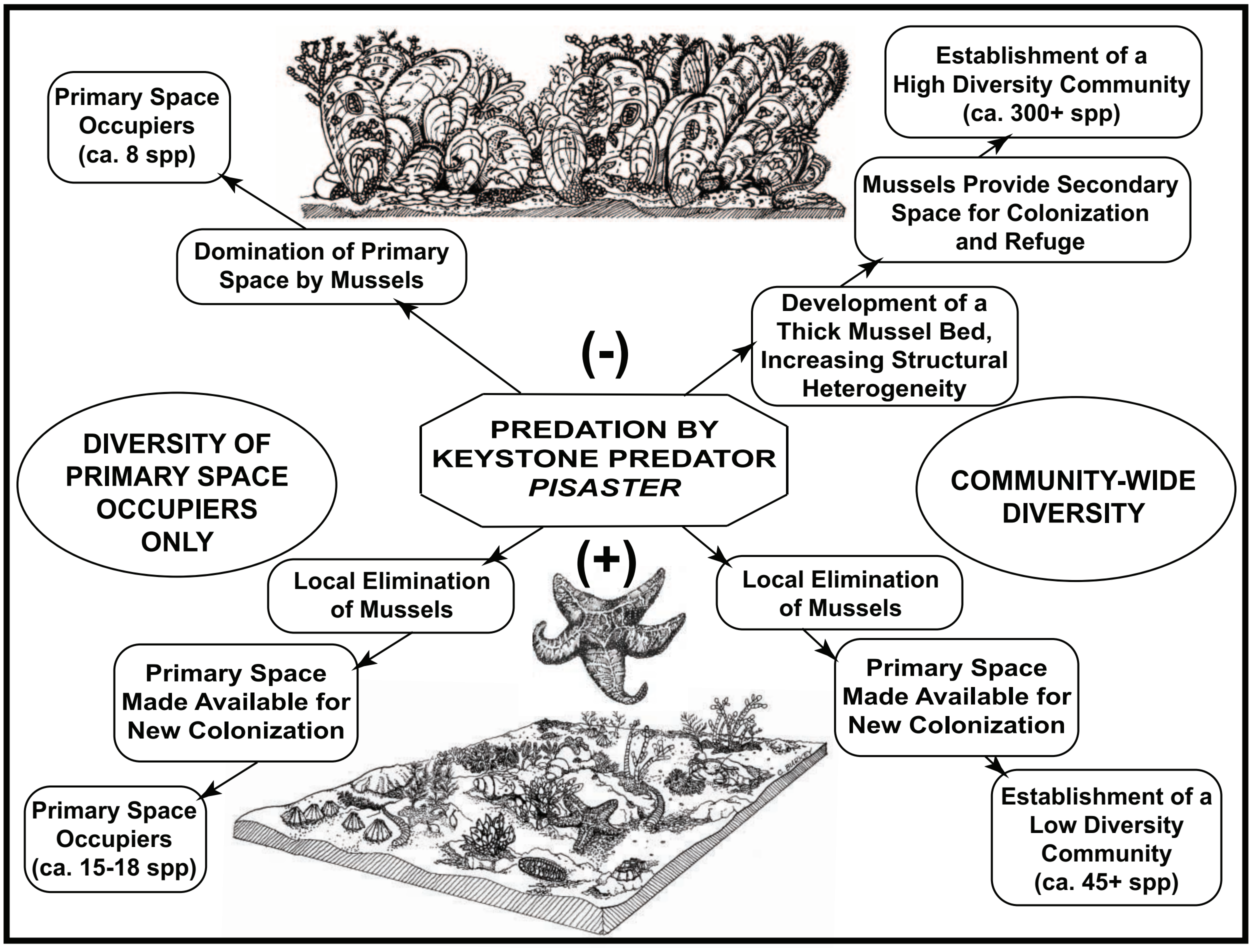

Figure 1: Response of primary space occupiers and community species richness to sea star removal at Tatoosh Island, Washington. Where the sea star *Pisaster* eliminates mussels, there are about 15–18 primary space-holding species, compared with only about 8 primary space-holding species and over 300 associated species comprising the total community-wide diversity where *Pisaster* is nearly absent and mussel beds are present. Data are from Paine (1966) and table A1.

this helps market predator conservation, classic ecological studies on predation (Estes and Palmisano 1974; Crooks and Soulé 1999; Ripple et al. 2001; Sergio et al. 2008) find that predators require biodiversity, and some can either increase or decrease diversity depending on their position in the food web, their ability to depress prey populations, the role of their prey as foundational species, and one's measure of diversity.

The success of "Food Web Complexity and Species Diversity," along with his other accomplishments, eventually helped Paine become president of the Ecological Society of America in 1983, the same year he received the prestigious MacArthur Award. He was also elected to the National Academy of Sciences in 1986 and awarded the International Cosmos Prize in 2013. However, when we asked him what Paine (1966) meant to him personally, Paine noted that, in retrospect, "Food Web Complexity and Species Diversity" was "a rush job characteristic of an eager assistant professor." Only after a sabbatical in New Zealand studying a similar system with a similar result did he begin to sense that his findings were general, and his key insights matured and solidified (Paine 1974). On a visit back home to Cambridge, he boasted, "Mother, I've gotten 1,600 reprint requests for this 1966 paper." Paine's mother, who wrote brief science pieces for the *New York Times*, responded, "That's great, but you know my article on water conservation? Senator Proxmire wants 200,000 copies to send out to every voter in Wisconsin." That put an end to Paine's boasting.

Fifty Years Later

Paine's final paper (Pfister et al. 2016) contemplates a sea star removal experiment orders of magnitude greater than his own. Starting in June 2013, Paine's sea star removal was repeated on a grand scale. From southern Alaska to Baja California, Mexico, *Pisaster ochraceus* and several other sea star species died en masse in association with a novel virus (Hewson et al. 2014). The die-off was termed a marine emergency due to its unprecedented scope. In communicating the importance of the die-off to the press, marine biologists explained that because sea stars promote intertidal diversity, the virus would be an ecological disaster. Although Paine (1966) shows the power of sea stars to control mussels and structure the intertidal, the net effects on biodiversity depend on one's perspective. A skeptic might say that the virus releases mussels from predation, promoting the diverse set of species that depend on mussels for habitat. Time will tell what happens in the rocky intertidal and whether conservation biologists will view sea star wasting disease as an impact or a boon to biodiversity.

Acknowledgments

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APPENDIX

Species List

Table A1: Species associated with the three-dimensional matrix of *Mytilus californianus* beds from Tatoosh Island (three sites) and Shi Shi (one site) from July 1974 to July 1976 in Washington State

	Functional group	Taxonomic group	Cumulative numerical abundance by species	Paine's spp. with *Pisaster*	Paine's spp. without *Pisaster*
		CHLOROPHYTA:			
1	E	*Cladophora* spp.	2		
2	E	Ulvoids	68		
3	E	*Urospora* sp.	301		
		PHAEOPHYTA:			
4	E	*Alaria marginata* Postels & Ruprecht, 1840	15		
5	E	*Analipus japonicus* (Harvey) Wynn, 1971	23		
6	E	*Fucus distichus* Linnaeus, 1767	1		
7	E	*Hedophyllum sessile* (C. Agardh) Setchell, 1901	24		
8	E	*Laminaria* spp.	1		
9	E	*Pelvitiopsis limitata* (Setchell) Gardner, 1910	5		
10	E	*Ralfsia pacifica* Hollenberg, 1944	17		
		RHODOPHYTA:			
11	E	*Callophyllis* spp.	5		
12	E	Corallines	1,689	P	P
13	E	*Endocladia muricata* (Postels & Ruprecht) J.G. Agardh, 1847	1,490	P	P
14	E	*Gigartina* sp. A	204		
15	E	*Gigartina* sp. B	154		
16	E	*Halosaccion glandiforme* (Gmelin) Ruprecht, 1850	33		
17	E	*Hildenbrandia* sp.	13		
18	E	*Mazaella laminarioides* (Bory de Saint-Vincent) Fredericq, 1993	50		
19	E	*Mazaella* sp.	24		
20	E	*Microcladia borealis* Ruprecht, 1850	150		
21	E	*Petrocelis* spp.	158		
22	E	*Polysiphonia* spp.	297		
23	E	*Porphyra* sp. A	16	P	P
24	E	*Porphyra* sp. B	78		
25	E	*Schizymenia* sp.	67		
		Rhodomela (from Paine 1966 only)		P	P

Table A1 (*Continued*)

	Functional group	Taxonomic group	Cumulative numerical abundance by species	Paine's spp. with *Pisaster*	Paine's spp. without *Pisaster*
		PROTOZOA:			
26	I	*Eponides columbiensis* (Cushman, 1925)	*		
		PORIFERA:			
		DEMOSPONGIAE:			
27	E	*Cliona celata* Grant, 1826	*		
28	E	*Halichondria panicea* Pallas, 1766	2,477		
29	E	*Haliclona cinerea* (Grant, 1826)	521	P	
30	E	*Clathria (Microciona) pennata* (Lambe, 1895)	*		
		CNIDARIA:			
		HYDROZOA:			
		Hydroida:			
31	E	*Abietinaria abietina* (Linnaeus, 1758)	908		
32	E	*Abietinaria inconstans* (Clark, 1877)	*		
33	E	*Abietinaria anguinea* (Trask, 1857)	*		
34	E	*Aglaophenia* sp.	*		
35	E	*Campanularia* sp.	*		
36	E	*Clytia hesperia* (Torrey, 1904)	*		
37	E	*Rhizorhagium roseum* (Sars, 1874)	21		
38	E	*Sertularella fusiformis* (Hincks, 1861)	4,446		
		Hydrocorallina:			
39	E	*Stylantheca papillosa* (Dall, 1884)	16		
		ANTHOZOA:			
		Actinaria:			
40	E	*Anthopleura elegantissima* (Brandt, 1835)	1,357	P	P
41	E	*Anthopleura xanthogrammica* (Brandt, 1835)	58		
42	E	*Diadumene* sp.	6		
		PLATYHELMINTHES:			
		TURBELLARIA:			
		Polycladida:			
43	M	*Notoplana* sp. (?*inquieta* (Heath & McGregor, 1912))	309		
		NEMERTEA:			
		ENOPLA:			
		Hoplonemertea:			
44	M	*Amphiporus* sp. (?*formidabilis* Griffin, 1898)	512		
45	M	*Emplectonema gracile* (Johnston, 1837)	294		
46	M	*Paranemertes peregrina* Coe, 1901	127		
		NEMATODA:			
47	M	Unidentified sp. A	2,561		
48	M	Unidentified sp. B	464		
		MOLLUSCA:			
		POLYPLACOPHORA:			
		Neoloricata:			
49	M	*Cyanoplax dentiens* (Gould, 1846)	1,105		
50	M	*Katharina tunicata* (Wood, 1815)	19	P	
51	M	*Mopalia ciliata* (Sowerby, 1840)	78	P?	
52	M	*Mopalia muscosa* (Gould, 1846)	1		
		GASTROPODA:			
		PROSOBRANCHIA:			
		Archaeogastropoda:			
53	M	*Acmaea mitra* Rathke, 1833	1		

Table A1 (*Continued*)

	Functional group	Taxonomic group	Cumulative numerical abundance by species	Paine's spp. with *Pisaster*	Paine's spp. without *Pisaster*
54	M	*Calliostoma ligatum* (Gould, 1849)	138		
55	M	*Lottia digitalis* (Rathke, 1833)	2,092	P?	
56	M	*Lottia pelta* (Rathke, 1833)	1,978	P?	
57	M	*Lottia scutum* (Rathke, 1833)	271		
58	M	*Lottia strigatella* (Carpenter, 1864)	3,908		
59	M	*Diodora aspera* (Rathke, 1833)	4		
60	M	*Homolapoma lacunatum* (Carpenter, 1864)	4,677		
61	M	*Homolapoma luridum* (Dall, 1885)	11		
62	M	*Lirularia lirulata* (Carpenter, 1864)	*		
63	M	*Lirularia succincta* (Carpenter, 1964)	372		
64	M	*Littorina scutulata* Gould, 1849	1,861		
65	M	*Littorina sitkana* Philippi, 1846	2,158		
66	M	*Tegula funebralis* (A. Adams, 1855)	203	P	
		Mesogastropoda:			
67	M	*Onoba carpenteri* (Weinkauff, 1885)	31		
68	M	*Alvnia compacta* (Carpenter, 1864)	37		
69	M	*Onoba mighelsii* (Stimpson, 1851)	8		
70	M	*Balcis* sp.	2		
71	M	*Barleeia sanjuanensis* Bartsch, 1920	45,692		
72	M	*Neostylidium eschrichtii* (Middendorff, 1849)	2		
73	M	*Cerithiopsis stejnegeri* Dall, 1884	1,192		
74	M	*Crepidula adunca* G.B. Sowerby I, 1825	2		
75	M	*Crepidula convexa* Say, 1822	1		
76	M	*Crepidula fornicata* (Linnaeus, 1758)	*		
77	M	*Crepidula plana* Say, 1822	10		
78	M	*Crepipatella lingulata* (Gould, 1846)	*		
79	M	*Lacuna vincta* (Montagu, 1803)	81		
80	M	*Opalia wroblewskyi* (Mörch, 1875)	6		
81	M	*Trichotropis cancellata* Hinds, 1843	2		
82	M	*Velutina velutina* (O.F. Müller, 1776)	4		
		Neogastropoda:			
83	M	*Alia carinata* (Hinds, 1884)	731		
84	M	*Amphissa columbiana* Dall, 1916	749		
85	M	*Ceratostoma foliatum* (Gmelin, 1791)	98		
86	M	*Granulina margaritula* (Carpenter, 1857)	18		
87	M	*Mitrella tuberosa* (Carpenter, 1865)	2		
88	M	*Nassarius mendicus* (Gould, 1850)	3		
89	M	*Ocinebrina lurida* (Middendorf, 1848)	17		
90	M	*Lirabuccinum dirum* (Reeve, 1846)	1		
91	M	*Nucella canaliculata* (Duclos, 1832)	348		
92	M	*Nucella emarginata* (Deshayes, 1839)	582	P	
		Anisodoris (from Paine 1966 only)		P	
		OPISTHOBRANCHIA:			
		Pyramidellida:			
93	M	*Odostomia deliciosa* Dall & Bartsch, 1907	178		
		Onchidiacea:			
94	M	*Onchidella borealis* Dall, 1872	2,492		
		PULMONATA:			
		Basommatophora:			
95	M	*Siphonaria thersites* Carpenter, 1864	42		

Table A1 (*Continued*)

	Functional group	Taxonomic group	Cumulative numerical abundance by species	Paine's spp. with *Pisaster*	Paine's spp. without *Pisaster*
		BIVALVIA:			
		PTERIOMORPHA:			
		Mytiloida:			
96	E	*Adula californiensis* (Philippi, 1847)	374		
97	E	*Modiolus* sp.	625		
98	E	*Musculus taylori* (Dall, 1897)	4,789		
99	—	*Mytilus californianus* Conrad, 1837	27,018		P
100	E	*Mytilus trossulus* Gould, 1850	7,536		
		Pterioida:			
101	E	*Chlamys* sp.	1		
102	E	*Pododesmus macrochisma* (Deshayes, 1839)	*		
		HETERODONTA:			
		Veneroida:			
103	I	*Kellia suborbicularis* (Montagu, 1803)	54		
104	I	*Lasaea adansoni* (Gmelin, 1791)	24		
105	I	*Lasaea subviridis* Dall, 1899	18,158		
106	I	*Macoma inquinata* (Deshayes, 1855)	4		
107	I	*Kurtiella tumida* (Carpenter, 1864)	2		
108	I	*Petricola carditoides* (Conrad, 1837)	0		
109	I	*Leukoma staminea* (Conrad, 1837)	1,317		
110	I	*Saxidomus gigantea* (Deshayes, 1839)	7		
		Myoida:			
111	E	*Hiatella arctica* (Linnaeus, 1767)	374		
112	I	*Mya arenaria* Linnaeus, 1758	*		
		ANOMALODESMATA:			
		Pholadomyoida:			
113	I	*Entodesma navicula* (Adams & Reeve, 1850)	16		
		ANNELIDA:			
		OLIGOCHAETA:			
114	M	Unidentified spp.	585		
		POLYCHAETA:			
		Orbiniida:			
		Orbiniidae:			
115	I	*Naineris dendritica* (Kinberg, 1867)	20		
		Spionida:			
		Spionidae:			
116	E	*Boccardia proboscidae* Hartman, 1940	9		
		Cirratulidae:			
117	I	*Cirratulus cirratus* (O.F. Müller, 1776)	1		
118	I	*Tharyx multifilis* Moore, 1909	4		
		Opheliida:			
		Opheliidae:			
119	I	*Armandia brevis* (Moore, 1906)	8		
120	I	*Travisia* sp.	1		
		Phyllodocida:			
		Phyllodocidae:			
121	M	*Eulalia levicornuta* Moore, 1909	7		
122	M	*Eulalia viridis* (Linneaus, 1767)	1		
		Polynoidae:			
123	M	*Arctonoe vittata* (Grube, 1855)	23		
124	M	*Eunoe senta* (Moore, 1902)	1		

Table A1 (*Continued*)

	Functional group	Taxonomic group	Cumulative numerical abundance by species	Paine's spp. with *Pisaster*	Paine's spp. without *Pisaster*
125	M	*Halosydna brevisetosa* Kinberg, 1855)	282		
126	M	*Harmothoe extenuata* (Grube, 1840)	2		
127	M	*Malmgreniella lunulata* (Delle Chiaje, 1830)	1		
128	M	*Harmothoe multisetosa* (Moore, 1902)	1		
129	M	*Hesperone ?adventor* (Skogsberg in Fisher & MacGinitie, 1928)	4		
130	M	*Lepidasthenia longicirrata* Berkeley, 1923	3		
131	M	*Lepionotus squamatus* (Linnaeus, 1758)	57		
132	M	*Grueopolynoe tuta* (Grube, 1855)	3		
		Sigalionidae:			
133	I	*Pholoe minuta* (Fabricius, 1780)	149		
		Chrysopetalidae:			
134	M	*Paleanotus bellis* (Johnson, 1897)	9		
135	M	*Chrysopetalum occidentale* Johnson, 1897	1		
		Hesionidae:			
136	M	*Micropodarke dubia* (Hessle, 1925)	1		
		Syllidae:			
137	M	*Syllis adamantea* (Treadwell, 1914)	358		
138	M	*Syllis alternata* Moore, 1908	93		
139	M	*Syllis armillaris* (Müller, 1776)	33		
140	M	*Syllis elongata* (Johnson, 1901)	16		
141	M	*Syllis gracilis* Grube, 1840	3		
142	M	*Typosyllis harti* Berkeley & Berkeley, 1938	15		
143	M	*Syllis heterochaeta* Moore, 1909	19		
144	M	*Typosyllis pigmentata* Berkeley & Berkeley, 1938	85		
145	M	*Typosyllis stewarti* Berkeley & Berkeley, 1941	663		
146	M	*Syllis variegata* Grube, 1860	*		
147	M	*Syllis* spp.	153		
		Nereidae:			
148	M	*Cheiloneries cyclurus* (Harrington, 1897)	*		
149	M	*Hediste limnicola* (Johnson, 1903)	8		
150	M	*Nereis vexillosa* Grube, 1851	336		
151	M	*Nereis* sp. A	3		
152	M	*Nereis* sp. B	2		
		Sphaerodoridae:			
153	M	Unidentified sp.	1		
		Eunicida:			
		Lumbrineridae:			
154	I	*Lumbrineris zonata* (Johnson, 1901)	1		
		Arabellidae:			
155	I	*Arabella iricolor* (Montagu, 1804)	81		
156	I	*Arabella semimaculata* (Moore, 1911)	1		
		Terebellida:			
		Sabellariidae:			
157	E	*Idanthyrsus macropaleus* (Schmarda, 1861)	9		
158	E	*Neosabellaria cementarium* Moore, 1906	2		
		Pectinariidae:			
159	I	*Pectinaria californiensis* Hartman, 1941	3		
160	I	*Cistenides granulata* (Linnaeus, 1767)	1		
161	I	*Amphictene moorei* (Annenkova, 1929)	1		
		Amparetidae:			
162	I	Unidentified sp. A	2		

Table A1 (*Continued*)

	Functional group	Taxonomic group	Cumulative numerical abundance by species	Paine's spp. with *Pisaster*	Paine's spp. without *Pisaster*
		Terebellidae:			
163	I	*Eupolymnia ?heterobranchia* (Johnson, 1910)	26		
164	I	*Laphania boecki* Malmgren, 1866	1		
165	I	*Streblosoma bairdi* (Malmgren, 1866)	2		
		Sabellida:			
		Sabellidae:			
166	E	*Parasabella media* Bush, 1904	3		
167	E	*Parasabella rugosa* Moore, 1904	2		
168	E	*Eudistylia polymorpha* (Johnson, 1901)	2		
169	E	*Eudistylia vancouveri* (Kinberg, 1866)	9		
170	E	*Laonome kroyeri* Malmgren, 1866	2		
171	E	*Myxicola infundibulum* (Montagu, 1808)	3		
172	E	*Pseudopotamilla intermedia* Moore, 1905	5		
173	E	*Pseudopotamilla myriops* Marenzeller, 1884	4		
174	E	*Potamilla neglecta* (Sars, 1851)	1		
175	E	*Schizobranchia insignis* Bush, 1905	24		
		Serpulidae:			
176	E	*Serpula vermicularis* Linnaeus, 1767	127		
177	E	Unidentified sp. A	*		
		Spirorbidae:			
178	E	Unidentified sp. A	16,272		
179	E	Unidentified sp. B	7,848		
		SIPUNCULIDA:			
180	I	*Phascolosoma agassizii* Keferstein, 1866	1,289		
		ARTHROPODA:			
		PYCNOGONIDA:			
181	M	*Achelia latifrons* (Cole, 1904)	7		
182	M	*Nymphopsis spinosissimum* (Hall, 1912)	1		
183	M	*Phoxichilidium fermoratum* (Rathke, 1799)	28		
184	M	*Pycnogonum stearnsi* (Ives, 1883)	3		
		ARACHNIDA:			
		Pseudoscorpionida:			
185	M	*Halobisium occidentale* Beier, 1931	30		
186	M	Unidentified sp. A	5		
		Acari:			
187	M	Unidentified sp. A	98		
188	M	Unidentified sp. B	2		
189	M	Unidentified sp. C	2		
190	M	Unidentified sp. D	2		
191	M	Unidentified sp. E	46		
192	M	Unidentified sp. F	12		
193	M	Unidentified sp. G	1		
194	M	Unidentified sp. H	2		
195	M	Unidentified sp. I	1		
196	M	Unidentified sp. J	1		
		CRUSTACEA:			
		CIRRIPEDIA:			
		Thoracica:			
197	E	*Semibalanus cariosus* (Pallas, 1788)	12,675	P	
198	E	*Balanus crenatus* (Bruguière, 1789)	257		
199	E	*Balanus glandula* Darwin, 1854	20,949	P	P

Table A1 (*Continued*)

	Functional group	Taxonomic group	Cumulative numerical abundance by species	Paine's spp. with *Pisaster*	Paine's spp. without *Pisaster*
200	E	*Balanus nubilus* Darwin, 1854	65		
201	E	*Chthamalus dalli* Pilsbry, 1916	65,416	P	
202	E	*Pollicipes polymerus* Sowerby, 1833	1,018	P	P
		MALACOSTRACA:			
		Tanaidacea:			
203	I	*Zeuxo normani* (Richardson, 1905)	16		
204	I	*Leptochelia dubia* (Krøyer, 1842)	1		
205	I	*Pancolus californiensis* Richardson, 1905	2,900		
206	I	*Synapseudes intumescens* Menzies, 1949	2		
		Isopoda:			
207	M	*Cirolana harfordi* Lockington, 1877	12,240		
208	M	*Dynamenella dilitata* (Richardson, 1899)	438		
209	M	*Dynamenella sheareri* (Hatch, 1947)	6,372		
210	M	*Edotia sublittoralis* Menzies & Barnard, 1959	*		
211	M	*Exosphaeroma amplicauda* (Stimpson, 1857)	1		
212	M	*Exosphaeroma octoncum* (Richardson, 1897)	2		
213	M	*Exosphaeroma rhomburum* (Richardson, 1899)	6		
214	M	*Gnorimosphaeroma oregonensis* (Dana, 1853)	76		
215	M	*Ianiropsis analoga* Menzies, 1952	134		
216	M	*Ianiropsis kincaidi* Richardson, 1904	3,684		
217	M	*Pentidotea schmitti* (Menzies, 1950)	6		
218	M	*Pentidotea wosnesenskii* Brandt, 1851	93		
219	M	*Joeropsis dubia* Menzies, 1951	11		
220	M	*Joeropsis ?lobata* Richardson, 1899	*		
221	M	*Munna chromatocephala* Menzies, 1952	1,212		
222	M	*Synidotea bicuspida* (Owen, 1839)	3		
		Amphipoda:			
223	M	*Ampithoe simulans* Alderman, 1936	92		
224	M	*Aoroides* sp.	5		
225	M	*Caprella angusta* Mayer, 1903	3		
226	M	*Caprella greenleyi* McCain, 1969	34		
227	M	*Corophium brevis* Shoemaker, 1949	21		
228	M	*Deutella ?californica* Mayer, 1890	2		
229	M	*Hyale anceps* (Barnard, 1969)	3,490		
230	M	*Protohyale frequens* Stout, 1913	5,566		
231	M	*Hyale grandicornis californica* Barnard, 1969	234		
232	M	*Ptilohyale plumulosus* (Stimpson, 1857)	778		
233	M	*Ischyrocerus anguipes* Krøyer, 1838	200		
234	M	*Ischyrocerus serratus* Gurjanova, 1938	124		
235	M	*Jassa falcata* (Motagu, 1808)	6,041		
236	M	*Megalorchestia* sp.	*		
237	M	*Desdimelita californica* (Alderman, 1936)	1,589		
238	M	*Desdimelita desdichada* Barnard, 1962	2		
239	M	*Metopa cistella* Barnard, 1969	100		
240	M	*Najna* sp.	5		
241	M	*Oligochinus lighti* J.L. Barnard, 1969	254		
242	M	*Orchomene* sp. A	1		
243	M	*Orchomene* sp. B	4		
244	M	*Parallorchestes* spp. (a complex of 12 spp.)	79		
245	M	*Paramoera suchaneki* Staude, 1995	750		
246	M	*Paramoera* sp. (undescribed species of Armstrong et al., 1976)	93		

Table A1 (*Continued*)

	Functional group	Taxonomic group	Cumulative numerical abundance by species	Paine's spp. with *Pisaster*	Paine's spp. without *Pisaster*
247	M	*Foxiphalus* cf. *obtusidens* (Alderman, 1936)	2		
248	M	*Parapleustes* den Barnard, 1969	180		
249	M	*Micropleustes nautilus* J.L. Barnard, 1969	377		
250	M	*Parapleustes pugettensis* (Dana, 1853)	1,312		
251	M	*Photis* sp.	1		
252	M	*Pontogeneia intermedia* Gurjanova, 1938	118		
253	M	*Stenothoides burbanki* J.L. Barnard, 1969	1		
		Decapoda:			
254	E	*Fabia subquadrata* Dana, 1851	213		
255	M	*Romaleon branneri* (Rathbun, 1926)	16		
256	M	*Hemigrapsus nudus* (Dana, 1851)	114		
257	M	*Oedignathus inermis* (Stimpson, 1860)	697		
258	M	*Pachycheles rudis* Stimpson, 1859	251		
259	M	*Pagurus* spp.	80		
260	M	*Petrolisthes cinctipes* (Randall, 1840)	1,157		
261	M	*Petrolisthes eriomeris* Stimpson, 1871	5		
262	M	*Pugettia gracilis* Dana, 1851	1		
263	M	*Pugettia richii* Dana, 1851	146		
		INSECTA:			
		PTERYGOTA:			
		Diptera:			
264	M	*Coelopa* sp.	64		
265	M	*Oedoparena glauca* (Coquillett, 1900)	35		
266	M	*Paraclunio alaskensis* (Croquillett, 1900)	604		
267	M	*Paraphrosylus nigripennis* (VanDuzee, 1924)	36		
268	M	Unidentified sp. A	*		
269	M	Unidentified sp. B	*		
270	M	Unidentified sp. C	*		
		Coleoptera:			
271	M	*Diaulota densissima* Casey, 1894	119		
272	M	*Liparocephalus brevipennis* (Mäklin, 1853)	300		
273	M	Unidentified sp. A	1		
		BRYOZOA:			
		GYMNOLAEMATA:			
		Ctenostomata:			
274	E	*Alcyonidium polyoum* (Hassall, 1841)	661		
275	E	*Flustrellidra corniculata* (Smitt, 1872)	12		
		Cyclostomata:			
276	E	*Crisia occidentalis* Trask, 1857	25		
277	E	*Crisia pugeti* Robertson, 1910	85		
278	E	*Tubulipora pacifica* Robertson, 1910	*		
		Cheilostomata:			
279	E	*Bugulina pugeti* (Robertson, 1905)	44		
280	E	*Callopora horrida* (Hincks, 1880)	1,220		
281	E	*Cellaria mandibulata* Hincks, 1882	5		
282	E	*Dendrobeania curvirostrata* (Robertson, 1905)	1		
283	E	*Dendrobeania ?laxa* (Robertson, 1905)	15		
284	E	*Primavelans insculpta* (Hincks, 1883)	14		
285	E	*Celleporella hyalina* (Linnaeus, 1767)	30,045		
286	E	*Microporella californica* (Busk, 1856)	*		
287	E	*Microporella ?marsupiata* (Busk, 1860)	*		
288	E	*Schizomavella linearis* (Hassall, 1841)	56		
289	E	*Smittina retifrons* (Osburn, 1952)	2,859		
290	E	*Tricellaria ternata* (Ellis & Solander, 1786)	570		

Table A1 (*Continued*)

	Functional group	Taxonomic group	Cumulative numerical abundance by species	Paine's spp. with *Pisaster*	Paine's spp. without *Pisaster*
		ECHINODERMATA:			
		ASTEROIDEA:			
		Spinulosida:			
291	M	*Henricia leviuscula* (Stimpson, 1857)	13		
		Forcipulatida:			
292	M	*Leptasterias hexactis* (Stimpson, 1862)	458		
293	M	*Pisaster ochraceus* (Brandt, 1835)	3	P	
		ECHINOIDEA:			
294	M	*Strongylocentrotus droebachiensis* (O.F. Müller, 1776)	11		
295	M	*Strongylocentrotus franciscanus* (A. Agassiz, 1863)	*		
296	M	*Strongylocentrotus purpuratus* (Stimpson, 1857)	7		
		HOLOTHUROIDEA:			
297	M	*Cucumaria pseudocurata* Deichmann, 1938	20,733		
298	M	*Cucumaria miniata* (Brandt, 1835)	14		
299	M	*Eupentacta quinquesemita* (Salenka, 1867)	34		
		OPHIUROIDEA:			
300	I	*Ophiopholis aculeata* (Linnaeus, 1767)	87		
		CHORDATA:			
		UROCHORDATA:			
		ASCIDIACEA:			
301	E	*Pyura haustor* (Stimpson, 1864)	2		
		VERTEBRATA:			
		OSTEICHTHYES:			
302	M	*Clinocottus embryum* (Jordan & Starks, 1895)	1		
303	M	*Phytichthys chirus* (Jordan & Gilbert, 1880)	19		
304	M	*Xiphister atropurpureus* (Kittlitz, 1858)	2		
		Total abundance	389,271	NA	NA
		Total species richness	304	18	8

Note: Modified from Suchanek (1979). Species identities are consistent with the 2015 World Register of Marine Species (http://www.marinespecies.org). Species with an asterisk in the abundance column represent species identified within the mussel bed matrix but not represented in the formal counts. E = epizoans; I = infauna; M = mobile fauna; NA = not applicable. Cumulative numerical abundance for each species of associated fauna or flora derives from 54 samples (each ~0.1 m^2) of mussel beds from high intertidal (20 samples), mid-intertidal (19 samples), and low intertidal (15 samples) sites, for a total of over 304 documented species and over 389,000 individual organisms in a total area of 5.4 m^2 of mussel beds sampled for all sites, tidal heights, and sampling dates. For comparison, species cited in Paine (1966) with and without *Pisaster ochraceus* are identified with the letter P.

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Example of a live *Mytilus californianus* mussel shell (central image) nearly overgrown by several species of the diverse *Mytilus*-associated community, including, among others, *Semibalanus cariosus*, *Balanus glandula*, and *Chthamalus dalli* acorn barnacles; *Pollicipes polymerus* gooseneck barnacles; *Nucella canaliculata* dog whelk; *Mytilus trossulus* mussels; *Lottia digitalis* limpets; and *Endocladia muricata* red algae. Photo: Tom Suchanek.