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A comparison of intertidal species richness and composition between Central California and Oahu, Hawaii

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Abstract

The intertidal zone of tropical islands is particularly poorly known. In contrast, temperate locations such as California's Monterey Bay are fairly well studied. However, even in these locations, studies have tended to focus on a few species or locations. Here we present the results of the first broadscale surveys of invertebrate, fish and algal species richness from a tropical island, Oahu, Hawaii, and a temperate mainland coast, Central California. Data were gathered through surveys of 10 sites in the early 1970s and again in the mid-1990s in San Mateo and Santa Cruz counties, California, and of nine sites in 2001–2005 on Oahu. Surveys were conducted in a similar manner allowing for a comparison between Oahu and Central California and, for California, a comparison between time periods 24 years apart. We report a previously undocumented richness of intertidal species in both locations: 516 for Oahu and 801 for Central California. Surprisingly, when differences in search efforts are controlled, overall (alpha) diversity appears to be similar between locations, although site level (beta) diversity is much higher in California. Species richness in California generally increased along a wave exposure gradient and distance from an urban area. Much higher numbers of both invasive and endemic species were found on Oahu. In California, more invertebrate species were found in the 1990s, likely due to an improvement in taxonomic resources since the 1970s, and species composition was different in the two surveys due to the high incidence of rare species. Although some southern species increased in number between the two time periods and some northern species decreased, we detected little evidence of change favoring southern or northern species. These results are in line with recent findings that water temperatures in the Monterey Bay have been in a cooling trend since the 1980s, in contrast to many locations elsewhere in the world.

Introduction

One of the most striking patterns in nature is the increase in species richness with decreasing latitude (Hillebrand 2004; Clarke & Gaston 2006; Valentine *et al.* 2008). This general trend holds for a great number of plant and animal taxa in marine and terrestrial environments and has been attributed variously to higher productivity in the tropics, less climatic variation, and the greater evolutionary age of tropical regions. None of these factors would, however, be likely to apply to rocky intertidal organisms on a relatively recently formed tropical oceanic island. Most tropical waters are not as productive as those of many temperate locations, and for marine organisms exposed at low tides, the climate is harsh relative to mainland coasts, particularly those influenced by mild maritime climates. In addition, the theory of island biogeography predicts species richness on islands should be lower than that of similar habitats on continents (Whittaker & Fernández-Palacios 2007). Thus, we might expect intertidal species richness in the isolated Hawaiian Island chain to be lower than that of the mainland coast of California. Some differences in insular species composition can also be predicted based on ecological theory: (i) a greater number of endemic species and (ii) a greater number of non-native species (*i.e.* Elton 1958; MacArthur & Wilson 1967; Begon *et al.* 1996; Lonsdale 1999; but see D'Antonio & Dudley 1995; Sol 2000; Jeschke 2008; Vila *et al.* 2010).

A second dramatic pattern is increasingly being reported from multiple habitat types: the shift of species towards higher latitudes, presumably in response to global climate change (Parmesan & Yohe 2003; Perry *et al.* 2005; Mieszkowska *et al.* 2006; Sunday *et al.* 2012). Such a change was reported from the rocky intertidal zone in Monterey, California, by Barry *et al.* (1995) and Sagarin *et al.* (1999), who enumerated species along a single transect initially surveyed in the early 1930s (Hewitt 1937). They found an increase in the abundance of several southern ('warmer-water') species and a decrease in several northern ('cold water') species, which they attributed to a rise in the mean annual sea temperature of 0.7 °C. These were among the first reports of a possible biotic response to the global warming of the latter half of the 20th century. However, although analyses of long-term records in Monterey Bay found significantly higher surface sea temperatures in the 1990s than in the 1920s, they have not shown a significant increase since the 1930s (Breaker 2005). Instead, wind-induced storminess and upwelling has increased, consistent with climate change predictions, leading to decreasing sea temperatures along the coast of Oregon and California (García-Reyes & Largier 2010; Iles *et al.* 2012). The degree to which intertidal species might respond to these fluctuations is not clear.

Here we compare patterns of species richness and composition of invertebrates, fishes and algae from the rocky intertidal zone on the tropical island of Oahu in the isolated Hawaiian Island chain, to that of a temperate, mainland location, Central California. For California we also compare between two time periods, the early 1970s and the mid-1990s. In both locations, these surveys represented the first broad-based look at species richness. The data were generated from three extensive presence/absence surveys: (i) in southern San Mateo and Santa Cruz counties, California, in the early 1970s; (ii) at the same sites in the mid-1990s; and (iii) on Oahu in the mid-2000s. Survey methods were shared among the three studies, allowing for a spatial comparison of richness and composition between California and Hawaii and a temporal comparison across a 24-year time period in California.

Background

Central California

Whereas the macrobiota of the rocky intertidal of Central California is well known (*e.g.* Abbott & Hollenberg 1976; Morris *et al.* 1980; Ricketts *et al.* 1985; Yoshiyama *et al.* 1986; Carlton 2007), most of our understanding is based on detailed work on specific groups of organisms at specific sites, in particular at Point Cabrillo on the Monterey Peninsula, the site of the Hopkins Marine Station of Stanford University (*e.g.* Hewatt 1937; Glynn 1965; Feder 1970; Haven 1973; Johnson 1976; Foster 1982; Smith & Berry 1985; Gaines & Roughgarden 1987; Sagarin *et al.* 1999; Denny *et al.* 2004; Pearse *et al.* 2010; Watanabe 2010). Less is known about the coast immediately north in San Mateo and Santa Cruz counties on the western and southern portion of the San Francisco Peninsula, with most accounts also limited to single sites (*e.g.* Kopp 1979; Beauchamp & Gowing 1982; Hansen 1981; Pearse 1981; Niesen 1999; Van De Werfhorst & Pearse 2007). Nearly all the earlier studies in Central California have been focused either on a restricted taxonomic group (*e.g.* limpets, Haven 1973; isopods, Johnson 1976; nudibranchs, Nybakken 1978; Schultz *et al.* 2010; Goddard *et al.* 2011; algae, Foster 1982; Smith & Berry 1985) and/or as mentioned above, a single site. Although many of them did provide quantitative data for specific species and areas that could be used for later comparisons, as done by Barry *et al.* (1995), Sagarin *et al.* (1999), Van De Werfhorst & Pearse (2007) and Pearse *et al.* (2010), between-site variation on the coast of California is substantial, making generalizations based on one or a few sites difficult (Foster 1990). In addition, much of the earlier work lacked an assessment of habitat diversity relative to species diversity, and many of the more recent and ongoing multi-taxa surveys, such as LiMPETS (http://limpetsmonitoring.org/), MARINe (http://www.marine.gov/), and PISCO (http://www.piscoweb.org/) purposely use standardized survey techniques across flat surfaces to reduce statistical variability (Foster *et al.* 1988, 2003; Steinbeck *et al.* 2005; Murray *et al.* 2006; Schoch *et al.* 2006; Blanchette *et al.* 2008). Such surveys miss a diverse assortment of cryptic species in major taxa that inhabit pools, crevices, undersides of rocks, and overhangs. Moreover, surveys using quadrats or transects overlook rare species, even on exposed surfaces. Consequently, species richness, especially of invertebrates and fishes, is underestimated and almost certainly too low, even in well studied areas such as Central California.

Hawaii

While the intertidal zone in temperate regions has been the subject of study for decades, significantly less is known about all aspects of the tropical rocky intertidal (but see Stephenson & Stephenson 1972; Bertness 1981; Menge & Lubchenco 1981; Garrity 1984; Menge *et al.* 1986; Sutherland & Ortega 1986; Sutherland 1990; Smith *et al.* 2007), and even less about the intertidal zone of tropical islands (exceptions include Stephenson & Stephenson 1972; Lubchenco *et al.* 1984; Yipp & Carefoot 1988; Nagelkerken & Debrot 1995). Not surprisingly, then, in contrast to Central California, Hawaii's intertidal zone has been poorly studied altogether. A small tidal excursion (~1 m), high air temperatures, current patterns that can move larval settlers away from appropriate habitats, among other factors, result in low biomass and an inconspicuous intertidal zone relative to temperate areas. With few exceptions, marine scientists in Hawaii have tended to focus on the more extensive and species-rich subtidal reef habitats.

To date, the rocky intertidal zone of Hawaii has not been comprehensively characterized. Virtually nothing has been written on the diversity or the community ecology of Hawaii's intertidal (exceptions are Kay 1979, 1987; Smith 1992; Cox & Smith 2011). A literature search of Zoological Records and BIOSIS databases (1978 to current) using the key words 'Hawaii AND rocky intertidal OR rocky shores' uncovered 12 journal articles, most of which dealt with taxonomy. Some 20 theses in the archives of the Zoology Department at the University of Hawaii deal with some aspect of the intertidal but, with a few exceptions (*i.e.* Strasburg 1953) these generally focus on a single species or genus.

Strasburg (1953) used poison stations to enumerate tide pool fish species on Oahu. He found 30 'common' inhabitants, and another 58 he considered 'stragglers' – reef fish that are occasionally found in the intertidal zone. He also identified 41 algal species and 34 species of common invertebrates but did not make an attempt to enumerate species such as xanthid crabs, whose taxonomy has not been well defined in Hawaii. Cox *et al.* (2011) in a study of tidepool fishes from six sites on Oahu found far fewer: 19 species inhabiting 40 pools. Smith (1992) found 100 species of macroalgae and turf algae at three locations on Oahu, and 60 turf species from a single location on the island of Hawaii. Despite these findings, the perception has continued within the scientific community that Hawaii's intertidal is species-poor and relatively barren (Southward *et al.* 1998; Coles & Eldredge 2002).

Several volumes deal with the taxonomy of Hawaii's marine invertebrates, algae and fish (Edmondson 1946, 1949; Hiatt 1954; Devaney & Eldredge 1977, 1987; Kay 1979; Randall 1996, 2005; Abbott *et al.* 1997; Abbott 1999; Hoover 1998, 2003; Abbott & Huisman 2004). Although these include many species that are found in the intertidal zone, only one, an introductory guide to the intertidal zone for school children (Edmondson 1949), focuses on intertidal species. Major groups, such as crabs, shrimps and sponges are inadequately covered in the taxonomic literature. Habitat descriptions are not included in many of the above publications, so lists of intertidal species cannot be confidently constructed from them.

Documenting changes in the intertidal zone

One of the first baseline studies of intertidal algae in California was done in Southern California by Dawson (1965). He produced voucher collections of more than 7500 specimens with over 180 species of algae found during surveys in 1956–1959 of 44 shoreline transects between Point Conception and the Mexican border. The transects were re-surveyed by several groups over the following 20 years (summarized by Thom & Widdowson 1978) and dramatic changes were documented. Further work (*e.g.* Murray *et al.* 1999) has indicated that much in coast of Southern California changed over the latter half of the 20th century, as species richness and diversity decreased due to human activities (harvesting, trampling, polluting). Some of the more harmful activities such as harvesting are now more tightly regulated but only recently have efforts been made to monitor the intertidal biota to document recovery or further degradation [*e.g.* the LiMPETS (http://limpetsmonitoring.org/), MARINe (http://www.marine.gov/) and PISCO (http://www.pisco-web.org/) programs]. There have been few published studies in Central or Northern California that clearly document changes in the intertidal biota due to human activities, and these indicate minor disturbance due to trampling (see Tenera Environmental 2003; Van De Werfhorst & Pearse 2007).

As mentioned above, Barry *et al.* (1995) and Sagarin *et al.* (1999) detected changes in the abundance of some species along a transect at Point Cabrillo in Monterey Bay initially surveyed in the early 1930s (Hewitt 1937). Changes included increases in warmer water species and decreases in cooler water species, which they attributed to a long-term trend in higher ocean temperatures (see Discussion). In fact, there could be many reasons for the changes at Point Cabrillo, including a response to a short-term warm water phase and to changes in other conditions at the site, such as harbor seals hauling out on and near the transect in the 1990s and their absence earlier, much lower algal cover in the 1990s, and fewer loose stones and boulders on the transect, which provide shelter for cooler-water species (Sagarin *et al.* 1999). Although the causes of these changes are ambiguous, the Point Cabrillo surveys highlight the value of having baseline data available for comparing changes over time.

The data provided here were collected to compare species richness and composition between locations and among sites within locations that differ in exposure, geology and human activity. For Central California, the re-survey of the original 10 sites from the 1970s provides an opportunity for evaluating long-term changes. Unlike almost all other surveys to date, which were quantitative and focused on a few species that could be counted or otherwise easily quantified, the focus of our surveys was on species richness, that is, the number and identity of species of most taxa present at specific sites. The data are not quantitative or, at best, they are semi-quantitative, but they can be used to see where specific species of algae and invertebrates were found for comparison with future surveys.

Fig. 1. Study sites in Central California.

Methods

Survey sites and personnel

Between November 1971 and September 1973, students from the University of California, Santa Cruz (UCSC), surveyed macroalgae and invertebrates at 10 sites (Fig. 1) between Capitola in Santa Cruz County and Pigeon Point in San Mateo County. These sites were selected because they were accessible rocky benches and outcrops that were well spaced along the coast and differed in exposure and rock substrate. Teams of students visited each site during minus spring tides at least once a quarter for seven quarters, recording all the species they found on each visit. Quantitative sampling was also done at five of the sites, and some of the data have been published elsewhere (Foster *et al.* 1988; Osborn *et al.* 2005) and are available at http://limpetsmonitoring.org/; these will not be included here. In 1996–1997, the survey was repeated, following as closely as possible the procedures developed in 1972–1973. Fishes were added to the study in the 1996–1997 surveys.

General surveys along the coast to determine subsequent site selection were done as an undergraduate class project in the Fall quarter of 1971. In the Spring of 1972, we divided the student teams into groups of five to 10 people, each with a faculty member or graduate teaching assistant, with each team responsible for surveying all taxa at two adjacent sites. Beginning in Fall 1972, and continuing through the 1996–1997 surveys, the students were divided into taxonomic teams, and all went to each of the 10 sites on the same dates. This later approach allowed students to develop greater familiarity with specific groups of organisms and standardized the sampling effort among sites.

The Oahu study combines species richness data from cursory surveys made in 2001 by graduate and undergraduate marine biology students with more thorough surveys conducted in 2003, 2004 and 2005 (Fig. 2) through a partnership between University of Hawaii Manoa (UHM) graduate students and local middle and high schools, with assistance from the Bernice P. Bishop Museum (BPBM). In 2001, one of us (C.J.Z., who was a student in the 1996–1997 California surveys) led surveys of 11 sites around the island of Oahu. Each site was visited once during minus spring tides from June to August. There were between two and eight participants in these surveys, mostly biology undergraduate and graduate

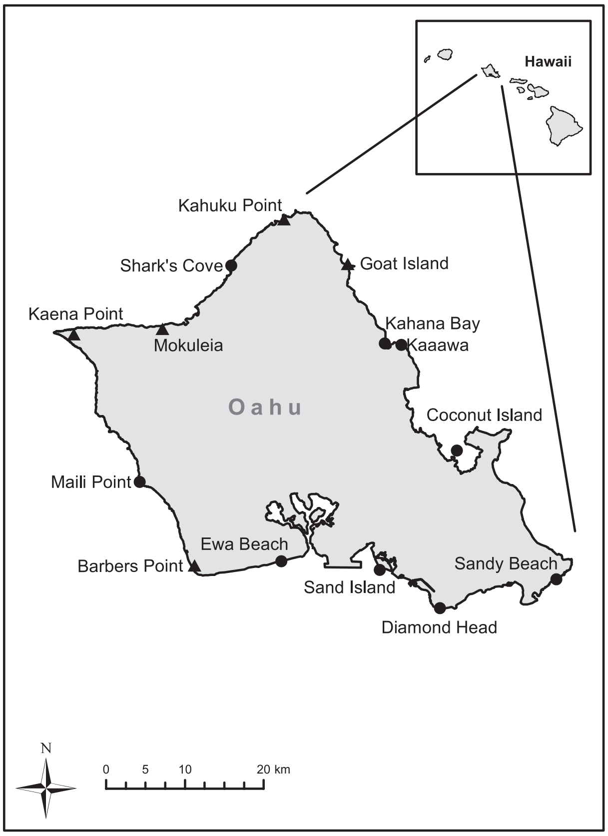

Fig. 2. Study sites on Oahu. Circles indicate sites surveyed for species richness by students. Triangles indicate sites surveyed by one of the authors (C.J.Z.) or quantitative study sites: species lists from these sites are included in Appendix 2 but are not used in the analysis in the text.

students. These were preliminary surveys and we included fish at only some sites, and algae not at all.

The majority of the Oahu survey work was done by the 9th grade Marine Science class at the University Laboratory School (ULS) through a partnership sponsored by the National Science Foundation Graduate Fellowship in K-12 Teaching program. The class surveyed four to five sites each year from 2003 to 2005 for fishes, algae and invertebrates, visiting each site once during minus spring tides from mid-February through mid-May. Nine sites were surveyed by the high school students. We attempted to survey a representative sample of rocky intertidal habitats with regard to wave exposure, substrate type, and proximity to urban areas, and to survey the different sides of the island. For safety reasons, the island's most wave-exposed sites were not visited. Some of the sites were visited only once, and others were visited two or three times.

In 2003, each site was surveyed by 54 ULS students; in 2004 and 2005, we took 26–28 students to each site. As in the California study, students were divided into teams, with each team focusing their search on a specific taxonomic group. During each survey, we were generally assisted by four to eight graduate students from UH Zoology and Botany departments and volunteers from the community and from BPBM. In July 2003, two additional trips were made to Sandy Beach, one with seven high school students from the Drew School in San Francisco and three adults, and one with a group of 15 science teachers and marine science teacher-trainers. Additional species were added to species lists from Sand Island, Barber's Point and Kahuku Point in 2005 by students from two Oahu schools, Farrington High and Kahuku Intermediate, who were participating in a separate intertidal monitoring program; the quantitative data collected by these students is summarized elsewhere (Cox *et al.* 2012b).

For both the California and Oahu surveys, searches were haphazard, and except where otherwise noted, focused on macro-invertebrates (generally >5 mm), macroalgae, and fishes. Searches were made in tide pools, under rocks, in shallow channels, and on rocky benches and other hard substrates from water's edge into the splash zone. The only major groups of macro-invertebrates not included were amphipods and, for California, flatworms. Search time was 2–3 h at each site. Small hand nets were used to catch fishes, shrimps and crabs. Turfs and coralline algae were excluded from the Oahu survey because of difficulty identifying them.

Species identifications and voucher specimens

Keys and identification manuals were limited during the 1972–1973 survey, and for many groups we relied on dated materials to identify the species. For general use, we had Light *et al.* (1954) to identify invertebrates, and Smith (1944) to identify algae. In addition, original taxonomic treatments were used for specific invertebrate taxa: de Laubenfels (1932; sponges), Fraser (1937; hydroids), Osborn (1950, 1952, 1953; bryozoans), Hartman (1968, 1969; polychaetes), Schmitt (1921; decapod crustaceans), and Van Name (1945; ascidians). Moreover, we were able to use and test draft keys that were being prepared for *Marine Algae of California* (Abbott & Hollenberg 1976) and the 3rd edition of *Light's Manual* (Smith & Carlton 1975).

Representative specimens of algae found during the 1972–1973 survey were pressed and used for teaching the marine botany courses at UCSC during succeeding years. The collection has been maintained at UCSC; however, field notes on the quarters in which species were found were lost. Representative specimens of most of the invertebrates found were relaxed with MgCl, fixed in formalin

(10% buffered formaldehyde) when appropriate, and/or preserved in 70% ethanol. These were kept for reference during the 1972–1973 survey. When the survey was complete, a collection of all the vouchered species was donated to the California Academy of Sciences where they are held in perpetuity; duplicate species were kept for teaching purposes and eventually dispersed.

Keys and identification manuals had improved by the 1996–1997 survey, *e.g.* Abbott & Hollenberg (1976), Smith & Carlton (1975) and Lindberg (1981). We added fishes to the survey using Miller & Lea (1972) and Fitch & Lavenberg (1975) for identification. The authors J.S.P. and K.A.M. and other taxonomic experts assisted students with identifications and checked voucher specimens for algae (both time periods), and sponges and bryozoans (1996–1997) (see Acknowledgements).

Vouchers were prepared for only a few invertebrates during the 1996–1977 survey, and only a few of these were transferred to the California Academy of Sciences for their collections. Dried specimens of the algae were added to the teaching collection at UCSC.

The taxonomy of invertebrates and algae on the California coast has undergone repeated revision during the past several decades. The names of invertebrate species used here follow those in Carlton (2007); those of algae follow the University and Jepson Herbaria website (University of California, Berkeley): http://ucjeps.berkeley.edu/californiaseaweeds.html/, draft April 2010.

A number of the Hawaiian fish and invertebrate species collected during the 2001–2005 surveys were easily identified in the field; others were known to the authors or scientist-volunteers from previous work. In the initial surveys on Oahu, we generally recorded species that could be identified in the field using available field guides (*e.g.* Kay 1979; Bertsch & Johnson 1981; Randall 1996; Hoover 1998, 2003). An occasional specimen was collected and preserved for later identification. For the work with ULS, we recorded and released at the field sites animals that were easy to identify. Other animals were kept live in classroom aquaria and then released after being identified. The specimens that were more difficult to identify were frozen or relaxed, fixed and preserved as above. Algae were pressed and/or preserved in formalin. In accordance with state and federal regulations, coral species were not collected; these were photographed in the field. Sponges and tunicates were also photographed *in situ* before being collected. Sponges were matched to a botanical color field guide (Munsell Color Charts for Plant Tissues, Gretag MacBeth LLC, New York) immediately after collection because they lose color upon preservation.

The authors C.J.Z., E.P.B. and D.S. double-checked identifications made by the Hawaii students in our areas of expertise. We were assisted with identifications of algae, fishes, hydroids, bivalves, limpets, polychaetes, molluscs and crustaceans by taxonomists at the BPBM and UHM (see Acknowledgements). In each case, we identified species to the lowest taxonomic level possible. Because the Hawaiian sponges are largely undescribed (R. deFelice, personal communication), they were sorted to morphospecies only. Voucher specimens for all collected animal taxa have been deposited with the BPBM (accession number BPBM 2005.164). The algae were kept by ULS for a teaching collection.

Data analysis

Alpha diversity

Data from all the surveys were combined to create species lists (alpha diversity) and used for overall totals by taxonomic group at each location (full species lists: Appendix S1 for the Central California study, Appendix S2 for the Oahu study). Although methods were comparable between the two study locations, the search effort was much greater in California. In addition, differences between the sizes of the study sites might be a factor in the number of species found at the site; on the whole, Central California study sites were larger than Oahu study sites. To compare richness between the two locations more confidently, we controlled for possible effects of different size study sites and differences in search effort in the following ways: (i) we calculated the area of each study site and standardized species per unit area for each site to arrive at a mean number of species per square meter for each location, then tested for differences between the means with a two-sample *t*-test; and (ii) we compared total Oahu richness to that from the California study for only one academic quarter in the 1990s. This was appropriate, as each site was visited two times per quarter for the California study, and two times on average for the Oahu study. While the taxonomic materials available in 2002–2004 for many of the intertidal organisms in Hawaii are similar to the state they were in for Central California in the 1970s, the early California survey did not include fishes, so the 1990s surveys are more appropriate for a comparison with Oahu.

For more detailed analyses comparing the species assemblages of each location, we excluded from the overall species lists organisms described only to genus or family except when they were the only representatives of those groups. For organisms recorded as morphospecies, we made conservative estimates of the likely number of species based on descriptions (for example, although 68 sponge taxa were recorded from Oahu, these likely represent about 40 species, based on conspicuous morphological differences). We used a chi-squared test to test for differences in the species richness by phyla between the two locations.

As an estimate of how close we may have come to characterizing the true species richness of intertidal species in the two locations, we reviewed available literature for some of the better-studied taxonomic groups: macro-molluscs on Oahu (Kay 1979), red algae on Oahu (Abbott 1999) and California (Abbott & Hollenberg 1976), and gastropod molluscs in Central California (Carlton 2007).

We used plots of cumulative species *versus* search effort to determine whether we approached an asymptote of species richness. Such plots require that search effort be equivalent at each time point. For Central California, search effort for invertebrate species was roughly equivalent over five quarters (Fall 1972, Spring 1973, Spring 1996, Fall 1996, Spring 1997). On Oahu, we had only two sites where effort was roughly equivalent and that were surveyed more than twice: Shark's Cove (algae, fishes and invertebrates, 2003, 2004, 2005) and Sandy Beach (fishes and invertebrates, 2003, 2004, 2005).

Beta diversity

For the Oahu data, the search effort was the most uniform between the nine sites surveyed by the ULS students, so we used only these sites for the remaining analyses. For comparisons of species richness by site in the Central California study, we used data from the quarters in which students visited all sites (Fall 1972, Spring 1973, Spring 1996, Fall 1996 and Spring 1997). Beta diversity was calculated using Whittaker's diversity index $\beta_w = (C/S)-1$, where C is the total number of species in the study location (Central California or Oahu), S is the mean number of species per site and $\beta_w = 0$ when C and S are equal; the higher β_w, the lower the diversity. For both locations, physical site variables of wave exposure, substrate structure, the proximity of sites to urban areas, and for the Oahu data, number of visits to each site, were informally examined using non-metric multidimensional scaling plots (MDS) for their potential effects on species richness.

Species characteristics

We designated a species as common if it was found half or more of the times when it could have been found, *i.e.* each visit to each site. Theoretically this method could include as 'common' a species that is rare, but happened to be found at all sites; an informal review of this list confirmed that this did not happen – no species known to be truly rare appeared on the list of common species. Field notes were missing for the algae collected in the 1970s, so we were unable to construct such a list for them. We compared the number of common species to overall lists to determine what percent of species richness at our study sites was the result of common *versus* rare species and whether that differed between locations or between time periods for the Central California study.

In addition, where possible based on available literature, we designated organisms as endemic (occurring only in Hawaii or only in Central and Northern California, from Point Conception to the Oregon border), native, and introduced or non-native (human-mediated range expansion). Many species are cryptogenic, meaning that biogeographic status is unknown; these include widely distributed species with insufficient information to determine whether they are native or introduced and species complexes which have not be adequately resolved. Wasson *et al.* (2005) and Carlton & Eldredge (2009) reviewed the biogeographic status of intertidal organisms in Central California and Oahu, respectively; we relied on their determinations and our determinations of species ranges (see below) for our analysis. We informally examined the data for differences in the percentages of common, endemic and non-native species for each location and site, and for the Central California data, between time periods.

Changes over time: species richness

For comparisons over time for the Central California study, we compared species lists from Fall 1972 and Spring 1973 with those from Fall 1996 and Spring 1997. Since fishes were not included in the 1970s surveys, these were not used for the comparison between time periods. Algae were also excluded from this comparison due to lost field notes (see above). Differences in species richness by time period among sites were informally examined to look for outliers (>1.5 interquartile range).

Changes over time: species composition

We used MDS plots to informally assess the similarity in invertebrate species composition among sites and between time periods for the Central California data. These plots were used to examine the potential effects of the above-mentioned site characteristics on the species assemblages. The plots were generated using Bray–Curtis similarity indices from presence/absence data for each species.

Changes over time: range shifts

Literature reviews were used to determine latitudinal range for the invertebrate and algal species found in the Central California study. Organisms were categorized as northern (southern limit Point Conception), southern (northern limit California–Oregon border), endemic (those found only between the two limits, except for rare occurrences), coastwide (those found along the entire West Coast, including Southern California and north of the California–Oregon border), or cosmopolitan, for those found on the West Coast as well as other locations around the world (determinations given in Appendix 1). Barry *et al.* (1995) and Sagarin *et al.* (1999) used Cape Mendocino as the northern limit of southern species but we found that the Oregon-California border is more often used in the literature as a boundary for species distributions in this category. Our 'endemic' category corresponds closely to the northern and Central Californian domains in Schoch *et al.* (2006), the restricted Oregonian Province as defined by Niesen (2007) (Point Conception to Central Oregon), and cluster groups 4–9 in Blanchette *et al.* (2008) (mainly Point Conception to Oregon). We used a chi-squared test to evaluate differences in the proportions of northern *versus* southern species in the Central California study between the two time periods. To meet the assumptions of the test, we used species found only in the 1970s or only in the 1990s, and excluded categories for which expected counts were much lower than five. For the algae, we were unable to standardize search effort (due to lost data from the 1970s; see above); however, we have no reason to suspect that uneven search effort between time periods would affect proportions of southern or northern species found. We compared the algae separately from the invertebrates.

Results

Alpha diversity: Oahu *versus* Central California

Our surveys documented high levels of species richness (Table 1): a total of 801 species of algae, invertebrates and fishes were recorded during the two time periods in the Central California surveys and 516 in the Oahu surveys (morphospecies were included in the Oahu totals, see Methods). Three groups – Chlorophyta, Heterokontophyta (class Phaeophyceae) and Mollusca – represented similar proportions of total species at each of the two study locations (~5%, ~4%, and ~23%, respectively). However, overall differences in species richness by taxonomic groups between the two locations were statistically significant ($\chi^2 = 67.8$, df = 11, $P < 0.0005$). The biggest contributors to the differences between locations were Annelida, Bryozoa and Rhodophyta, which all had disproportionately more species on the Central California coast, and Echinodermata and fishes, which had higher species richness on the Oahu coast than would be expected based on chance alone.

When we corrected for search effort, comparing number of species found in a single quarter in Central California to the total found on Oahu, richness is similar: in Central California, 508 species were found in Spring 1996, 457 species in Fall 1996, and 600 in Spring 1997, compared to Oahu's 516. Oahu sites were in general smaller than Central California sites, however differences in mean number of species per square meter were not statistically significant between the two locations.

Table 1. Species richness by taxonomic group, both locations across all time periods.

Phylum/Division	Central California total taxa (percent of total)	Oahu total taxa (percent of total)
Annelida[a]	71 (9)[b]	20 (3.9)
Arthropoda	87 (11)	83 (16.0)
Brachiopoda	1 (0.1)	0
Bryozoa[a]	38 (4.9)[b]	6 (1.2)
Chlorophyta	**42 (5.1)**	**28 (5.4)**
Chordata (tunicates)	30 (3.7)	13 (2.5)
Chordata (fish)[a]	34 (4.2)	50 (9.7)[b]
Cnidaria	28 (3.5)	28 (5.4)
Cyanobacteria	0	2 (0.4)
Echinodermata[a]	23 (2.9)	36 (7.0)[b]
Echiura	1 (0.1)	0
Hemichordata	0	1 (0.2)
Heterokontophyta	**36 (4.1)**	**22 (4.3)**
Kamptozoa	1 (0.1)	0
Mollusca	**183 (22.9)**	**124 (24)**
Nemertea	12 (1.5)	4 (0.8)
Platyhelminthes	n.a.	13 (2.5)
Porifera	44 (5.5)	~40 (7.8)
Rhodophyta[a]	164 (20.4)[b]	45 (8.7)
Sipuncula	4 (0.5)	1 (0.2)
Tracheophyta	2 (0.3)	0
Total	801 (100)	516 (100)

[a] Groups that contribute to the biggest differences between locations.
[b] Taxa with higher than expected species richness. Groups that are in similar proportions between locations are in bold.

Based on reported numbers of some of the better characterized taxonomic groups, our study appears to have recorded 25–50% of known species in each location. Some 238 molluscs are recorded as occurring in the intertidal zone in Hawaii (Kay 1979), not including 76 micromolluscs (<5 mm length). We found 120 (50%). For Central California, Carlton (2007) reports 384 gastropod species from the open coast; we found 183 (48%). Abbott (1999) reports 177 species of red algae from the intertidal zone in Hawaii, including turfs; we found 45 (25%). Abbott & Hollenberg (1976) treat 459 species of red algae in California (including Southern California); we have 164 (36%) for the intertidal of Central California.

Cumulative numbers of invertebrate species plotted against number of surveys for all California sites and for invertebrates and fishes for Sandy Beach and all organisms at Shark's Cove suggest that discoveries of additional species are not leveling off (Fig. 3).

Beta diversity: Oahu *versus* Central California

In the California study, per-site species richness ranged from 300 to 438 (Table 2), with a mean of 383 (SD ±45)

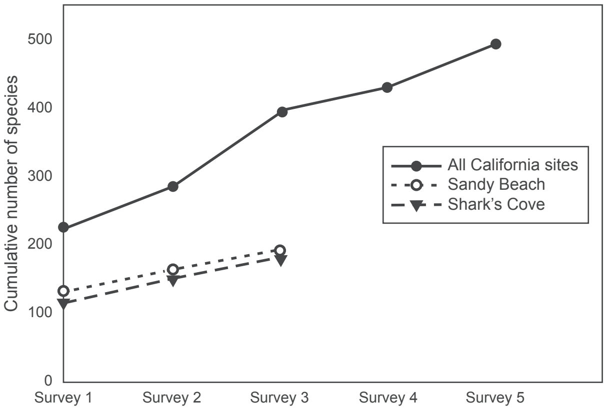

Fig. 3. Cumulative number of species found over the course of repeated surveys of equivalent effort. Solid line indicates total invertebrate species across all Central California sites; Fall 1972, Spring 1973, Spring 1996, Fall 1996, Spring 1997. Dotted line indicates number of invertebrates and fish found at one Oahu site, Sandy Beach, 2003, 2004, 2005; dashed line indicates number of invertebrates, fish and algae found at another Oahu site, Shark's Cove, 2003, 2004, 2005.

species per site and $\beta_w = 1.0$. Per-site species richness on Oahu ranged from 78 to 221 (Table 3), with a mean of 142 (SD ±41); beta diversity was considerably lower ($\beta_w = 2.6$).

In Central California, as a general rule, species richness was higher at the more remote sites with the most complex topography: Pigeon Point North and South, Año Nuevo Point and Cove, and Scott Creek. Soquel Point, which has an extensive low zone and is a relatively flat bench in an urban area, was the exception. Although the relationship between study site size (log scale) and number of species was roughly linear, site size was not a good predictor of species richness ($R^2 = 31.5$, $P = 0.05$), and there were no other clear patterns linking species richness to the site variables considered.

On Oahu, there were no obvious patterns linking species richness to the site variables considered. Again, although the relationship between site size and species number was roughly linear, study site area was not a good predictor for species richness ($R^2 = 22.2$, $P = 0.20$). We recorded the highest species richness at the two sites

Table 2. Site characteristics and number of species per site, Santa Cruz and San Mateo counties, all time points for algae, five quarters for invertebrates (during which all sites were surveyed same number of times, see Methods), three quarters for fishes. Sites arranged from highest to lowest species richness.

Site	Rural/Urban	Predominant substrate structure	Predominant substrate type	Wave exposure	Area (m^2)	No. of species
Pigeon Point South	R	Bench	Conglomerate	Semi	19,399	438
Año Nuevo Point	R	Cobble/bench	Shale	Semi	23,716	434
Año Nuevo Cove	R	Mixed cobble/bench	Shale	Semi	5466	434
Pigeon Point North	R	Mixed cobble/bench	Conglomerate	Exposed	17,192	398
Scott Creek	R	Bench	Mudstone	Exposed	12,782	382
Soquel Point	U	Bench	Mudstone	Semi	31,280	380
Davenport Landing	R	Bench	Mudstone	Semi	9458	376
Santa Cruz Point East	U	Cobble/boulder/bench	Mixed rip-rap/mudstone	Semi	2250	361
Natural Bridges	U	Bench	Mudstone	Semi	5971	332
Almar Street	U	Bench	Mudstone	Semi	2208	300
Mean (SD)						383 (45)

Table 3. Site characteristics, number of surveys, and number of species per site, Oahu, all time points. Sites arranged from highest to lowest species richness.

Site	Urban/rural	Predominant substrate structure	Predominant substrate type	Wave exposure	No. of surveys	Area (m^2)	No. of species
Sandy Beach	R	Bench	Basalt	Exposed	3	5808	221
Shark's Cove	R	Bench	Basalt	Protected	3	22,077	181
Sand Island	U	Cobble	Mixed rip-rap	Semi	1	2479	156
Coconut Island	R	Cobble	Mixed rip-rap	Protected	2	780	144
Kaaawa	R	Cobble	Basalt	Protected	1	1405	138
Ewa Beach	U	Bench	Limestone	Semi	2	5039	131
Maili Point	R	Bench	Basalt	Exposed	1	5206	122
Diamond Head	U	Bench	Limestone	Semi	2	3464	104
Kahana Bay	R	Cobble	Basalt	Protected	2	1322	78
Mean (SD)							142 (41)

that were surveyed three times; the other sites were surveyed one or two times.

Changes in diversity over time: Central California

Many more invertebrate species, 420 *versus* 287, were found in the Central California study during 1996–1997 than from 1971–1973, even with the correction for search effort (comparing only two quarters from each time period). Increases in the number of species were not proportional across all groups; the greatest gains were made in enumerating annelid worms and bryozoans (Table 4).

More invertebrate species were recorded at all sites in the second time period, with a mean per-site increase of 70.5% (Table 5). Soquel Point, with a gain of 115%, is a high outlier (>1.5 interquartile range 33–87%); although Año Nuevo Cove is low, it falls just inside this range (Fig. 4). Number of species per site for the 1970s ranged from 93 to 161, with a mean of 119, in comparison with a range of 155–235, with a mean of 200 for the 1990s (using data from two quarters only). Beta diversity was slightly lower in the 1970s, $\beta_w = 1.4$ *versus* 1.1 in the 1990s.

Site variables and species composition: Oahu and Central California

Species composition at the Central California sites varied along a north–south gradient. MDS plots using the combined 1990s and 1970s datasets can be roughly divided into southern sites on the left and northern sites on the right (Fig. 5). This geographic pattern is overlaid with a gradient of decreasing wave exposure, increasing human impacts and a shift in rock type from hard substrate (conglomerate rock at the Pigeon Point sites and Monterey Shale at the Año Nuevo sites) to various types of mudstone for the remaining sites. The most northern sites, the two Pigeon Point sites and the two Año Nuevo sites, shared the most species in common. Species assemblages at these sites were typical of high-wave exposure sites, characterized by such organisms as sea palms (*Postelsia palmaeformis*), cup corals (*Balanophyllia elegans*), octocorals (*Thrombophyton trachydermum*), black chitons (*Katharina tunicata*), veiled chitons (*Placiphorella velata*), red abalones (*Haliotis rufescens*), rock snails

Table 4. Species richness by phyla, Central California, across two time periods, one Fall and one Spring academic quarter only.

Phylum	Fall 72-Spring 73	Fall 96-Spring 97	Difference (No. of species)	Percent change
Annelida	20 (6.9)	60 (14.2)	40	**200**
Arthropoda	52 (18)	67 (15.9)	15	29
Brachiopoda	0 (0)	1 (0.24)	1	n.a.
Bryozoa	8 (2.7)	36 (8.5)	28	**350**
Chordata (excluding fishes)	20 (6.9)	22 (5.2)	2	10
Cnidaria	20 (6.9)	23 (5.5)	3	15
Echinodermata	16 (5.5)	18 (4.3)	2	12.5
Echiura	0 (0)	1 (0.2)	1	n.a.
Kamptozoa	0 (0)	1 (0.2)	1	n.a.
Mollusca	117 (40)	146 (34.6)	29	24.8
Nemertea	9 (3.1)	7 (1.7)	−2	−22
Porifera	22 (7.6)	35 (8.3)	13	60
Sipuncula	3 (0.6)	3 (0.7)	0	0
Total	287	420	133	46

Fishes and algae were not included in the analysis (see Methods).
Percentage of total species richness for each time period in parentheses.
Largest proportional gains are in bold.

Table 5. Species richness by site, across two time periods, one Fall and one Spring academic quarter only, fishes and algae excluded (see Methods).

Location	Fall 1972–Spring 1973	Fall 1996–Spring 1997	% change
Pigeon Point North	125 (43.6)	209 (49.8)	67.2
Pigeon Point South	142 (49.5)	235 (56.0)	65.5
Año Nuevo Point	146 (50.9)	229 (54.5)	56.8
Año Nuevo Cove	161 (56.1)	216 (51.4)	34.2
Scott Creek	118 (41.1)	197 (46.9)	66.9
Davenport Landing	114 (39.7)	203 (48.3)	78.1
Natural Bridges	97 (33.8)	174 (41.4)	79.4
Almar Street	97 (33.8)	155 (36.9)	59.8
Santa Cruz Point East	100 (34.8)	182 (43.3)	82.0
Soquel Point	93 (32.4)	200 (47.6)	115.1
Totals	287	420	70.5

Sites arranged north to south.
Percentage of total species found in each time period given in parentheses.

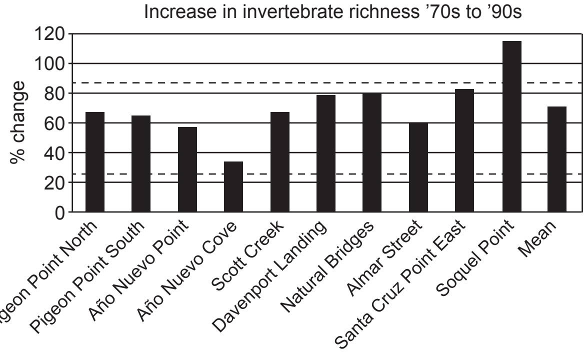

Fig. 4. Percent increase in the number of invertebrates species found in the 1970s *versus* the 1990s. Dashed line shows the 1.5 inner quartile range. One site, Soquel Point, is a high outlier.

(*Ocinebrina interfossa*), diamondback tritonias (*Tritonia festiva*), and purple shore crabs (*Hemigrapsus nudus*). The remainder of the sites cluster less tightly. The four most southern and urban sites, Natural Bridges, Almar Street, Santa Cruz Point and Soquel Point, were different from each other and from the more northern sites. With the possible exception of the introduced, largely terrestrial, urban isopod *Porcellio scaber* and species in the bryozoan genus *Membranipora* associated with intertidal giant kelp, *Macrocystis pyrifera*, these sites did not include any species in common that were not found in more exposed sites or that might be considered more typical of protected shores. Instead these sites had lower species diversity and were missing species commonly found in more exposed sites (*e.g.* the green alga, *Codium setchellii*, flattened rockweed, *Fucus distichus*, the red algae *Erythrophyllum delesserioides* and *Neoptilota densa*, dunce-cap limpets, *Acmaea mitra*, black abalones, *Haliotis cracherodii*, hoof snails, *Antisabia panamensis*, leather stars, *Dermasterias imbricata*, and six-rayed sea stars, *Leptasterias* spp.). Because data were recorded as presence–absence only, the percent similarity between sites in the distance matrix (Table 6) represents the percent of species shared between any two sites: these ranged from 62% to 80%, with a mean of 70.8%.

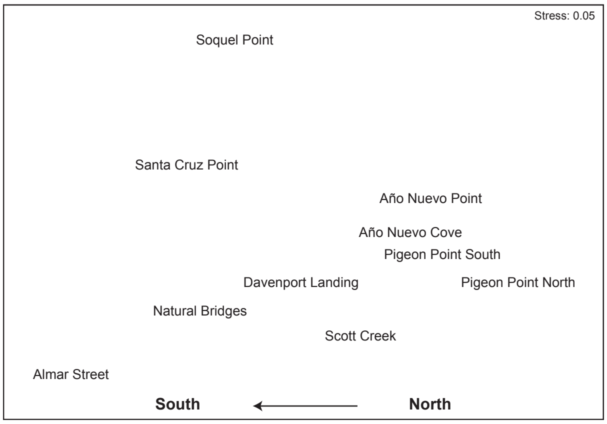

Fig. 5. Multidimensional scaling plot of Central California sites, using data from all quarters. Sites closest to one another are more similar in terms of shared species. Species similarity falls out along a north to south (also rural to urban) gradient and northern sites are more alike than the sites further into Monterey Bay, which are more distinct from one another.

The MDS plot for species assemblages for the nine Oahu sites can be roughly divided by substrate structure, with cobble sites on the left side of the plot and bench sites on the right (Fig. 6). Generally, cobble sites are less like one another, while bench sites cluster more closely. Coconut Island and Kahana Bay were least like any of the other sites; Kaaawa and Sand Island were at intermediate distances to other sites, and the rest of the sites cluster more closely together. High numbers of filter feeders, including sponges, bivalves, and tube-dwelling worms, found only at Coconut Island, distinguished this site from the others. Kahana Bay was a species-poor site with the lowest numbers of molluscs, fishes, polychaetes, sponges and cnidarians of any of the sites. The spatial pattern does not appear to be explained by the number of surveys per site, wave exposure or substrate type.

The number of species in common among Oahu sites was much lower than for the Central California sites (Table 7): species shared between pairs of sites ranged from 23% to 48%, with a mean of 36.4%.

Differences in species composition over time: Central California

Of the 523 invertebrate species in our Central California survey, 63%, or 327, were found in both time periods (Appendix 1); 38 were found in the 1970s only and 167 only in the 1990s. With few exceptions, species common in the 1970s were also common in the 1990s (Table 8). However, there were more common species in the 1990s,

Table 6. Bray–Curtis distance matrix, Central California sites, all data combined.

	Pigeon Point North	Pigeon Point South	Año Nuevo Point	Año Nuevo Cove	Scott Creek	Davenport Landing	Natural Bridges	Almar Street	Santa Cruz Point
Pigeon Point South	79.6								
Año Nuevo Point	76.0	80.1							
Año Nuevo Cove	61.5	78.6	79.4						
Scott Creek	71.6	73.3	72.7	75.3					
Davenport Landing	70.0	75.3	74.1	79.4	80.3				
Natural Bridges	66.2	70.0	70.0	70.4	71.3	75.9			
Almar Street	61.5	65.2	62.2	64.7	65.9	71.0	73.6		
Santa Cruz Point	64.8	70.6	68.8	70.5	69.4	73.8	71.2	70.5	
Soquel Point	65.0	67.6	67.6	68.8	66.5	68.2	68.6	65.0	74.5

Sites arranged north to south.

with 141 species found at half or more of the site visits; only 67 such species met this criterion in the 1970s (Table 9). As a result, across sites, species assemblages from the 1990s were more alike than any of those from the 1970s. Assemblages from the two time periods cluster separately, with the north-to-south site separation present within the temporal clusters (Fig. 7).

The vast majority of the invertebrate species for which we could determine range information occur broadly across the West Coast, from Alaska or British Columbia well into Mexico (Table 10). Between the two time periods these species increased by 50 species (a change of 32%). In contrast, southern species increased by 24 (77%) and northern species by 11 (41%) between the 1970s and the 1990s. However, southern *and* northern species found only in one time period approximately quadrupled: eight southern and four northern in the 1970s, and 33 southern and 15 northern in the 1990s (Table 9). Thus differences between the time periods for the three major range categories (northern, southern and coastwide) are not statistically significant ($\chi^2 = 0.21$, $P = 0.90$, df = 2). Of the species common in the 1990s but not the 1970s, eight were northern and six were southern; of the species common in the 1970s but not the 1990s, one was a northern species (*Semibalanus cariosus*) and none was southern (see Table 8).

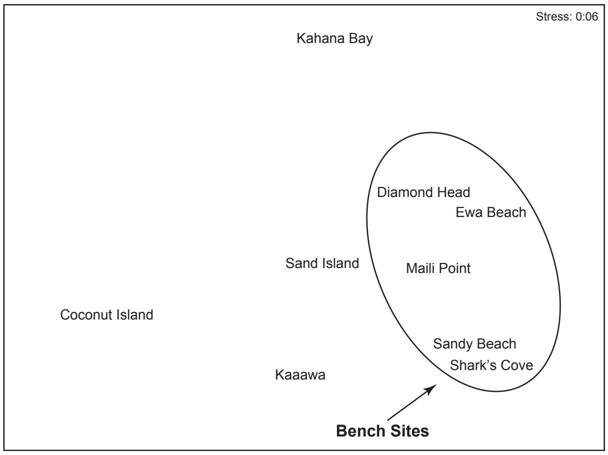

Fig. 6. Multidimensional scaling plot of Oahu sites. Sites closest to one another are more similar in terms of shared species. Bench sites are more alike than cobble sites. There is no apparent pattern in terms of proximity: for example, Sandy Beach and Shark's Cove, which share many species, are located on the island's south and north shores respectively.

Many of the organisms that were found at nearly all sites in the 1990s but were rarely found in the 1970s were in two of the groups that increased most in richness between the two time periods: Bryozoa and Annelida. Additional challenging taxa, such as Porifera and Ascidia, also made up many of these.

However, there were some changes in conspicuous and easy to identify taxa. The distinctive southern worm snail *Serpulorbis squamigerus*, for example, was not noted in the 1970s but was found in nine of the 10 sites the 1990s, and the striking southern nudibranch *Phidiana hiltoni* was not found in the 1970s but was found in four sites in the 1990s (see Appendix 1). The northern barnacle *Semibalanus cariosus* was found at nine of the 10 sites in the 1970s but in only four in the 1990s, while the distinctive northern limpet *Lottia persona* was found at five sites in the 1970s but only one in the 1990s.

For the algal species found only in the 1970s, 14 (35%) were northern species and six (15%) were southern species (Table 10). Four northern species (15%) and six southern species (25%) were found only in the 1990s. However, these apparent differences in algal assemblages between the time periods appear to be mostly due to species that either (i) were small, easily missed, or challenging to identify (*e.g. Amplisiphonia pacifica, Collinsiella tuberculata, Endophyton ramosum, Peyssonnelia* spp.), (ii) have undergone taxonomic revisions and were not distinguished as separate species during one time period (*e.g. Prionitis andersoniana/Prionitis sternbergii; Mazzaella flaccida/Mazzaella splendens*; *Ulva*

Table 7. Bray–Curtis similarity matrix for species composition, Oahu sites.

	Diamond Head	Sand Island	Ewa Beach	Maili Point	Shark's Cove	Kaaawa	Kahana Bay	Coconut Island
Sand Island	40.2							
Ewa Beach	43.9	36.8						
Maili Point	44.2	41.9	43.6					
Shark's Cove	36.7	35.4	36.2	48.2				
Kaaawa	35.8	39.8	32.8	37.3	34.2			
Kahana Bay	36.0	28.4	30.7	34.6	23.1	27.1		
Coconut Island	25.9	30.4	25.6	26.9	23.4	33.3	27.6	
Sandy Beach	37.3	37.8	41.3	48.0	48.6	33.6	27.0	28.3

Sites arranged clockwise around the island, starting on the south shore.

Table 8. Central California common invertebrate species (found in half or more of our surveys of 10 sites surveyed in Fall and Spring of 1972–1973 and 1996–1997).

Species/taxa	Phylum	Range	1972–1973	1996–1997	Combined
Anthopleura elegantissima	Cnidaria	C	20	20	40
Balanus glandula	Arthropoda	C	20	20	40
Chthamalus spp.	Arthropoda	C	20	20	40
Lottia scabra	Mollusca	C	20	20	40
Mytilus californianus	Mollusca	C	20	20	40
Chlorostoma funebralis	Mollusca	C	20	19	39
Cyanoplax dentiens	Mollusca	N	20	18	38
Lottia digitalis/austrodigitalis	Mollusca	C	18	20	38
Pisaster ochraceus	Echinodermata	C	18	20	38
Pugettia producta	Arthropoda	C	18	20	38
Distaplia occidentalis	Chordata	C	18	19	37
Lacuna marmorata	Mollusca	C	17	19	36
Lottia insessa	Mollusca	C	16	20	36
Lottia paleacea	Mollusca	C	16	20	36
Nucella emarginata/ostrina	Mollusca	C	17	19	36
Pollicipes polymerus	Arthropoda	C	17	19	36
Anthopleura artemisia	Cnidaria	C	18	17	35
Anthopleura xanthogrammica	Cnidaria	C	16	19	35
Littorina scutulata/plena	Mollusca	C	16	19	35
Mopalia muscosa	Mollusca	C	18	17	35
Eudistoma psammion	Chordata	C	16	18	34
Garnotia adunca	Mollusca	C	16	18	34
Pagurus hirsutiusculus/venturensis	Arthropoda	C	14	20	34
Alia carinata	Mollusca	C	16	17	33
Aplidium californicum	Chordata	C	13	20	33
Balanus crenatus	Arthropoda	N	14	19	33
Lottia paradigitalis	Mollusca	C	14	19	33
Haliclona spp.	Porifera	W	17	16	33
Pachygrapsus crassipes	Arthropoda	C	13	20	33
Tetraclita rubescens	Arthropoda	S	14	19	33
Cancer antennarius	Arthropoda	C	13	19	32
Lottia asmi	Mollusca	C	13	19	32
Lottia limatula	Mollusca	C	12	20	32
Nereis grubei	Annelida	C	12	20	32
Strongylocentrotus purpuratus	Echinodermata	C	12	20	32
Chlorostoma brunnea	Mollusca	C	15	16	31
Haliclona sp. A of Hartman 1975	Porifera	U	12	19	31
Lottia scutum	Mollusca	C	13	18	31
Mopalia ciliata	Mollusca	C	13	18	31
Paranemertes peregrina	Nemertea	C	15	16	31
Phragmatopoma californica	Annelida	S	11	20	31
Acanthinucella spirata	Mollusca	C	14	16	30
Epiactis prolifera	Cnidaria	C	16	14	30
Halichondria panicea	Porifera	W	11	19	30
Mopalia hindsii	Mollusca	N	11	19	30
Nuttallina californica	Mollusca	S	12	18	30
Tonicella lineata/lokii	Mollusca	N	15	15	30
Styela montereyensis	Chordata	C	10	19	29
Suberites sp.	Porifera	U	12	17	29
Tricellaria spp.	Bryozoa	U	4	20	29
Cliona californica	Porifera	C	11	17	28
Phascolosoma agassizii	Sipuncula	C	9	19	28
Amphissa versicolor	Mollusca	C	11	16	27
Eudistoma ritteri	Chordata	C	9	18	27

Table 8. (Continued).

Species/taxa	Phylum	Range	1972–1973	1996–1997	Combined
Aglaophenia sp.	Cnidaria	U	8	18	26
Amphiporus imparispinosus	Nemertea	C	10	16	26
Aplysilla glacialis	Porifera	W	6	20	26
Epitonium tinctum	Mollusca	C	11	15	26
Idotea stenops	Arthropoda	C	7	19	26
Naineris dendritica	Annelida	C	7	19	26
Plumularia sp.	Cnidaria	U	9	17	26
Trimusculus reticulans	Mollusca	C	8	18	26
Celleporella spp.	Bryozoa	U	2	13	25
Clathria originalis	Porifera	C	6	19	25
Pagurus granosimanus	Arthropoda	C	11	14	25
Clathria pennata	Porifera	C	10	14	24
Doris montereyensis	Mollusca	C	9	15	24
Heptacarpus taylori	Arthropoda	C	11	13	24
Idotea wosnesenskii	Arthropoda	N	11	13	24
Leptasterias sp.	Echinodermata	N	12	12	24
Littorina keenae	Mollusca	C	11	13	24
Arabella iricolor	Annelida	W	4	19	23
Diaulula sandiegensis	Mollusca	C	9	14	23
Emplectonema gracile	Nemertea	W	5	18	23
Idotea montereyensis	Arthropoda	C	4	19	23
Pagurus samuelis	Arthropoda	C	10	13	23
Platynereis bicanaliculata	Annelida	W	9	14	23
Ritterella aequalisiphonis	Chordata	C	5	18	23
Antho karykina	Porifera	C	4	18	22
Cirolana harfordi	Arthropoda	C	6	16	22
Eurystomella bilabiata	Bryozoa	C	4	18	22
Flabellina trilineata	Mollusca	C	13	9	22
Hiatella arctica	Mollusca	W	3	19	22
Pinauay spp.	Cnidaria	U	6	16	22
Rostanga pulchra	Mollusca	C	7	15	22
Serpula columbiana	Annelida	C	2	20	22
Calliostoma ligatum	Mollusca	C	7	14	21
Haliclona sp. X	Porifera	U	11	10	21
Halosydna brevisetosa	Annelida	C	3	18	21
Lottia instabilis (rock form)	Mollusca	C	5	16	21
Nereis vexillosa	Annelida	N	3	18	21
Petrolisthes cinctipes	Arthropoda	C	9	12	21
Triopha maculata	Mollusca	C	6	15	21
Acmaea mitra	Mollusca	C	8	12	20
Euherdmania claviformis	Chordata	S	4	16	20
Henricia sp.	Echinodermata	U	10	10	20
Leucilla nuttingi	Porifera	C	5	15	20
Pisaster brevispinus	Echinodermata	C	7	13	20
Themiste dyscrita	Sipuncula	N	5	15	20
Antho lithophoenix	Porifera	S	3	16	19
Fissurellidea bimaculata	Mollusca	C	10	9	19
Heptacarpus sitchensis	Arthropoda	C	7	12	19
Katharina tunicata	Mollusca	N	8	11	19
Lottia gigantea	Mollusca	C	3	16	19
Sertularella/Symplectoscyphus	Cnidaria	U	7	12	19
Abietinaria spp.	Cnidaria	C	5	13	18
Cirriformia spp.	Annelida	S	4	14	18
Cyanoplax hartwegii	Mollusca	S	5	13	18
Eulithidium pulloides	Mollusca	C	8	10	18
Heptacarpus brevirostris	Arthropoda	N	2	16	18

Table 8. (Continued).

Species/taxa	Phylum	Range	1972–1973	1996–1997	Combined
Pachycheles rudis	Arthropoda	C	3	15	18
Spirorbinae	Annelida	U	2	16	18
Cauloramphus californiensis	Bryozoa	C	0	17	17
Haliotis cracherodii	Mollusca	C	5	12	17
Hemipodia simplex	Annelida	W	3	14	17
Hermissenda crassicornis	Mollusca	C	5	12	17
Leukoma staminea	Mollusca	C	4	13	17
Onchidella borealis	Mollusca	N	7	10	17
Perophora annectens	Chordata	C	6	11	17
Salmacina tribranchiata	Annelida	C	1	16	17
Scoletoma zonata	Annelida	C	7	10	17
Ascidia ceratodes	Chordata	C	5	11	16
Corynactis californica	Cnidaria	C	6	10	16
Patiria miniata	Echinodermata	C	5	11	16
Penitella penita	Mollusca	C	2	14	16
Pugettia richii	Arthropoda	C	10	6	16
Cystodytes lobatus	Chordata	C	5	10	15
Dodecaceria fewkesi	Annelida	C	1	14	15
Idotea aculeata	Arthropoda	C	2	13	15
Microporelloides cribrosa	Bryozoa	S	0	15	15
Mopalia lignosa	Mollusca	C	4	11	15
Petrolisthes eriomerus/manimaculus	Arthropoda	C	5	10	15
Boccardia proboscidea	Annelida	C	3	11	14
Lacuna porrecta	Mollusca	C	4	10	14
Nucella analoga	Mollusca	N	1	13	14
Semibalanus cariosus	Arthropoda	N	12	2	14
Crangon nigricauda	Arthropoda	C	1	12	13
Didemnum carnulentum	Chordata	C	3	10	13
Flustrellidra spinifera	Bryozoa	N	1	12	13
Serpulorbis squamigerus	Mollusca	S	0	13	13
Hymeniacidon sinapium	Porifera	I	0	12	12
Hamacantha hyaloderma	Porifera	N	0	10	10
Rhynchozoon rostratum	Bryozoa	C	0	10	10

Table 9. Geographic ranges for invertebrate species found during two academic quarters in the 1970s and 1990s, invertebrates only (see Methods).

Range	Fall 1972–Spring 1973 No. of species (%)	Fall 1996–Spring 1997 No. of species (%)	1970s only No. of species (%)	1990s only No. of species (%)
Northern	27 (11.9)	38 (12.0)	4 (11.8)	15 (12.0)
Southern	31 (13.7)	55 (17.4)	8 (23.5)	33 (26.4)
Coastwide	155 (68.6)	205 (64.9)	19 (55.9)	67 (53.6)
Endemic	3 (1.3)	4 (1.3)	1 (2.9)	3 (2.4)
Introduced	1 (0.4)	2 (0.6)	0	1 (0.8)
Cosmopolitan	9 (4.0)	12 (3.8)	2 (5.9)	6 (4.8)
Total with known range	226	316	34	125
Range unknown	47	89	5	42
Total species	273	405	39	167

Numbers in parentheses are the percent of species for which range information is available.

spp.) or (iii) are specialists in ephemeral habitats, such as sand-covered rock, which may have changed between years (*e.g. Stenogramma californica*) or are usually subtidal species that might be found only rarely on extreme low tides (*e.g. Bossiella schmittii*). However, one easily identifiable species that is more common south of our study area, *Chondracanthus spinosus*, was more abundant in the 1990s than in the 1970s.

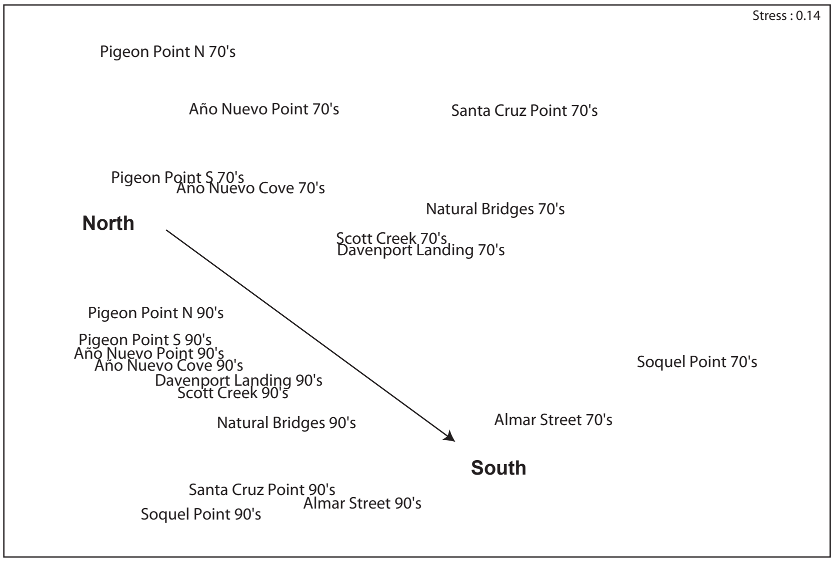

Fig. 7. Multidimensional scaling plot of Central California sites, using invertebrate data from two quarters in the 1970s and two in the 1990s (see Methods). Sites closest to one another are more similar in terms of shared species. Sites in the 1990s, on the left side of the plot, are more like each other than sites in the 1970s, shown on the right side of the plot. However, the north to south gradient in species similarity is apparent in each time period.

Table 10. Geographic ranges for algal species found during all quarters for two time periods 1970s and 1990s (see Methods).

Range	1970s No. of species (%)	1990s No. of species (%)	1970s only No. of species (%)	1990s only No. of species (%)
Northern	59 (29.2)	49 (26.3)	14 (17.9)	4 (8.5)
Southern	19 (9.4)	19 (10.2)	6 (7.7)	6 (12.8)
Coastwide	102 (50.5)	98 (52.7)	13 (16.7)	9 (19.1)
Endemic	2 (1.0)	2 (1.1)	0	0
Cosmopolitan	22 (9.9)	20 (9.7)	4 (5.1)	2 (4.3)
Total with known range	202	186	78	47
Range unknown	16	17	4	5
Total species	218	203	82	52

Differences in effort disallow comparisons of species numbers but percentages can be compared.
Numbers in parentheses are the percent of species for which range information is available.

Species characteristics: Oahu and Central California

Common versus rare

As suggested by the differences in the distance matrices and MDS plots, sites in Central California shared more species than those on Oahu. Common species represented a much greater proportion of the total fauna for the Central California study: 32% compared with 6% on Oahu. By all accounts, species richness of both locations is largely driven by rare organisms that are encountered in only a few locations or/and a few times. The higher proportion of rare species in Hawaii may reflect a pattern of increasing numbers of rare species with decreasing latitude, as found by Okuda *et al.* (2004) in Japan. Many (but not all) of the 'rare' species are common in the subtidal, and it may be that subtidal species do not survive as well in the intertidal in the tropics as in cooler temperate areas, and are thus restricted to microhabitats not present at all sites.

Non-native species

Four invertebrates found in the Central California study are not natives [the arthropods *Armadillidium vulgare* and *Porcellio scaber* (both essentially terrestrial species), and the sponges *Halichondria bowerbankia* and *Hymenacidon sinapium*], representing <1% of the species for which we have range information. The non-native invertebrate sponge species were also found in Elkhorn Slough in Monterey Bay (Wasson *et al.* 2005), where they are particularly abundant and conspicuous (J.S.P. personal observation). *Hymeniacidon sinapium* was found at the Año Nuevo sites, Natural Bridges, and Soquel Point in the 1990s but not at all in the 1970s. No non-native algae or fishes were found.

On the other hand, several species are ambiguous, being perhaps introduced to Central California long ago, widely distributed around the world or, most likely (J. T. Carlton, personal communication) undescribed members of species complexes. These are species that were originally described from European localities in the 18th, 19th and early 20th centuries (*e.g.* the sponges *Aplysilla glacialis* and *Halichondria panicea,* the nemertean *Emplectonema gracile,* the polychaetes *Arabella iricolor*, *Eumida sanguinea, Hemipodia simplex* and *Platynereis bicanaliculata,* the bryozoans *Bugula neritina, Cryptosula pallasiana, Membranipora membranacea*, and the bivalve *Hiatella arctica.*)

Two of the three southernmost sites, Natural Bridges and Soquel Point, each had three non-native species, and Almar Street, Año Nuevo Point and Año Nuevo Cove had one each.

In contrast to the Californian sites, on Oahu, non-native species made up 4% of the fishes (two species), 5% of the algae (five species) and 7% of the invertebrates (26 species) for which we could find range information. On average, non-native species represented about 4% of total species at each site, but Coconut Island and Kahana Bay had much higher percentages of non-natives at 20% and 10%, respectively. Two non-native species, the barnacle *Chthamalus proteus* and the red alga *Acanthophora spicifera*, were among the most common species, having been found at nearly every site.

Endemism

Fourteen of the invertebrate species and two algal species found in the Central California study can be considered endemic to Central and Northern California. Of these species, five were found during the study periods we used for time comparisons, representing ~1.3% of the invertebrate species for which we have range information.

In contrast, endemics made up 10–12% of the total species found on Oahu. The higher percentage includes those species described in the literature as ‘probable’ or ‘possible’ endemics. Endemism was highest in the fishes at 26% (13 species); 11–12% of algae (11–12 species) and 6–11% (22–41 species) of invertebrate species are endemic. At the phylum level, endemism in Hawaii was highest for brown algae at 23% (five species), due in part to several endemic species of *Sargassum.* Endemism among molluscs was also high, up to 19% (24 species) with possible/probable endemics included. Platyhelminthes had the highest rate of any phylum at 40%, but there were only five platyhelminth species for which biogeographical status is known, so it is unclear whether this percentage is truly representative of intertidal flatworms.

Endemic species represented about 12–14% of total species at most sites. Maili Point had the most, at 18%, and Coconut Island, at half that, had the lowest.

Range expansions

There were only five species found in our surveys that had not been previously recorded from Central California. Three had only been reported previously from Southern California (the annelid *Scoletoma erecta* and the bryozoans *Microporelloides catalinensis* and *Retevirgula areolata*), one from Northern California (the isopod *Ianiropsis minuta*), and one from Alaska to Oregon (the hydroid *Thuiaria* sp., which also has been observed on the Sonoma coast by J. Goddard, personal communication). No species in our Oahu surveys were new to the island.

Discussion

A comparison of species richness: Oahu and Central California

Alpha diversity

Our surveys reveal a previously undocumented richness of intertidal species in both locations. Richness was greater in Central California, where search effort was also greater. When we correct for differences in search effort, our data suggest that richness is roughly equivalent between locations.

For Oahu, certainly, our results provide a gross underestimate of true species richness, as small organisms, turfs and coralline algae were not enumerated, and many individuals of large families of crabs and shrimp were recorded only to family and thus counted as just one species. We were conservative in our estimates of organisms recorded as morphospecies and believe that more detailed taxonomic investigation will lead to higher numbers of species in these groups.

The available literature also indicates that our study underestimates species richness of at least two groups at both locations, macro-molluscs and red algae. For gastropods, we found approximately 48% and 50% of the species reported for Central California and Oahu, respectively, and for red algae it was 36% and 25%. If this is any indication of our general effectiveness across other taxonomic groups, we may have found between 25% and 50% of the total intertidal macro-organisms on Oahu and in Central California. Based on the limited number of surveys for two Oahu sites, it does not appear that the rate of new discoveries is decreasing; likely many additional species will be recorded in subsequent surveys.

In Central California sites, this is also probably true and, given the high percentage of rare species, not surprising.

Although total species richness may be roughly equivalent between the two locations, there are some differences in the contributions of various animal phyla to the total species richness: in particular greater fish and echinoderm diversity on Oahu. Hawaii's marine flora and fauna are largely derived from that of the Indo-Pacific, especially the East Indies Triangle, which is a hot spot of diversity and speciation for many organisms, including fishes and echinoderms (Hoeksema 2007). We are less inclined to believe that bryozoans and annelid worms are less speciose on Oahu than in Central California. Bryozoans and annelids were among the groups that increased dramatically in number in Central California in the 1990s with the availability of better taxonomic references and assistance from taxonomic experts. In their survey on Hawaii Island, which focused on intertidal bryozoans, Dick *et al.* (2006) found richness comparable to that of many temperate latitudes (32 species) at one high-wave exposure site, but numbers more similar to ours at their remaining sites (zero to five species). It may be that the sites selected for our study (see Methods) are not optimal bryozoan habitat. In addition, we are disinclined to accept the relatively low richness of red algae found in the Oahu survey as a true reflection of differences between the two locations. Our exclusion of turfs and coralline algae automatically eliminated two groups that contribute to richness in Hawaii. On the other hand, macroalgae have been noted elsewhere to increase in diversity with increasing latitude (Bolton 1994; Santelices & Marquet 1998), and that also may be the case in our comparison between California and Hawaii.

Beta diversity

Another striking difference between the two locations is the significantly higher per-site richness for Central California. Whereas total species richness in Central California was only 55% higher than in Oahu, mean richness per site was more than double that of Oahu, resulting in lower β_w. It is likely that the Oahu survey underestimates the true species richness on a per-site basis. However, surveys in Central California in a single quarter in the 1990s found nearly 90 more species on average per site than on Oahu, so the difference in per-site richness does not appear to be an artifact of differences in effort between the surveys.

In addition to having more species, Central California intertidal sites tend to be more alike in terms of shared species than do Oahu sites. Pairs of sites in Central California on average shared two times as many species as those on Oahu, and common species represented a much greater proportion of the total species. The higher similarities between sites might be due to their location along a geographic gradient that includes changes in wave exposure, human impacts, and rock types. Indeed, sites on the MDS plot fell out along these gradients. Sites on Oahu are not located along a comparable gradient. Sites close to one another geographically could vary in a number of factors such as shoreline orientation, wave exposure, substrate type and formation, and exposure to human impacts. Although we did not find it a good explanatory variable for overall species richness, other studies in Hawaii have linked species composition of dominant species to substrate type (Kay 1979; Cox *et al.* 2011). The numerous rare species in our study may have swamped such a signal.

Species richness was more easily linked to site characteristics in Central California. With the exception of one site, species richness was generally greatest at the outer coast sites and decreased along a gradient toward the Monterey Bay. Because several factors co-vary along this geographic gradient, including two factors expected to impact richness, wave exposure and proximity to urban areas, it is not clear what is driving this trend. For Oahu, richness seems to be linked only to the number of site visits; underlying patterns will likely only be revealed with subsequent site surveys.

Species characteristics

As predicted by the theory of island biogeography, endemic species made up a sizable proportion of the intertidal species found on Oahu. Endemism on Oahu was higher in some groups and at some locations. The central coast of California had few endemics, which is not surprising considering the lack of a physical barrier north and south strong enough to restrict movement of adults or propagules, resulting in speciation through isolation. This finding contrasts with Niesen (2007), who makes a point of the high levels of endemism in the restricted Oregonian faunal province extending from Central Oregon to Point Conception. Our Central California sites, in fact, are within the much larger Oregonian biogeographic province, which contains genetically well-mixed species (Wares *et al.* 2001).

The high numbers of non-native species on Oahu relative to Central California fits the idea that islands are more easily invaded than continents. These numbers may have been slightly exaggerated by the inclusion of Coconut Island, the most protected site. Coconut Island alone accounted for 12 non-native species, including two species, *Diadumene lineata* and *Crassostrea gigas*, which are found in harbors and estuaries in Central California but not in the open coast rocky intertidal (Wasson *et al.* 2005; Carlton & Cohen 2007). However, even with Coconut Island excluded, non-native species richness is twice as high overall and higher on a per-site basis than for Central California. In addition, only one of the exotic species we found in Central California is common (*Hymeniacidon sinapium*), and even that species has not yet achieved widespread distribution in coastal California.

Changes over time: Central California

Species richness

In Central California, despite increased urbanization and various natural and anthropogenic stressors, we find no suggestion of a loss of species richness over the 24-year period between our two survey periods. The apparent increase in invertebrate species richness from the 1970s to the 1990s in the Central California study is certainly the result of improvements in the availability of taxonomic references and increased experience on the part of the principal investigator (J.S.P.), rather than a reflection of an actual increase in richness between the two time periods.

For the invertebrates, various sources were used for identifications in the 1971–1973 surveys. For some taxa we used draft keys prepared for the 3rd edition of *Light's Manual* (Smith & Carlton 1975) but we did not have the final versions or keys for all the taxa; we largely relied on the published keys in *Light's Manual* for the 1996–1997 survey. In addition, in the 1996–1997 survey we had two consultants help with particularly difficult groups (Welton Lee, sponges; Judith Winston, bryozoans). Not surprisingly, while increases occurred across all invertebrate groups, the greatest gains were made in the more difficult groups, including sponges and bryozoans.

In Central California, per-site species richness increased between the two time periods. At one site, Soquel Point, invertebrate species richness more than doubled compared with a mean increase of 65.5% across the other sites. In 1972–1973, domestic sewage was being discharged on the seaward side of the site, and was swept shoreward by incoming waves, visibly impacting the northeast portion of the site with the loss of surfgrasses (*Phyllospadix* spp.) and its replacement with the coralline alga *Corallina chilensis* (Pearse 1992). Particularly noticeable at the time was the absence of most species of sponges and ascidians, as well as their nudibranch predators. Sewage discharge was terminated in 1976, and species sensitive to the sewage, including surfgrasses, sponges, ascidians, and nudibranchs were able to reestablish themselves by 1996–1997 (Pearse *et al.* 1998, see Appendix 1).

In contrast to Soquel Point, the increase in invertebrate species richness (34%) at Año Nuevo Cove was only about half the mean increase for the other sites. During the early 1970s, large numbers of pinnipeds, especially elephant seals, hauled out on Año Nuevo Island, 800 m offshore from Año Nuevo Point, and nutrients from their excrement enhanced the population of marine algae (Hansen 1981), perhaps also favoring invertebrate populations in the area. However, elephant seals began hauling out on the mainland at the Año Nuevo Cove site in the 1960s and in 1975 the first pup was born on the mainland (Le Boeuf & Panken 1977). The new breeding colony increased rapidly and by the 1990s a major rookery was present at that site as well as on the island (Stewart *et al.* 1994). It is possible that the much increased organic enrichment, as well as physical disturbance by elephant seals, decreased invertebrate diversity at the Año Nuevo Cove site. However, no difference was seen in the occurrence of sponges and ascidians between the two time periods.

Species composition

The MDS plot for Central California indicates a shift in species composition between the two time periods. This is likely due to the fact that only about half of the species of invertebrates were found in both surveys. Considering that most of the species recorded appeared to be relatively uncommon and unpredictable in their occurrence, the relatively low number of species found in both surveys is not surprising.

However, there have been some shifts in species composition during the interval between the two surveys, some of which would seem to fit a pattern driven by a change to warmer sea temperatures. For example, the brightly colored, southern nudibranch *Phidiana hiltoni,* which has been expanding northward in Central California (Goddard *et al.* 2011), was not found in our 1972–1973 survey, but was found at four sites in the 1996–1997 survey. Another example is the worm snail *Serpulorbis squamigerus*, a conspicuous and abundant inhabitant of Southern California, which until recently was rarely found in Central California. In the Point Cabrillo transect (Sagarin *et al.* 1999), 872 individuals were found in 1993, whereas none was found in the same transect in 1933. Similarly, we did not find any specimens of *S. squamigerus* in the 1972–1973 survey, but they were found at nine of our 10 sites in the 1996–1997 survey. In a before and after study of an area in the thermal plume of a nuclear power plant in Central California, Steinbeck *et al.* (2005) also found a marked increase in *S. squamigerus*, as well as the other warmer-water species (such as *Tetraclita rubescens* and *Anthopleura elegantissima/sola*, two species which had also increased along the Point Cabrillo transect), suggesting that the abundance of these species can be influenced by water temperatures. Other conspicuous warm-water species such as the alga *Chondracanthus spinosus* and the sponge *Hymeniacidon sinapium* were more abundant in our study in the 1990s than the 1970s. The cooler water barnacle *Semibalanus cariosus* and the northern limpet *Lottia persona* were also found at fewer sites in the 1990s than in the 1970s. These findings align with those of Barry *et al.* (1995) and Sagarin (1999).

On the other hand, a closer examination of species that we found frequently during one survey period but which were rare or not found in the other survey period did not reveal a consistent pattern. Many conspicuous, easy-to-recognize species that occur along the whole coast, from Alaska to Southern or Baja California, were found at many sites during one survey but not at all during the other, and changes in these species were hardly different from those of northern and southern species. We found increases in both northern and southern species over the study period, and nearly all species that were common in the 1970s were also common in the 1990s. Thus, while there are compelling examples of northern shifts in some individual species, on the whole our data do not reflect an overall shift to warmer water species in Central California. This is not surprising, given that although sea surface temperatures in Monterey Bay were significantly higher in the 1990s than in the 1920s (which may have influenced species composition at Point Cabrillo), temperatures have not significantly increased since the 1930s (Breaker 2005). In fact, consistent with climate-change predictions, wind-induced upwelling and storminess along the coast of California and Oregon has increased, leading to decreasing sea temperatures over the past several decades (García-Reyes & Largier 2010; Iles *et al.* 2012). Consequently, lack of a shift toward southern species at our California intertidal sites between the early 1970s and mid-1990s, despite warming on a global scale, is consistent with the lack of observed sea temperature increase at a regional scale. If sea temperature is a major driver in species distribution, we would be more likely to see a decrease in southern species and an increase in northern species. In fact, we found little evidence of a net change.

The overall lack of a coherent pattern in our study is perhaps not surprising given that shorter-term and regional phenomenon can also be major forces regulating recruitment and composition of nearshore species, independent of the longer term trends linked to global climate change. Shifts in species composition and abundance have been well-documented in relation to oceanographic shifts such as the North Atlantic Oscillation (*i.e.* Southward *et al.* 1995; Oviatt 2004), El Niño-Southern Oscillation (ENSO) and Pacific Decadal Oscilliation (PDO) events (*i.e.* McGowan *et al.* 1998; Hilbish *et al.* 2010; Schultz *et al.* 2010; Wethey *et al.* 2011), extreme weather conditions such as cold snaps (Canning-Clode *et al.* 2011), and local tidal regimes that interact with climate change, resulting in heterogeneity in thermal stress along latitudinal gradients (Helmuth *et al.* 2002). It is possible that such phenomena also influenced some species abundances in our surveys: a weak El Niño phase occurred over the two years preceding the 1970s surveys (when many of the species we counted might have recruited), and a weak La Niña during the 2 years proceeding the 1990s surveys. Moreover, there were major oceanographic regime shifts in 1976–1977 and 1989 in the northern Pacific which resulted in warmer, fresher water and decreased zooplankton abundance, with effects measured across multiple nearshore and coastal taxa (McGowan *et al.* 1998; Breaker 2007). Shorter-term warming trends can result in shifts in species distributions in the same direction as predicted due to global warming (*e.g.* in the northeast Atlantic in the 1920s to 1930s and again in the 1980s to 1990s, Southward *et al.* 1995; in the northeastern Pacific from 1958 to 1960s and again in 1983 to 1984, McGowan *et al.* 1998); it is possible that the changes at Point Cabrillo might have been in response to warm years preceeding the resurvey of the transect there.

Shorter-term cooling trends have been found to reverse the global trends of sea surface warming elsewhere (*i.e.* Southward *et al.* 1995; Canning-Clode *et al.* 2011; Wethey *et al.* 2011). In an example from California, Hilbish *et al.* (2010) demonstrated that the non-native warm-water mussel *Mytilus galloprovincialis* contracted southward along the coast following an ENSO and PDO shift to a cold phase. Shifts back to cool-water phases ought to reverse gains made by warm-water species, but apparently this is not always the case. Goddard *et al.* (2011) reported an increase in the abundance of a southern nudibranch, *Phidiana hiltoni*, from 1977 to 1992 in Central California and a subsequent decrease in the abundance of the nudibranch species it consumes; Schultz *et al.* (2010) attributed this range expansion at least in part to the effect of El Niño-Southern Oscillation on larval delivery. However, the range of *P. hiltoni* has not contracted post-ENSO.

As more sophisticated monitoring and analytical techniques are developed, it is becoming increasingly clear that complex fluctuations in large-scale oceanic conditions are responsible for some of the major, long-term variation in recruitment and community composition of the rocky intertidal of the Eastern Pacific (Schultz *et al.* 2010; Menge *et al.* 2011). These phenomena interact with regional patterns, such as tidal regimes and internal waves (Woodson 2011), and with longer-term trends such as global climate change, resulting in biotic changes that are not entirely predictable.

Conclusions

On the whole, despite a number of natural and anthropogenic stressors, there has been little change in intertidal flora and fauna between the two time periods separated by 24 years in Central California. A gradient in species composition was apparent between the more diverse, rural, open coast and the more urbanized, protected coast. One site adjacent to a small domestic sewage outfall that was turned off shortly after being surveyed in the early 1970s showed a major increase in species richness by the time the survey was repeated in the mid-1990s. There was little indication of a loss of species richness at any of the sites except perhaps at one that has become a major elephant seal rookery. Most species found are widespread on the West Coast and endemic species are rare, invasive species remain few in number, and there was no indication of a general shift between northern and southern species.

Ours is not the only long-term study reporting little change over time in a rocky intertidal zone. Surveys of the fauna of the rocky intertidal on the east coast of Australia, separated by 50 years, also found little evidence of change in species distributions (Poloczanska *et al.* 2011). Both our surveys and those of Poloczanska *et al.* (2011) indicate that rocky intertidal communities may be quite resilient over time, and their composition is highly influenced by regional and local conditions, which may not match global trends. On the other hand, surveys separated by 52 years in southern Florida found a general degradation of the sites, probably due to pollution and reef erosion (Smith *et al.* 2007).

Our Hawaiian surveys are preliminary and have not fully characterized the intertidal zone on Oahu, much less the rest of the Hawaiian Islands. However, three of our findings are particularly striking: (i) species richness is high, comparable to that of Central California, (ii) high numbers of species are endemic, about one third of which are restricted to the intertidal zone (not found in shallow reef habitats), and (iii) high numbers of species are introduced, some of which have become invasive and widespread. Without more comprehensive work, new invasions or local extinctions of native species will necessarily go undetected. Although the intertidal zone is included in several of the marine protected areas in the islands, we suggest that further protection and management of intertidal assemblages in the islands is needed, especially in the light of the fact that some of the harvested algae and animals are becoming increasingly harder to find.

We expect that our use of students to conduct surveys will be of concern to some readers. Certainly, there are limitations to a study that relies upon non-professionals, as shown for programs monitoring the spread of low-density invasive species (Fitzpatrick *et al.* 2009); however, neither of our surveys, or similar surveys done by students and other citizen scientists (Silvertown 2009; Dickinson *et al.* 2010), would likely have been done without the extensive labor students can provide. While there may be some biases in sampling and errors in identifications, just as there would be in any such survey, even with highly trained personnel, recent studies by Osborn *et al.* (2005), Cox & Philippoff (2008), Delaney *et al.* (2008), and Cox *et al.* (2012a), demonstrated little or no significant difference in data collected between student teams such as we used and research science teams. We are confident that the data collected by the students are reliable for these surveys.

Finally, we highlight the unexpected finding that species richness on the geographically isolated tropical island of Oahu appears to be on a par with, and perhaps exceeds, that of intertidal sites in Central California. Further surveys of the intertidal zone in temperate and tropical locations are needed before we can say with confidence that intertidal assemblages fit within predicted patterns of increasing species richness with decreasing latitude.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Master Species List, California.

Appendix S2. Master Species List, HI.

Appendix S3. References for Master Species List, California.

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