David Lohse[1], **Karah Ammann,** Department of Ecology and Evolutionary Biology, Long Marine Lab, 115 McAllister Way, University of California, Santa Cruz, California 95060

and

Eric C. Dinger, US National Park Service, Inventory and Monitoring Division, Southern Oregon University, 1250 Siskiyou Blvd, Ashland, Oregon 97520

Long-term Monitoring of Rocky Intertidal Communities: Lessons and Implications from the Redwood National and State Parks, Northern California

Abstract

A challenge modern-day ecologists and resource managers face is how to separate natural variations in populations from changes caused by human activities (e.g., climate change). Long-term monitoring programs provide valuable information to assist in this endeavor. This study details the initial findings of a long-term monitoring program initiated in 2004 to monitor changes in rocky intertidal communities within Redwood National and State Parks, located in northern California. Permanent plots were established at three sites using protocols developed by the Multi-Agency Rocky Intertidal Network, a consortium that monitors rocky intertidal communities along the western coast of North America. Replicate plots were established to monitor changes in abundance of key intertidal taxa, including mussels (*Mytilus californianus*), barnacles (*Chthamalus dalli* and *Balanus glandula*), red alga (*Endocladia muricata*), and rockweeds (*Pelvetiopsis limitata* and *Fucus gardneri*). Plots were sampled annually since they were established. Results from the first 15 years of this study indicate that all taxa exhibited substantial short-term (annual) variation, with barnacles and *E. muricata* exhibiting the most. For barnacles, such variations were correlated with measures of recruitment. Except for *P. limitata*, all other target taxa experienced at least one period of large-scale major change, where abundances decreased dramatically (> 50% of long term mean) and simultaneously in most plots. However, in almost all cases abundances recovered, resulting in no apparent long-term changes. For the few instances where long-term changes were detected, it is possible this result may be an artifact of the analytical methods used to assess them. The potential implications of this finding are discussed.

Keywords: rocky intertidal, long-term monitoring, Redwood National and State Parks, disturbance, recruitment

Introduction

It can be a challenge to assess the effects of human activities on ecosystems, a problem of increasing interest and concern, because populations vary naturally over time (e.g., Andrewartha and Birch 1954). Whether trying to assess the effects of oil spills (e.g., Peterson et al. 2003, Barron et al. 2020, Lewis et al. 2020), overfishing (e.g., McCauley et al. 2015, Gordon et al. 2018, Sumaila and Tai 2020), invasive species (e.g., Molnar et al. 2008; Simberloff 2013; Iacarella et al. 2019a, b), or human-induced climate change (e.g., Harley et al. 2006; Hawkins et al. 2008, 2016; Bindoff et al. 2019), it is important to know the "natural", pre-disturbance condition of an ecosystem to assess potential effects of human activity. Long-term monitoring studies can provide the information necessary to address this issue (e.g., Magnuson 1990).

Lindemayer and Likens (2010) define a long-term monitoring study as a field study in which data are repeatedly and continuously collected for a period of at least 10 years. Numerous authors have discussed the importance of such studies (e.g., Magurran et al. 2010; Hughes et al. 2017; Miner et al. 2018, 2021). They can establish a baseline set of conditions against which future changes to the community can be measured. Such data are useful not only to interpret short-term ecological experiments (Magnuson and Bowser 1990), but to inform policy makers and resource managers

---

[1] Author to whom correspondence should be addressed. E-mail: dlohse@ucsc.edu

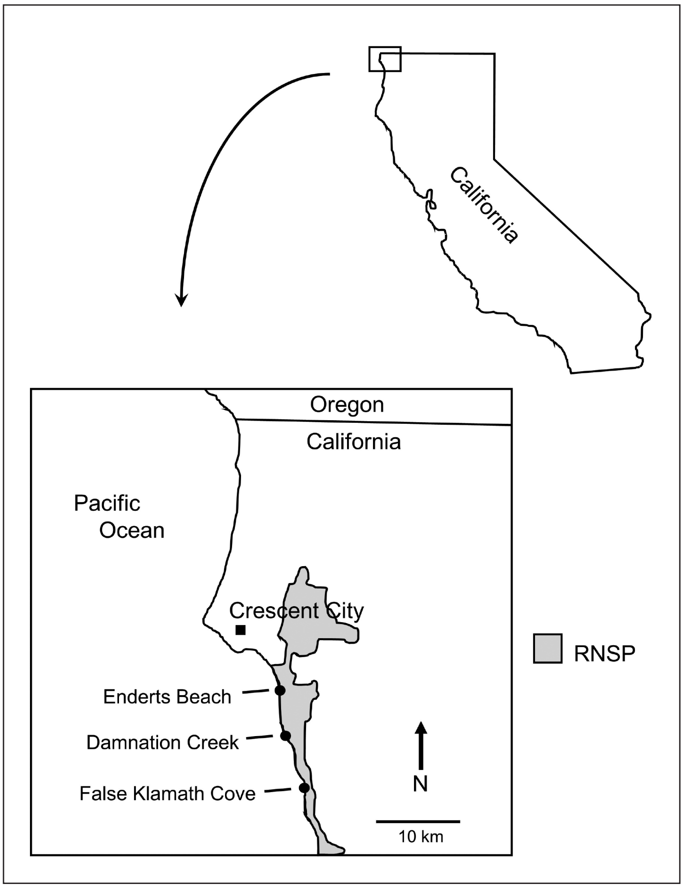

Figure 1. Map showing location of the three study sites in Redwood National and State Parks (RNSP).

tasked with mitigating the effects of natural and human-caused changes (e.g., Lindenmayer et al. 2012, Schuurman et al. 2020).

Recognizing the importance and benefits of long-term monitoring, in 1999 the National Park Service (NPS) established the Inventory and Monitoring Program, a nation-wide effort to provide park managers with scientific information about both the natural resources within the parks and how they are changing over time (Fancy et al. 2009). In 2004, the Klamath Inventory and Monitoring Network (KLMN) of the NPS, a unit of this monitoring network, initiated a long-term monitoring study to document the status and temporal dynamics of common intertidal invertebrate and algal taxa found within Redwood National and State Parks (RNSP). Established in 1994, this approximately 560 sq km park, located in northern California, is visited by an estimated 700,000 people annually. Although perhaps best known for its old-growth redwood forests, RNSP also includes 56 km of coastline.

Here, we present some initial findings from this ongoing long-term monitoring study. We utilized data from the first 15 years (2004 to 2018) of this study to describe the temporal changes in abundance of a select group of common intertidal organisms. We then used several different analyses to detect both short- and long-term patterns and trends in species abundance, and then discuss potential mechanisms driving these patterns. Finally, we offer insights into ways of improving future analyses of long-term change.

Methods

This ongoing study was initiated in 2004, when permanent plots were established at three sites within RNSP (Figure 1) to monitor changes in abundance of several common and ecologically important intertidal taxa. The site at Enderts Beach consists of several rocky benches separated by boulder-filled channels, while the site at Damnation Creek is an extensive channel-cut bench surrounded by a boulder and cobble beach. Both sites experience moderate to high wave exposure, and due to accessibility issues, receive few visitors. In comparison, the site at False Klamath Cove consists of several small benches within a large boulder field. It is somewhat more protected from waves and more accessible than the other two sites.

At each site, permanent plots were established to monitor abundance of six target species: 1) California mussel (*Mytilus californianus* Conrad), 2) red turfweed alga (*Endocladia muricata* Postels & Ruprecht), 3) common brown rockweed (*Fucus gardneri* Linnaeus), 4) dwarf rockweed

(*Pelvetiopsis limitata* Gardner), 5) small acorn barnacle (*Chthamalus dalli* Pilsbury), and 6) common acorn barnacle (*Balanus glandula* Darwin). The plots were established using protocols developed by the Multi-Agency Rocky Intertidal Network (MARINe), a consortium of various governmental agencies, universities, and private organizations that monitors the intertidal community at sites along the western coast of North America; a detailed description of these protocols and their rationale can be found in Ammann and Raimondi (2008). Briefly, five permanent plots, each measuring 50 × 75 cm, were established per taxon; the corners of each plot were marked using stainless steel bolts and marine epoxy. The plots were installed where the abundance of targeted taxa was high (ideally > 80% cover); since each of these taxa is dominant at a different height on the shore, the monitoring plots were spread throughout the intertidal zone. At False Klamath Cove (FKC), plots were established for all target taxa, with one set of plots used to monitor the two barnacle species. However, at Enderts Beach (END) and Damnation Creek (DMN), only four plot types were established; *F. gardneri* was not common enough to establish plots at Enderts Beach, nor was *P. limitata* at Damnation Creek.

Since 2004, the abundance (% cover) of taxa within each plot have been assessed annually in May or June of each year (note: Enderts Beach was inaccessible in 2017). Initially, this was done in the lab by identifying and counting individuals under a grid of 100 uniformly spaced points overlaid onto photographs taken of the plots using imaging software (points spaced the digital equivalent of 5 cm apart widthwise, 7.5 cm apart lengthwise). However, starting in 2007, abundances were measured directly in the field by placing a quadrat, strung with line to create a grid of 100 uniformly spaced points (spaced approximately 5 × 7.5 cm apart as noted above) over the permanent plots. Again, the individuals under each point were identified and counted. Although there can be multiple taxa under each point due to layering, those on the bottom layer(s) were usually not visible in the early photographs scored in the lab. Therefore, for the sake of consistency, only the data for the top layer were considered for this study. The exception was the mussels in the mussel plots, where their presence was scored regardless of layer. Note that during the first two years of the study, barnacles were not identified to species, but they were from 2006 onward. Thus, percent barnacle cover represents the combined abundance of both *C. dalli* and *B. glandula* (except for recruitment, see below). This paper includes the data collected from 2004 to 2018.

In 2006, five 10 × 10 cm plots, one adjacent to each barnacle plot, were established to monitor barnacle recruitment. The corners of the plots were marked with marine epoxy, and then the plots were scraped clean. A 2-cm border around the plots was also scraped to minimize edge effects. The following year (2007), all barnacle recruits in the plots were identified and counted, after which the plots were again scraped clean. This was repeated every year until 2016.

Because mussel beds often consist of multiple rather than single layers of mussels, percent cover alone often does not provide a complete measure of mussel abundance. Thus, beginning in 2010, the size distribution of mussels in the *M. californianus* plots was also measured annually (but beginning in 2011 at END). The size measurements were taken by placing a small 10 × 10 cm quadrat in the four corners and center of each plot and measuring the length of the mussels under two corners of each quadrat. If there was more than one layer of mussels, as many additional individuals as possible were measured under each corner without physically altering the bed. Thus, a minimum of 10 individuals were measured per plot (2 corners × 5 quadrats), but sometimes more. Beginning in 2011 the thickness of the mussel bed was also determined by measuring the distance from the primary substrate (i.e., rock) to the top of the top-most mussel, with the aid of a metal skewer, in the center of each 10 × 10 cm quadrat. All measurements were taken to the nearest 1 cm.

Temporal Analyses

Several analyses were used to investigate temporal changes in abundance of the target taxa in their designated plots during the period from 2004 to 2018. Short-term annual changes were investigated by first using correlation analysis to compare abundances in sequential years: year(x) versus year(x+1).

Second, periods of major change were identified by determining when the change in abundance between sequential surveys exceeded 50% of the long-term mean.

Two different statistical analyses were used to detect longer term changes in abundance. First, two-way randomized block analysis of variance (ANOVA) was used to detect non-linear changes in abundance over short (3 years), medium (5 years), or long (7 years) time scales. For each, the 15 annual surveys were divided into chronological groups containing the appropriate number of samples (e.g., for the short time scale there were 5 groups, each containing 3 surveys). Note that because there were 15 surveys, to maintain a balanced comparison (i.e., to compare equal time periods), the year 2011 was not used for the long time scale (7 years per group) analysis. Prior to analysis, the average abundance of the target taxa was first calculated for each replicate plot within each group; this mean was then log(x + 1) transformed. Any significant differences detected by the ANOVA were further investigated using Tukey's *a posteriori* test.

For the second analysis, we used the unweighted linear mixed model of Piepho and Ogutu (2002) to detect any linear trends in the abundance of the target taxa; Starcevich et al. (2018b) found this method was robust for trend detection. The analyses were done using the R package TrendNPS (Starcevich et al. 2018b), and all data were log(x + 1) transformed prior to analysis. When possible, the model included a site-level slope variable, a random variable that captured spatial variation at the plot level (Starcevich et al. 2018a). However, when the model was singular or failed to converge (likely due to over parameterization), this variable was omitted. Tests for significance were conducted by comparing the Wald statistic for the trend coefficient (i.e., slope) against the *t*-distribution, with degrees of freedom determined by the Satterthwaite method (Satterthwaite 1946).

Results

A total of 42 taxa were counted within the plots during the study, but the vast majority (76%) of these taxa had mean cover < 2%. The three most common in each plot, which included some combination of the five target taxa, plus open space and the two crustose algae (*Ralfsia* spp. and Petrocelis [the tetrasporophyte phase of the red algae *Mastocarpus* spp.]) accounted for, on average, 77 to 98% of all points scored (Table 1). Open space, which in most cases was second in abundance after the target taxa in each plot, tended to be strongly, and negatively, correlated with cover of the target taxa (Table 2).

The target taxa exhibited varying degrees of annual variation in abundance (Figure 2), with the barnacle and *Endocladia* plots appearing to exhibit the most (Figure 3). The pattern of variation often differed among the sites. For example, barnacle abundances at both Enderts Beach and Damnation Creek were lowest in 2010, while at False Klamath Cove, they were lowest at the start (2004) and end (2018) of the 15-year study period (Figure 2). *E. muricata* abundances started high and then dropped precipitously at all three sites, but only at Enderts Beach and False Klamath Cove did abundances quickly recover (Figure 2). Starting in 2014, percent cover again declined at Enderts Beach before beginning to recover (Figure 2). In the mussel (*Mytilus*) plots, mussel abundances were dramatically lower at Enderts Beach in 2015 and 2016, which coincided with a reduction in mussel bed thickness (Figure 4); there were no changes at the other two sites (Figure 2). Although less striking, site differences were also evident in the cover of *F. gardneri* and *P. limitata* in their respective plots (Figure 2). For the barnacle plots, the observed variation in cover was correlated with annual differences in barnacle recruitment (Figure 5).

While many of the short-term (annual) changes were small (< 10%), there were several instances where the differences were large (> 40%; Figure 3). Major changes occurred with some frequency at a small scale (i.e., occurring in ≤ 2 of the 5 replicate plots), but also occasionally at a larger scale (≥ 3 of the plots) (Figure 6). Undoubtedly, the frequency of such changes contributed to the fact that, with a few exceptions, there was no temporal autocorrelation among samples (Table 3), this despite the fact that the taxa were sessile and abundances were measured in fixed, not random, plots.

In the barnacle plots, a major loss in abundance was often immediately (the next year) followed

TABLE 1. The top three most abundant taxa or open space found in the top layer of each plot type at the three study sites. Numbers in parentheses are mean abundance (percent cover) over the course of the study. Non-coralline crust was Petrocelis plus *Ralfsia* spp. NP = plots of this type not present.

Plot type	Enderts Beach	Damnation Creek	False Klamath Cove
Barnacle	*Chthamalus / Balanus* (45)	*Chthamalus / Balanus* (44)	*Chthamalus / Balanus* (53)
	Open space (22)	Open space (33)	Open space (24)
	Mytilus californianus (10)	*Endocladia muricata* (7)	*Endocladia muricata* (7)
Endocladia	*Endocladia muricata* (54)	*Endocladia muricata* (44)	*Endocladia muricata* (73)
	Open space (14)	Open space (30)	Open space (11)
	Chthamalus / Balanus (11)	*Chthamalus / Balanus* (9)	*Fucus gardneri* (9)
Fucus	NP	*Fucus gardneri* (83)	*Fucus gardneri* (67)
		Open space (7)	Non-coralline crust (10)
		Endocladia muricata (5)	*Endocladia muricata* (6)
Mytilus	*Mytilus californianus* (82)	*Mytilus californianus* (95)	*Mytilus californianus* (86)
	Open space (6)	Open space (2)	Open space (3)
	Chthamalus / Balanus (4)	*Chthamalus / Balanus* (1)	*Chthamalus / Balanus* (3)
Pelvetiopsis	*Pelvetiopsis limitata* (55)	NP	*Pelvetiopsis limitata* (65)
	Open space (16)		*Chthamalus / Balanus* (12)
	Chthamalus / Balanus (11)		Open space (8)

by a major increase, but this was less common for the other taxa. There were several instances (e.g., 2005 at Enderts Beach and False Klamath Cove in the barnacle plots, and 2009 at Enderts Beach in the *Endocladia* plots) when some replicate plots exhibited major losses, while the others were exhibiting major increases (Figure 6). There were also several instances (e.g., 2005, 2010, 2012, and 2015) when major losses were recorded both across plot types within a site and across sites (Figure 6).

TABLE 2. Correlation coefficients (Spearman's rho) comparing percent cover of open space to the percent cover of the target taxa for the three study sites. Data were log(x +1) transformed prior to analysis. $^{a} = P < 0.1$, $* = P < 0.05$, $** = P < 0.01$, $*** = P < 0.001$. Study sites are END = Enderts Beach, DMN = Damnation Creek, FKC = False Klamath Cove. NP = plots of this type not present.

Taxa	END (*n* = 14)	DMN (*n* = 15)	FKC (*n* = 15)
C. dalli, B. glandulas	–0.75**	–0.72**	–0.56*
E. muricata	–0.37	–0.79***	–0.43
F. gardneri	NP	–0.75**	–0.44^{a}
M. californianus	–0.74**	–0.87***	–0.32
P. limitata	–0.76**	NP	–0.61**

For longer term changes, the results of the ANOVA analysis found significant differences in abundance at the short (3 yrs/group) and medium (5 yrs/group) time scales for many of the taxa in their designated plots (Figure 7, Table 4). In almost all cases, these differences suggest abundances were either higher or lower in the middle, rather than the beginning or end, of the study (Figure 7); *E. muricata* and *P. limitata* at Enderts Beach were the exceptions, as both had abundances lower at the end of the study than the beginning (Figure 7). However, at the longest time scale (7 yrs/group), there were only two instances when abundances differed between the first 7 years versus last 7 years of the study (Figure 7, Table 4): during the second half of the study, barnacle cover at Damnation Creek was higher, and at Enderts Beach *P. limitata* cover was lower. For *P. limitata*, this trend is consistent with the findings of the short and medium time scales, but for the barnacles, it is not. Similarly, the abundance of *E. muricata* at Enderts Beach, which appeared to decrease over time at the short and medium time scales, was only marginally different when examined at the longer time scale (Table 4).

Perhaps not unexpectedly, the results of the linear trend analysis most closely matched those of the long time scale (7 years per group) ANOVA analysis in that, in almost all cases, there were no significant linear temporal trends in abundance (Table 5). However, there were two important differences. First, neither of the two cases where a significant linear

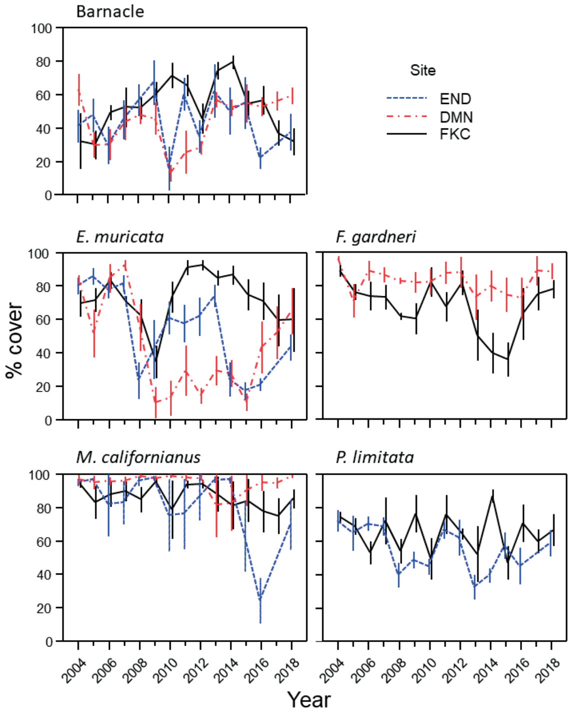

Figure 2. Patterns of abundance (mean % cover ± 1 standard error) of target taxa in their designated plots over the course of the study; the barnacle graph displays the two acorn barnacle species combined: *Chthamalus dalli* and *Balanus glandula*. Study sites are labeled as END = Enderts Beach, DMN = Damnation Creek, FKC = False Klamath Cove.

trend was detected (*E. muricata* and *M. californianus* at Enderts Beach) were significantly different in the ANOVA analysis. And second, neither *P. limitata* at Enderts Beach, nor the barnacles at Damnation Creek, which exhibited significantly different mean abundances in the two halves of the study, exhibited a significant linear trend (Table 5). In three cases (*P. limitata*, *E. muricata*, and *M. californianus* at Enderts Beach), there was a large-scale, major decline in abundance, albeit in different years, during the second half of the study (Figure 6). That both *M. californianus* and *P. limitata* abundances had recovered by the end of the study (assessed by comparing abundance in 2018 versus mean abundance from 2004 to 2011 in a paired t-test [$n = 5$], $t = 1.53$, $P > 0.05$ for *M. californianus*, and $t = 0.44$, $P > 0.05$ for *P. limitata*), but *E. muricata* had not (abundance in 2018 versus mean abundance from 2004 to 2011, $t = 3.34$, $P < 0.05$) contributed to these different results. Recovery of *M. californianus* was primarily due to an influx of small mussels (Figure 4).

Discussion

During the 15-year study period, all the target taxa showed some degree of temporal variation in abundance, including several instances of very large change. For the barnacles, there is evidence that variations in abundance were, in part, determined by variations in recruitment (see below). For the other taxa, the frequent incidents of both small- and large-scale major declines in abundance suggest that disturbance played a major role in determining their abundance. In general, disturbances are unexpected events that disrupt the structure of communities. However, here we use the term to represent events that kill or damage individuals (sensu Sousa 1984a). Although extreme temperatures can be agents of disturbance (e.g., Sebens and Lewis 1985, Suchanek 1985, Robles et al. 1995, Harley 2008, Harley and Paine 2009), in the rocky intertidal system along this coast, physical disturbances are usually related to high wave action and wave-borne objects striking the shore (e.g., Dayton 1971, 1973; Harger and Landenberger 1971; Paine 1979, 1988; Paine and Levin 1981; Sousa 1979, 1984b; Shanks and Wright 1986). Because such events create open space on the rock, they both renew an important and often limited resource (i.e., open space) and reset the successional sequence. Thus, disturbances play a key role in determining the structure in rocky intertidal systems (e.g., Levin and Paine 1974; Sousa 1979, 1984b; Paine and Levin 1981; Guichard et al. 2003).

Given the observed strong, negative correlations between the abundance of the target taxa and the amount of open space in the plots, sudden drops in abundance of the target taxa most likely represent disturbance events. As such, small-scale disturbances, as evidenced by losses in one or two replicate plots, appeared to happen with some frequency, particularly in the barnacle, *Endocladia*, and *Pelvetiopsis* plots. Why they were less common in the *Fucus* and *Mytilus* plots is unknown. For mussels, perhaps the protection offered by their shells (e.g., Burnett and Belk 2018, Crane et al. 2021), along with their ability to increase attachment strength in response to increased hydrodynamic forces (e.g., Witman and Suchanek 1984, Bell and Gosline 1997, Carrington 2002), offer them heightened levels of protection from some disturbances. For *F. gardneri,* because it is a canopy-forming species, the measures of its abundance reflect the size of the canopy, not the space it occupies on the rock. Because this canopy is quite flexible, it may be able to avoid damage from certain types of disturbances. Alternatively, if the density of *F. gardneri* is high enough, or individuals big enough, neighboring individuals drape over each other during low tide. Under these conditions, the loss of individuals due to disturbances may have more of an effect on the thickness of the canopy than on the measures of percent cover.

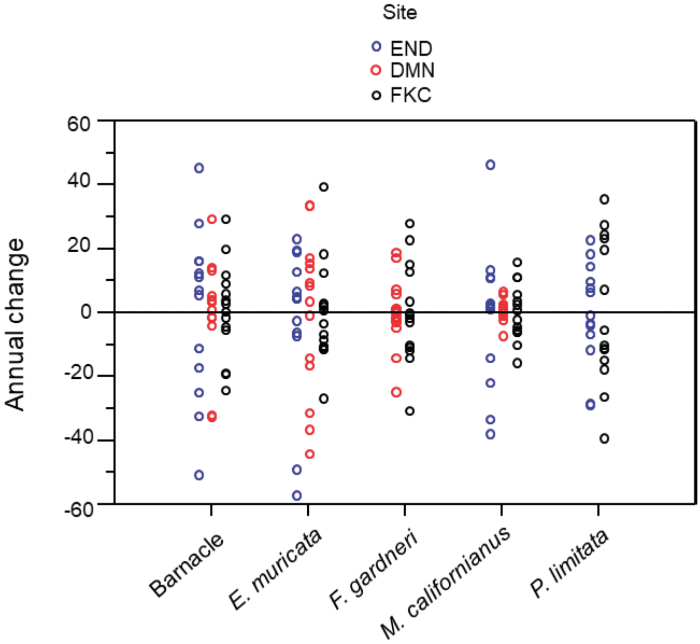

Figure 3. Values of annual change in abundance, i.e., year(x) versus year(x+1), observed in target taxa in their designated plots over the course of study, where barnacle data displays the two acorn barnacle species combined: *Chthamalus dalli* and *Balanus glandula*. Study sites are labeled as END = Enderts Beach, DMN = Damnation Creek, FKC = False Klamath Cove.

There were also instances when disturbances occurred on a larger scale, impacting multiple plots of a given taxon, or in several cases, plots of multiple taxa within and across sites. Again, the *Fucus* and *Mytilus* plots were the least affected. Although such instances represent periods of greater loss, when more individuals spread out over larger areas were eliminated from the population, given the sampling interval, it is unknown whether these disturbances happened all at once (e.g., one winter storm), or occurred over a longer period of time (e.g., one winter season). Since previous authors have had success linking offshore measures of oceanographic conditions to disturbances onshore (Denny 1995, Blanchette et al. 2002), this is clearly a topic deserving of further research.

Curiously, one large-scale event that apparently did not have much of an impact on the target taxa was the 2014 to 2016 marine heatwave (MHW). This MHW was an extended period of anomalously high water temperatures along much of the coastline of western North America (Gentemann et al. 2017); during this period we observed mean monthly water temperatures 1 to 3 °C above normal at the study sites. This MHW had major impacts on many nearshore and coastal communities (Cavole et al. 2016, Weitzman et al. 2021), including the rocky intertidal system, where it has been linked to the onset of sea star wasting syndrome (SSWS) and the subsequent coast-wide decline in sea star numbers (Eisenlord et al. 2016, Miner et al. 2018; however, see Menge et al. 2016). For example, numbers of adult ochre sea stars (*Pisaster ochraceus* Brandt) declined by more than 50% at the three study sites at the start of the MHW (Ammann et al. 2017). Thus, it is somewhat surprising that, except for widespread small-scale disturbances in 2015 and a major decline in mussels at Enderts Beach, the target taxa apparently were not greatly impacted

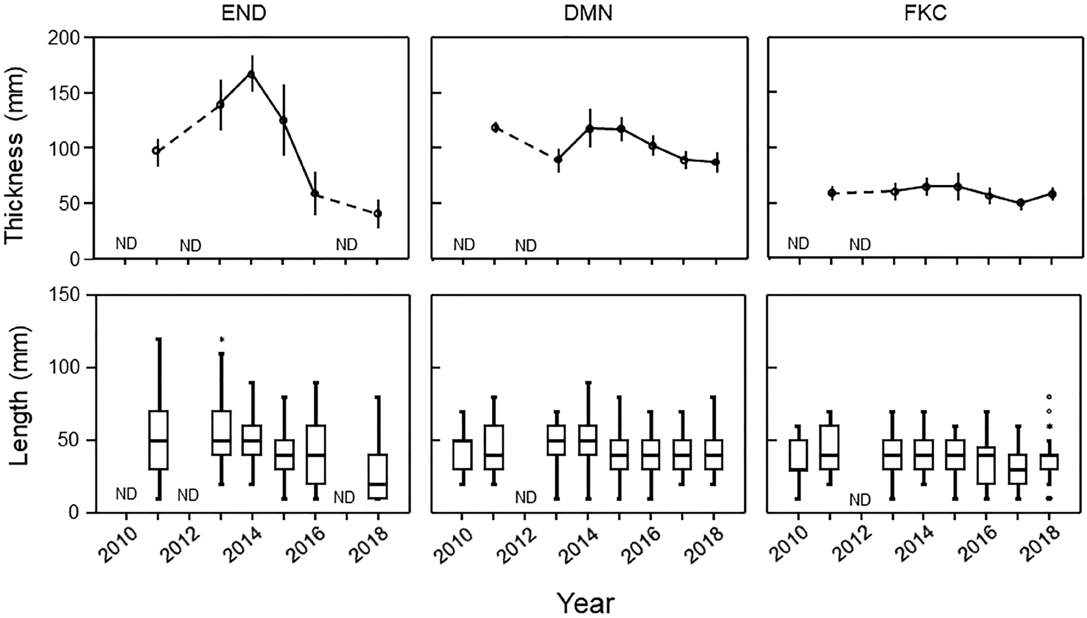

Figure 4. Temporal changes in mussel bed thickness (mean ± 1 standard error) and mussel size (length) distributions in the mussel plots at the three study sites. Study sites are labeled as END = Enderts Beach, DMN = Damnation Creek, FKC = False Klamath Cove. For the box plots, the bottom, middle, and top of the boxes represent the 1st quartile, the median, and the 3rd quartile, respectively. Whiskers extend from the 1st quartile –1.5 × interquartile range (bottom) to the 3rd quartile +1.5 × interquartile range (top). ND = no data collected for that year. Dashed lines connect means from non-sequential years.

by this MHW. Most marine taxa occupy the fullest range of latitudes allowed by their thermal tolerances (Sunday et al. 2012), and the target taxa at the three study sites are not close to their southern distributional limits (Table 6). This suggests that the above-normal temperatures experienced during the MHW were not high enough to cause widespread harm. This is supported by published temperatures tolerances (Table 6), which are much greater than the maximum water temperatures (< 17 °C, Ammann et al. 2017) observed at the study sites during this MHW. Since climate change is expected to cause an increase in the frequency and intensity of MHWs over the next century (Oliver et al. 2017, Frölicher et al. 2018, Collins et al. 2019, Darmaraki et al. 2019), how the target taxa respond to future MHWs is of interest. Similarly, since intertidal organisms must also deal with air temperatures during low tides, how they respond to climate-induced changes in air temperatures is also worthy of attention.

While the MHW may have played a role in the decline in mussel abundance at Enderts Beach, it could have also facilitated their subsequent recovery. While smaller gaps in mussel beds created by disturbances commonly fill in via encroachment of the surrounding mussels (Paine and Levin 1981, Sousa 1984b), the recovery of larger gaps depends more upon recruitment (Connell and Slatyer 1977, Paine and Levin 1981, Conway-Cranos 2012). The success of this process can depend on the actions of the ochre sea star (*Pisaster ochraceus*), a major predator on mussels (Paine 1966, 1974; Menge et al. 1994); previous studies have documented that this predator can eliminate patches of new mussel recruits (Sousa 1984b, Robles et al. 1995). However, Menge et al.(2016) found that the rate of predation on mussels was greatly reduced during the MHW, which they attributed to the loss of *P. ochraceus* due to SSWS. Since the loss of this predator has been linked to the post-SSWS downward (i.e., towards the water) expansion of mussel beds along the

California coast, due in part to recruitment (Moritsch 2021), it is plausible that it also contributed to the large influx of small mussels in the mussel plots at Enderts Beach beginning in 2016.

Although the recovery of mussels at Enderts Beach demonstrates the importance of recruitment following disturbances, the significant correlation between recruitment in the barnacle clearings and cover in the plots suggests that, for barnacles, recruitment plays a key role in the temporal dynamics of their populations. This finding is consistent with previous studies that concluded intertidal populations along the stretch of coastline encompassing the three study sites are recruitment limited (Connolly and Roughgarden 1998, Connolly et al. 2001, Broitman et al. 2008). For such populations, not enough recruitment occurs for open space to become limited. Consequently, post-settlement mortality is density independent, and variation in adult abundance reflects variation in recruitment (Caley et al. 1996). Additionally, although *B. glandula* can live up to 10 years, and *C. dalli* for up to 3 years (Newman and Abbott 1980), the significant correlation between recruitment and cover also suggests that the populations in the plots were comprised largely of a single generation. This further implies not only that some processes, such as winter storms or predation, remove most of the population each year, but that the long-term persistence of these populations is reliant on continual recruitment.

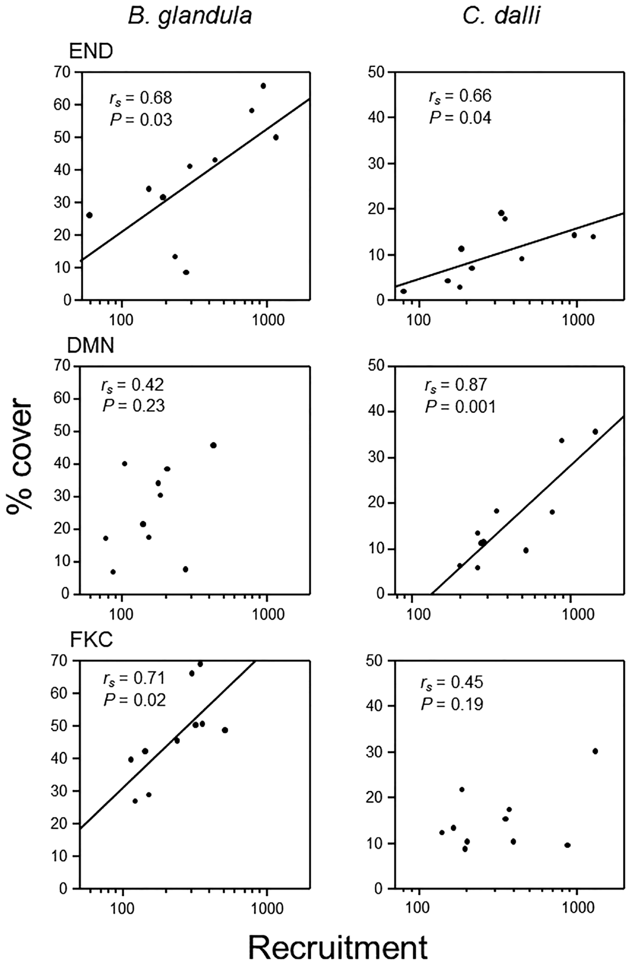

Figure 5. Barnacle recruitment in clearings versus existing barnacle percent cover in barnacle plots. r_s = Spearman's rho correlation coefficient. Lines are only present in plots with significant correlations ($P \leq 0.05$). Study sites are labeled as END = Enderts Beach, DMN = Damnation Creek, FKC = False Klamath Cove.

Long-term Changes

Despite evidence of disturbance, in most cases there were no significant long-term changes in abundance, most likely because following each disturbance was a period of "recovery"; this was true even for those exceptions that exhibited long-term declines (see below). In the barnacle plots, such periods often occurred immediately following the decline, but for the other taxa, it often took a little longer. Previous studies have found that not only are barnacles often the first to colonize following a disturbance, but that their presence can facilitate the appearance of later successional stages (Dayton 1971, Farrell et al. 1991, Van Tamelen and Stekoll 1996, Berlow 1997, Kim 1997, Menge et al. 2011). Thus, the apparent differences in the rate of recovery could reflect successional dynamics. Since reproductive seasons vary among the taxa, the timing (i.e., season) of the disturbance event could also play a role

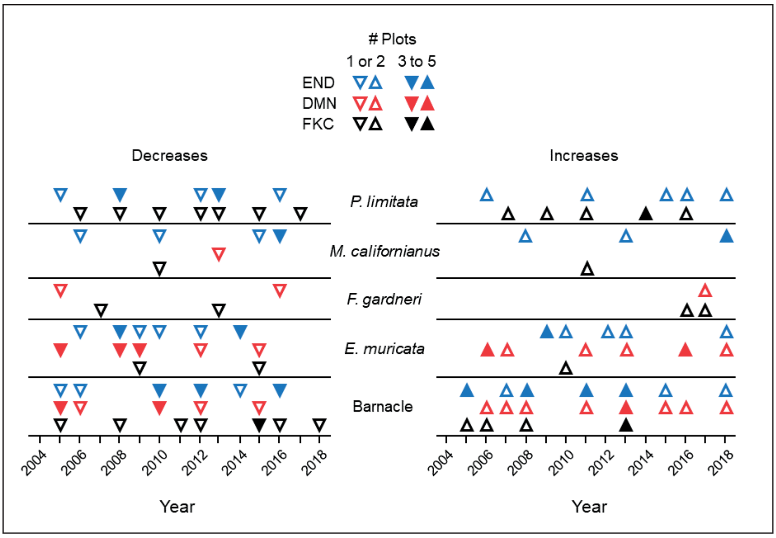

Figure 6. Instances of small (open symbols, change limited to 1 or 2 plots) and large (closed symbols, change in 3 to 5 plots) scale major changes (≥ 50% of long-term mean) in abundance of the target taxa; barnacle is the two acorn barnacle species combined: *Chthamalus dalli* and *Balanus glandula*. Study sites are labeled as END = Enderts Beach, DMN = Damnation Creek, FKC = False Klamath Cove.

TABLE 3. Correlation coefficients (Spearman's rho) comparing taxa abundance at time(t) versus time(t + 1). Data were log(x + 1) transformed prior to analysis. [a] = $P < 0.1$, * = $P < 0.05$, ** = $P < 0.01$. Study sites are END = Enderts Beach, DMN = Damnation Creek, FKC = False Klamath Cove. NP = plots of this type not present.

Taxa	END ($n = 13$)	DMN ($n = 14$)	FKC ($n = 14$)
C. dalli, B. glandulas	0.46	0.35	0.56*
E. muricata	0.55[a]	0.46[a]	0.34
F. gardneri	NP	0.19	0.52[a]
M. californianus	0.66*	0.45	0.08
P. limitata	0.24	NP	0.78**

(Kim and DeWreede 1996). Alternatively, since algae can expand via vegetative growth (Sousa 1980, 1984b; Sousa et al. 1981; Conway-Cranos 2012), it could simply reflect a different process of recovery (i.e., outward expansion of existing individuals versus colonization by planktonic larvae), one that operates at a different time scale.

For those cases that demonstrated long-term declines (*M. californianus*, *E. muricata*, and *P. limitata*, all at Enderts Beach), the timing and frequency of the disturbances played an important role in this outcome. For example, in the case of *M. californianus*, there was only one instance of a major disturbance, and it occurred near the end of the study. Although abundances had recovered by the last census (2018), it was depressed for long enough to reduce the mean abundance of the second half of the study relative to the first. As for *P. limitata* and *E. muricata,* both experienced two major disturbances, one in each half of the study. *P. limitata* recovered from both, but because it took longer to recover after the second disturbance, abundances were lower for a longer period during the second half of the study than during the first. Although its abundance had not yet fully recovered by the end of the study, the same was basically true for *E. muricata.* Thus, while in all three cases the statistical tests suggest overall abundances were lower in the second half of the study, which is suggestive of long-term change, arguably this result may have less to do with the actual state of the populations and more to do with the methodology of the analyses used to detect these changes (discussed further in the next section).

There are two additional points worth noting. First, the highest abundances of *E. muricata* at Enderts Beach over the course of the study were observed at the start. Although this could be an artifact of the criteria used to establish the plots (i.e., they were installed where abundances were high), it could also be an example of a shift in baseline abundance (that is, the level around which abundances vary over time). In this case, after both postulated major disturbance events, abundances of *E. muricata* increased, but after the second, they did not return to the same level. Whether, given more time, abundances will eventually do so, or

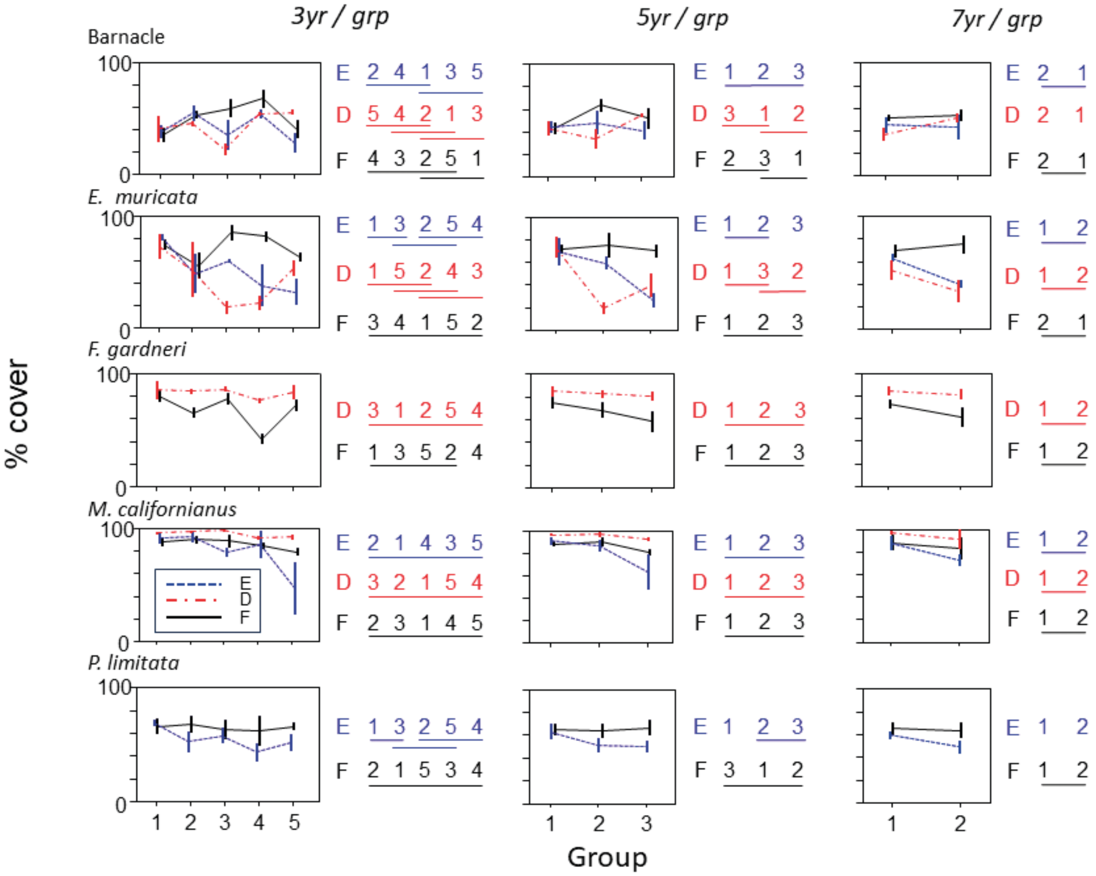

Figure 7. Changes in mean abundance (percent cover ± 1 standard error) over time (left) and results of Tukey's multiple comparison tests (right) for surveys grouped chronologically using 3 different time intervals. For the shortest interval there were 5 groups of 3 years each (e.g., group 1 = years 2004 to 2006), the medium interval had 3 groups of 5 years each (e.g., group 1 = years 2004 to 2008), and the longest interval had 2 groups of 7 years each (group 1 = 2004 to 2010, group 2 = 2012 to 2018). For multiple comparisons, group numbers are arranged from most (left) to least (right) abundant based on log-transformed data; groups connected by a line are not significantly different. See Table 4 for ANOVA results. E = Enderts Beach, D = Damnation Creek, F = False Klamath Cove.

whether they will remain at a lower level, can only be determined by continued monitoring.

Second, if this change truly represents a shift in the baseline, it only took place at one site, Enderts Beach. If it were due to some large-scale phenomenon, like climate change, similar changes would be expected at the other sites. Since this was not the case, the shift likely reflects a change in local, not global, conditions.

Implications

To understand how human activities affect natural communities, there has been renewed interest in observational ecology in general (Sagarin and Pauchard 2010) and a recognition of the importance of long-term monitoring studies (e.g., Lovett et al. 2007; Magurran et al. 2010; Lindenmayer et al 2012; Hughes et al 2017; Miner et al. 2018, 2021). By collecting data both continuously (i.e., annually in the current study) and over an extended period of time (Lindenmayer and Likens 2010), such studies provide a more complete picture of the temporal dynamics of a population. Both aspects of such studies are important. Because data are collected continuously, it is possible to determine whether an observed change is more extreme than

TABLE 4. *F*-statistics of 2-way analysis of variances comparing mean abundance among groups defined using three different intervals: 3, 5, or 7 years per group for study sites. Results of Tukey's multiple comparison tests are presented in Figure 5. df = degrees of freedom. [a] = $P < 0.1$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Study sites are END = Enderts Beach, DMN = Damnation Creek, FKC = False Klamath Cove.

		3 yr/group		5 yr/group		7 yr/group	
Taxa	Site	*F* (plot) df = 4, 16	*F* (group) df = 4, 16	*F* (plot) df = 4, 8	*F* (group) df = 2, 8	*F* (plot) df = 4, 4	*F* (group) df = 1, 4
C. dalli, B. glandulas	END	16.4***	5.8**	13.6**	0.4	7.9*	0.05
	DMN	2.6[a]	17.5***	2.2	14.2**	1.0	8.4*
	FKC	1.8	5.2**	1.5	4.6*	3.0	1.8
E. muricata	END	0.7	8.1***	0.4	9.0**	0.5	6.4[a]
	DMN	7.5**	9.5***	3.9*	14.1**	2.9	1.0
	FKC	2.3	2.9[a]	2.0	0.3	1.8	0.4
F. gardneri	DMN	4.3*	1.2	3.9*	0.6	10.8*	4.2
	FKC	4.0*	7.7**	3.8[a]	4.0[a]	1.7	3.6
M. californianus	END	0.9	1.9	0.9	2.4	1.3	4.3
	DMN	1.3	1.0	3.5[a]	0.6	0.9	0.7
	FKC	14.3***	1.1	11.8**	1.8	18.3**	1.2
P. limitata	END	4.2*	6.7*	8.1**	10.9**	5.1[a]	10.3*
	FKC	5.4**	0.7	5.3*	0.5	9.1*	0.03

TABLE 5. Annual percent change estimates of linear mixed models (Piepho and Ogutu 2002) used to detect linear trends of target taxa at study sites over time. Data were log(x+1) transformed prior to analysis, and results (i.e., estimates of slopes) were back-transformed. CI = confidence interval; * = slope significantly different than 0 (P < 0.1); ϕ = the random site-level slope variable was retained in the model. Study sites are END = Enderts Beach, DMN = Damnation Creek, FKC = False Klamath Cove.

Taxa	Site	Annual % change in slope (CI)
C. dalli, B. glandula	END	–1.3 (–7.9, 5.8)
	DMN	3.9 (–1.6, 9.6)
	FKC	2.9 (–1.7, 7.7)
E. muricata	END	–7.9 (–14.2, –1.3)*
	DMN ϕ	–5.7 (–16.0, 5.9)
	FKC ϕ	–1.0 (–6.0, 4.2)
F. gardneri	DMN	–0.6 (–1.7, 0.6)
	FKC	–2.8 (–5.8, 0.3)
M. californianus	END	–4.7 (–8.9, –0.2)*
	DMN ϕ	–0.7 (–2.8, 1.5)
	FKC	–1.0 (–2.0, 0.0)
P. limitata	END	–2.6 (–5.4, 0.2)
	FKC	–0.5 (–2.9, 1.9)

'normal', whether it is temporary or permanent, or whether or how often similar changes have occurred before. Such knowledge provides important context, making it possible to identify those changes that are unexpected or extreme. Also when data are collected over long periods of time, it is possible to establish a baseline measure of abundance, a value against which any observed change can be compared. Because all populations exhibit some degree of short-term variation, such information is essential for detecting long-term changes, like those predicted for climate change (e.g., Harley et al. 2006; Hawkins et al. 2008, 2016; Bindoff et al. 2019).

Results from the first 15 years of this ongoing study reinforce the importance of both aspects of long-term monitoring studies. Consider the mussel plots at Enderts Beach, one of the two instances (the other being *E. muricata* at Enderts Beach) that exhibited a significant linear change in abundance over the course of the study. Because the data were collected continuously over a long period of time, we know: 1) this population experienced only one major disturbance event, the only mussel population to do so, 2) this event occurred towards the end of the 15-year time period, and 3) abundance returned to pre-disturbance levels relatively quickly. Thus, while the mixed linear model suggested a decline in abundance, a closer look at the temporal dynamics of the population, possible because this was a long-term study, offered a different interpretation. Specifically, except for the short period encompass-

TABLE 6. Southern distributional limits and thermal tolerances of the target taxa. NI = no information.

Taxa	Southern limit	Thermal tolerance
B. glandula	Northern Baja CA[1]	33 °C (immersion)[2]
C. dalli	San Diego, CA[1]	NI
E. muricata	Northern Baja CA[3]	28 °C (immersion)[4]
F. gardneri	Pt Conception, CA[3]	23 °C (immersion)[4]
M. californianus	Southern Baja CA[1]	NI
P. limitata	Cambria, CA[1]	NI

[1]Newman and Abbott (1980); [2]Iwabuchi and Gosselin (2020); [3]Abbott and Hollenberg (1976); [4]Lüning and Freshwater (1988)

ing the disturbance/recovery event (2015 to 2018), abundances were relatively stable; abundances were no different in the short and medium time scales ANOVA analyses. Again, it was the timing of the one major disturbance event that led to the significant result. This suggests that care should be taken when using a linear model to analyze data that are either not necessarily linear or that have longer cyclical patterns (e.g., Denny and Paine 1998, Burnaford et al. 2014), which when analyzed over shorter time periods, could give alternate interpretations.

This study illustrates the importance of defining an appropriate baseline. Since baselines represent the condition against which future population change will be assessed, they should typify the average condition of the population, not an arbitrary point in time (e.g., the starting point of a project). An appropriate baseline could depend upon the question being addressed. For example, determining the effects of an oil spill could require a shorter temporal baseline than one to detect the effects of long-term climate change. We recommend that the minimum length of time needed to define an appropriate baseline, especially in a disturbance-prone community, include at least one major disturbance and recovery event. This may be taxa or site dependent; for example, based on this study, the baseline for *M. californianus* may need to be longer than one for *E. muricata*. Defining an appropriate baseline, especially one to detect longer term changes, should also consider periodic or cyclical events known to affect the intertidal communities; these include the El Nino-Southern Oscillation, the North Pacific Gyre Oscillation, and the Pacific Decadal Oscillation (e.g., Menge et al. 2009, 2011; Spiecker and Menge 2022), as well as the nodal tidal cycle (e.g., Denny and Paine 1998, Burnaford et al. 2014). While obtaining an appropriate baseline may encompass a length of time that can be both logistically and financially challenging, to assess the effects of long-term climate change, it may be necessary. Thus, there is a need for committed long-term monitoring studies, like the National Park Service Inventory and Monitoring Program.

Finally, the results from the current study support the idea that, when linked with other biological or physical measurements, long-term monitoring studies can help identify potentially important processes and mechanisms that determine population size. For example, combining the long-term abundance data with the data from the recruitment study revealed that the dynamics of the barnacle populations at the study sites were very dependent upon recruitment. Given the important role barnacles play in this system, from important prey item (e.g., Connell 1970, Spight 1982, Palmer 1984), to competitor (e.g., Choat 1977, Van Tamelen 1987), to facilitator (Dayton 1971, Farrell et al. 1991, Van Tamelen and Stekoll 1996, Berlow 1997, Kim 1997, Menge et al. 2011), fluctuations in barnacle abundance can have important consequences for the community. Similarly, by combining long-term abundance data with data on sea surface temperatures, Miner et al. (2021) were able to show that ocean temperatures play an important role in the stability of intertidal communities along the western coast of North America. Examples such as these demonstrate that, when combined with other relevant biological and physical data, long-term monitoring studies can be a powerful tool in helping further our understanding of what drives the temporal dynamics of natural populations and communities.

In conclusion, many resource managers, like those in the National Park Service, face the difficult task of both preserving natural resources and encouraging public use (e.g., recreation, fishing, etc.) of those same resources. In an environment of ever-increasing human influence, including climate change, there is a need for a more nuanced understanding of "baseline" when making management decisions (Schuurman et al. 2020). The types of information collected by long-term monitoring can help lead to better, more informed decisions about how to best achieve these often conflicting goals.

Acknowledgments

Funding for this effort was provided by the National Park Service through the Klamath Inventory and Monitoring Network, managed by Alice Chung-Maccoubrey. The principal investigator for this monitoring project is Dr. Peter Raimondi. We also thank the many non-author researchers, technicians, students, and volunteers who helped collect and manage data, including Allison Snyder, David Anderson, Heather Brown, Kyle Max, and Terri Williams from NPS, and Maya George, Melissa Douglas, Laura Anderson, Nathaniel Fletcher, Rani Gaddam, and Melissa Miner from UCSC. The manuscript was improved thanks to input from three reviewers. Authors have no conflicts of interest to declare.

Literature Cited

Abbott, I. A., and G. J. Hollenberg. 1976. Marine Aglae of California. Stanford University Press, Stanford, CA.

Ammann, K. N., and P. T. Raimondi. 2008. Long-term monitoring protocol for rocky intertidal communities of Redwood National and State Parks, California. Natural Resource Report NPS/KLMN/NRR—2008/034. National Park Service, Fort Collins, CO.

Ammann, K. N., P. T. Raimondi, and D. P. Lohse. 2017. Rocky intertidal monitoring: 2015 results from Redwood National and State Parks. Natural Resource Report NPS/KLMN/NRR—2017/1489. National Park Service, Fort Collins, CO.

Andrewartha, H. G., and L. C. Birch. 1954. The Distribution and Abundance of Animals. University of Chicago Press, Chicago, IL.

Barron, M., D. Vivian, R. Heintz, and U. H. Yim. 2020. Long-term ecological impacts from oil spills: comparison of Exxon Valdez, Hebei Spirit, and Deepwater Horizon. Environmental Science & Technology 11:6456-6467.

Bell, E. C., and J. M. Gosline. 1997. Strategies for life in flow: tenacity, morphometry, and probability of dislodgment of two *Mytilus* species. Marine Ecology Progress Series 159:197-208.

Berlow, E. L. 1997. From canalization to contingency: historical effects in a successional rocky intertidal community. Ecological Monographs 67:435-460.

Bindoff, N. L., W. W. L. Cheung, J. G. Kairo, J. Arístegui, V. A. Guinder, R. Hallberg, N. Hilmi, N. Jiao, M. S. Karim, L. Levin, S. O'Donoghue, S. R. Purca Cuicapusa, B. Rinkevich, T. Suga, A. Tagliabue, and P. Williamson. 2019. Changing ocean, marine ecosystems, and dependent communities. *In* H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, and N. M. Weyer (editors), IPCC Special Report on the Ocean and Cryosphere in a Changing Climate, Cambridge University Press, Cambridge, UK and New York, NY. Pp. 447-587.

Blanchette, C. A., B. G. Miner, and S. D. Gaines. 2002. Geographic variability in form, size and survival of *Egregia menziesii* around Point Conception, California. Marine Ecology Progress Series 239:69-82.

Broitman, B., C. Blanchette, B. Menge, J. Lubchenco, C. Krenz, M. Foley, P. Raimondi, D. Lohse, and S. Gaines. 2008. Spatial and temporal patterns of invertebrate recruitment along the West Coast of the United States. Ecological Monographs 78:403-421.

Burnaford, J., K. Nielsen, and S. Williams. 2014. Celestial mechanics affects emersion time and cover patterns of an ecosystem engineer, the intertidal kelp *Saccharina sessilis*. Marine Ecology Progress Series 509:127-136.

Burnett, N. P., and A. Belk. 2018. Compressive strength of *Mytilus californianus* shell is time-dependent and can influence the potential foraging strategies of predators. Marine Biology 165:42.

Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. Annual Review of Ecology and Systematics 27:477-500.

Carrington, E. 2002. Seasonal variation in the attachment strength of blue mussels: causes and consequences. Limnology and Oceanography 47:1723-1733.

Cavole, L., A. Demko, R. Diner, A. Giddings, I. Koester, C. Pagniello, M. L. Paulsen, A. Ramirez-Valdez, S. Schwenck, N. Yen, M. Zill, and P. Franks. 2016. Biological impacts of the 2013–2015 warm-water anomaly in the Northeast Pacific: winners, losers, and the future. Oceanography 29:273-285.

Choat, J. 1977. The influence of sessile organisms on the population biology of three species of Acmaeid limpets. Journal of Experimental Marine Biology and Ecology 26:1-26.

Collins, J. A., F. Lamy, J. Kaiser, N. Ruggieri, S. Henkel, R. D. Pol-Holz, R. Garreaud, and H. W. Arz. 2019. Centennial-scale SE Pacific sea surface temperature variability over the past 2,300 years. Paleoceanography and Paleoclimatology 34:336-352.

Connell, J. H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecological Monographs 40:49-78.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist 111:1119-1144.

Connolly, S. R., B. A. Menge, and J. Roughgarden. 2001. A latitudinal gradient in recruitment of intertidal invertebrates in the Northeast Pacific Ocean. Ecology 82:1799-1813.

Connolly, S. R., and J. Roughgarden. 1998. A latitudinal gradient in Northeast Pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. The American Naturalist 151:311-326.

Conway-Cranos, L. L. 2012. Geographic variation in resilience: an experimental evaluation of four rocky intertidal assemblages. Marine Ecology Progress Series 457:67-83.

Crane, R. L., J. L. Diaz Reyes, and M. W. Denny. 2021. Bivalves rapidly repair shells damaged by fatigue and bolster strength. Journal of Experimental Biology 224:jeb242681.

Darmaraki, S., S. Somot, F. Sevault, and P. Nabat. 2019. Past variability of Mediterranean Sea marine heatwaves. Geophysical Research Letters 46:9813-9823.

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41:351-389.

Dayton, P. K. 1973. Dispersion, dispersal, and persistence of the annual intertidal alga, *Postelsia palmaeformis* Ruprecht. Ecology 54:433-438.

Denny, M. 1995. Predicting physical disturbance: mechanistic approaches to the study of survivorship on wave-swept shores. Ecological Monographs 65:371-418.

Denny, M. W., and R. T. Paine. 1998. Celestial mechanics, sea-level changes, and intertidal ecology. Biological Bulletin 194:108-115.

Eisenlord, M. E., M. L. Groner, R. M. Yoshioka, J. Elliott, J. Maynard, S. Fradkin, M. Turner, K. Pyne, N. Rivlin, R. van Hooidonk, and C. D. Harvell. 2016. Ochre star mortality during the 2014 wasting disease epizootic: role of population size structure and temperature. Philosophical Transactions of the Royal Society B: Biological Sciences 371:20150212.

Fancy, S. G., J. E. Gross, and S. L. Carter. 2009. Monitoring the condition of natural resources in US national parks. Environmental Monitoring and Assessment 151:161-174.

Farrell, T. M., D. Bracher, and J. Roughgarden. 1991. Cross-shelf transport causes recruitment to intertidal populations in central California. Limnology and Oceanography 36:279-288.

Frölicher, T. L., E. M. Fischer, and N. Gruber. 2018. Marine heatwaves under global warming. Nature 560:360-364.

Gentemann, C., M. Fewings, and M. García-Reyes. 2017. Satellite sea-surface temperatures along the west coast of the United States during the 2014–2016 northeast Pacific marine heat wave. Geophysical Research Letters 44:312-319.

Gordon, T. A. C., H. R. Harding, K. E. Wong, N. D. Merchant, M. G. Meekan, M. I. McCormick, A. N. Radford, and S. D. Simpson. 2018. Habitat degradation negatively affects auditory settlement behavior of coral reef fishes. Proceedings of the National Academy of Sciences 115:5193-5198.

Guichard, F., P. Halpin, G. Allison, J. Lubchenco, and B. Menge. 2003. Mussel disturbance dynamics: signatures of oceanographic forcing from local interactions. The American Naturalist 161:889-904.

Harger, R., and D. Landenberger. 1971. The effect of storms as a density dependent mortality factor on population of sea mussels. Veliger 14:195-201.

Harley, C. D. G. 2008. Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores. Marine Ecology Progress Series 371:37-46.

Harley, C. D. G., A. R. Hughes, K. M. Hultgren, B. G. Miner, C. J. B. Sorte, C. S. Thornber, L. F. Rodriguez, L. Tomanek, and S. L. Williams. 2006. The impacts of climate change in coastal marine systems. Ecology Letters 9:228-241.

Harley, C. D. G., and R. T. Paine. 2009. Contingencies and compounded rare perturbations dictate sudden distributional shifts during periods of gradual climate change. Proceedings of the National Academy of Sciences 106:11172-11176.

Hawkins, E., R. S. Smith, J. M. Gregory, and D. A. Stainforth. 2016. Irreducible uncertainty in near-term climate projections. Climate Dynamics 46:3807-3819.

Hawkins, S. J., P. J. Moore, M. T. Burrows, E. Poloczanska, N. Mieszkowska, R. J. H. Herbert, S. R. Jenkins, R. C. Thompson, M. J. Genner, and A. J. Southward. 2008. Complex interactions in a rapidly changing world: responses of rocky shore communities to recent climate change. Climate Research 37:123-133.

Hughes, T. P., J. T. Kerry, M. Álvarez-Noriega, J. G. Álvarez-Romero, K. D. Anderson, A. H. Baird, R. C. Babcock, M. Beger, D. R. Bellwood, R. Berkelmans, T. C. Bridge, I. R. Butler, M. Byrne, N. E. Cantin, S. Comeau, S. R. Connolly, G. S. Cumming, S. J. Dalton, G. Diaz-Pulido, C. M. Eakin, W. F. Figueira, J. P. Gilmour, H. B. Harrison, S. F. Heron, A. S. Hoey, J. P. A. Hobbs, M. O. Hoogenboom, E. V. Kennedy, C. Kuo, J. M. Lough, R. J. Lowe, G. Liu, M. T. McCulloch, H. A. Malcolm, M. J. McWilliam, J. M. Pandolfi, R. J. Pears, M. S. Pratchett, V. Schoepf, T. Simpson, W. J. Skirving, B. Sommer, G. Torda, D. R. Wachenfeld, B. L. Willis, and S. K. Wilson. 2017. Global warming and recurrent mass bleaching of corals. Nature 543:373-377.

Iacarella, J. C., I. C. Davidson, and A. Dunham. 2019a. Biotic exchange from movement of 'static' maritime structures. Biological Invasions 21:1131-1141.

Iacarella, J. C., D. Saheed, A. Dunham, and N. C. Ban. 2019b. Non-native species are a global issue for marine protected areas. Frontiers in Ecology and the Environment 17:495-501.

Iwabuchi, B. L., and L. A. Gosselin. 2020. Implications of acute temperature and salinity tolerance thresholds for the persistence of intertidal invertebrate populations experiencing climate change. Ecology and Evolution 10:7739-7754.

Kim, J. H. 1997. The role of herbivory, and direct and indirect interactions, in algal succession. Journal of Experimental Marine Biology and Ecology 217:119-135.

Kim, J. H., and R. F. DeWreede. 1996. Effects of size and season of disturbance on algal patch recovery in a rocky intertidal community. Marine Ecology Progress Series 133:271-135.

Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation, and community structure. Proceedings of the National Academy of Sciences 71:2744-2747.

Lewis, J. P., J. H. Tarnecki, S. B. Garner, D. D. Chagaris, and W. F. Patterson. 2020. Changes in reef fish community structure following the Deepwater Horizon oil spill. Scientific Reports 10:1-13.

Lindenmayer, D. B., and G. E. Likens. 2010. The science and application of ecological monitoring. Biological Conservation 143:1317-1328.

Lindenmayer, D. B., G. E. Likens, A. Andersen, D. Bowman, C. M. Bull, E. Burns, C. R. Dickman, A. A. Hoffmann, D. A. Keith, M. J. Liddell, A. J. Lowe, D. J. Metcalfe, S. R. Phinn, J. Russell-Smith, N. Thurgate, and G. M. Wardle. 2012. Value of long-term ecological studies. Austral Ecology 37:745-757.

Lovett, G. M., D. A. Burns, C. T. Driscoll, J. C. Jenkins, M. J. Mitchell, L. Rustad, J. B. Shanley, G. E. Likens, and R. Haeuber. 2007. Who needs environmental monitoring? Frontiers in Ecology and the Environment 5:253-260.

Lüning, K., and W. Freshwater. 1988. Temperature tolerance of Northeast Pacific marine algae. Journal of Phycology 24:310-315.

Magnuson, J. J., and C. J. Bowser. 1990. A network for long-term ecological research in the United States. Freshwater Biology 23:137-143.

Magurran, A. E., S. R. Baillie, S. T. Buckland, J. M. Dick, D. A. Elston, E. M. Scott, R. I. Smith, P. J. Somerfield, and A. D. Watt. 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. Trends in Ecology & Evolution 25:574-582.

McCauley, D. J., M. L. Pinsky, S. R. Palumbi, J. A. Estes, F. H. Joyce, and R. R. Warner. 2015. Marine defaunation: animal loss in the global ocean. Science 347:1255641.

Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecological Monographs 64:250-286.

Menge, B. A., E. B. Cerny-Chipman, A. Johnson, J. Sullivan, S. Gravem, and F. Chan. 2016. Sea star wasting disease in the keystone predator *Pisaster ochraceus* in Oregon: insights into differential population impacts, recovery, predation rate, and temperature effects from long-term research. PLOS One 11:e0153994.

Menge, B. A., F. Chan, K. J. Nielsen, E. D. Lorenzo, and J. Lubchenco. 2009. Climatic variation alters supply-side ecology: impact of climate patterns on phytoplankton and mussel recruitment. Ecological Monographs 79:379-395.

Menge, B. A., T. C. Gouhier, T. Freidenburg, and J. Lubchenco. 2011. Linking long-term, large-scale climatic and environmental variability to patterns of marine invertebrate recruitment: toward explaining "unexplained" variation. Journal of Experimental Marine Biology and Ecology 400:236-249.

Miner, C. M., J. L. Burnaford, R. F. Ambrose, L. Antrim, H. Bohlmann, C. A. Blanchette, J. M. Engle, S. C. Fradkin, R. Gaddam, C. D. G. Harley, B.G. Miner, S. N. Murray, J. R. Smith, S. G. Whitaker, and P. T. Raimondi. 2018. Large-scale impacts of sea star wasting disease (SSWD) on intertidal sea stars and implications for recovery. PLOS One 13:e0192870.

Miner, C. M., J. L. Burnaford, K. N. Ammann, B. H. Becker, S. C Fradkin, S. Osterman-Kelm, J. R. Smith, S. G. Whitacker, and P. T. Raimondi. 2021. Latitudinal variation in long-term stability of North American rocky intertidal communities. Journal of Animal Ecology 90: 2077-2093.

Molnar, J. L., R. L. Gamboa, C. Revenga, and M. D. Spalding. 2008. Assessing the global threat of invasive species to marine biodiversity. Frontiers in Ecology and the Environment 6:485-492.

Moritsch, M. M. 2021. Expansion of intertidal mussel beds following disease-driven reduction of a keystone predator. Marine Environmental Research 169:105363.

Newman, W. A., and D. P. Abbott. 1980. Cirripedia: the barnacles. *In* R. H. Morris, D. P. Abbott, and E.C. Haderlie (editors), Intertidal Invertebrates of California, Stanford University Press, Stanford, CA. Pp 504-535.

Oliver, E. C. J., J. A. Benthuysen, N. L. Bindoff, A. J. Hobday, N. J. Holbrook, C. N. Mundy, and S. E. Perkins-Kirkpatrick. 2017. The unprecedented 2015/16 Tasman Sea marine heatwave. Nature Communications 8:16101.

Paine, R. T. 1966. Food web complexity and species diversity. The American Naturalist 100:65-75.

Paine, R. T. 1974. Intertidal community structure. Oecologia 15:93-120.

Paine, R. T. 1979. Disaster, catastrophe, and local persistence of the Sea Palm *Postelsia palmaeformis*. Science 205:685-687.

Paine, R. T. 1988. Habitat suitability and local population persistence of the Sea Palm *Postelsia palmaeformis*. Ecology 69:1787-1794.

Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs 51:145-178.

Palmer, M. A. 1984. Invertebrate drift: behavioral experiments with intertidal meiobenthos. Marine Behaviour and Physiology 10:235-253.

Peterson, C. H., S. D. Rice, J. W. Short, D. Esler, J. L. Bodkin, B. E. Ballachey, and D. B. Irons. 2003. Long-term ecosystem response to the Exxon Valdez oil spill. Science 302:2082-2086.

Piepho, H. P., and J. O. Ogutu. 2002. A simple mixed model for trend analysis in wildlife populations. Journal of Agricultural, Biological, and Environmental Statistics 7:350-360.

Robles, C., R. Sherwood-Stephens, and M. Alvarado. 1995. Responses of a key intertidal predator to varying recruitment of its prey. Ecology 76:565-579.

Sagarin, R., and A. Pauchard. 2010. Observational approaches in ecology open new ground in a changing world. Frontiers in Ecology and the Environment 8:379-386.

Satterthwaite, F. E. 1946. An approximate distribution of estimates of variance components. Biometrics Bulletin 2:110-114.

Schuurman, G., C. Hawkins-Hoffman, D. Cole, D. Lawrence, J. Morton, D. Magness, A. Cravens, S. Covington, R. O'Malley, and N. Fisichelli. 2020. Resist-accept-direct (RAD)—a framework for the 21st-century natural resource manager. Natural Resource Report. NPS/NRSS/CCRP/NRR—2020/ 2213. National Park Service. Fort Collins, CO.

Sebens, K. P., and J. R. Lewis. 1985. Rare events and population structure of the barnacle *Semibalanus cariosus* (Pallas, 1788). Journal of Experimental Marine Biology and Ecology 87:55-65.

Shanks, A. L., and W. G. Wright. 1986. Adding teeth to wave action: the destructive effects of wave-borne rocks on intertidal organisms. Oecologia 69:420-428.

Simberloff, D. 2013. Biological invasions: prospects for slowing a major global change. Elementa: Science of the Anthropocene 1:000008.

Sousa, W. P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecological Monographs 49:227-254.

Sousa, W. P. 1980. The responses of a community to disturbance: the importance of successional age and species' life histories. Oecologia 45:72-81.

Sousa, W. P. 1984a. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:353-391.

Sousa, W. P. 1984b. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. Ecology 65:1918-1935.

Sousa, W. P., S. C. Schroeter, and S. D. Gaines. 1981. Latitudinal variation in intertidal algal community structure: the influence of grazing and vegetative propagation. Oecologia 48:297-307.

Spiecker, B. J., and B. A. Menge. 2022. El Niño and marine heatwaves: Ecological impacts on Oregon rocky intertidal kelp communities at local to regional scales. Ecological Monographs 92:e1504.

Spight, T. M. 1982. Population sizes of two marine snails with a changing food supply. Journal of Experimental Marine Biology and Ecology 57:195-217.

Starcevich, L. A. H., K. A. Irvine, and A. M. Heard. 2018a. Impacts of temporal revisit designs on the power to detect trend with a linear mixed model: an application to long-term monitoring of Sierra Nevada lakes. Ecological Indicators 93:847-855.

Starcevich, L. A. H., T. McDonald, A. Chung-MacCoubrey, A. Heard, J. C. Nesmith, H. Coletti, and T. Philippi. 2018b. Methods for estimating trend in binary and count response variables from complex survey designs. Natural Resource Report NPS/ KLMN/NRR—2018/1641. National Park Service. Fort Collins, CO.

Suchanek, T. 1985. Mussels and their role in structuring rocky shore communities. *In* P. G Moore and R. Seed (editors), The Ecology of Rocky Coasts, Hodder and Stoughton, London. Pp. 70-96.

Sumaila, U. R., and T. C. Tai. 2020. End overfishing and increase the resilience of the ocean to climate change. Frontiers in Marine Science 7:523.

Sunday, J. M., A. E. Bates, and N. K. Dulvy. 2012. Thermal tolerance and the global redistribution of animals. Nature Climate Change 2:686-690.

Van Tamelen, P. G. 1987. Early successional mechanisms in the rocky intertidal: the role of direct and indirect interactions. Journal of Experimental Marine Biology and Ecology 112:39-48.

Van Tamelen, P. G., and M. S. Stekoll. 1996. The role of barnacles in recruitment and subsequent survival of the brown alga, *Fucus gardneri* (Silva). Journal of Experimental Marine Biology Ecology 208:227-238.

Witman, J. D., and T. H. Suchanek. 1984. Mussels in flow: drag and dislodgement by epizoans. Marine Ecology Progress Series 16:259-268.

Weitzman, B., B. Konar, K. Iken, H. Coletti, D. Monson, R. Suryan, T. Dean, D. Hondolero, and M. Lindeberg. 2021. Changes in rocky intertidal community structure during a marine heatwave in the Northern Gulf of Alaska. Frontiers in Marine Science 8:556820.

Submitted 30 November 2021
Accepted 03 August 2022