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Soundscapes indicate kelp forest condition

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ABSTRACT: Soundscapes are promising indicators of marine habitat condition, yet this approach remains untested in many ecosystems, and soundscape–ecological relationships remain unclear. In this study, we analyzed soundscapes in kelp forest habitats off the coast of California, USA, in Channel Islands National Park. We investigated if (1) soundscape features correlated with ecological variables and (2) these features differed inside and outside of marine protected areas (MPAs). We recorded 1 min every 15 min at 5 sites from 12 May to 23 June 2018. Three sites were in MPAs with high kelp cover and low urchin density, while 2 were in adjacent, unprotected habitats with low kelp cover and high urchin density. To analyze the data, we calculated soundscape features using detection algorithms and acoustic indices, which we then correlated with annual ecological data from 2016 to 2018. We found that drivers of regime shifts in kelp forests, i.e. sea urchin density, kelp cover, and fish diversity, were significantly related to soundscape features. Sea urchin density was positively correlated and kelp cover negatively correlated with the rate of shrimp snaps. Fish species richness and abundance were positively correlated with the intensity and diel dynamics in the low-frequency bands that contained most fish vocalizations. This study demonstrates that marine soundscapes indicate the condition of kelp forests, which are vulnerable to destruction from urchin overgrazing. If marine soundscapes can reliably indicate the status of ecological drivers, then this approach could be a valuable complement to diver surveys in fully assessing marine ecosystem health.

KEY WORDS: Marine soundscape · Acoustic monitoring · Soundscape ecology · Ecoacoustics · Kelp forest · Regime shift analysis

1. INTRODUCTION

Human activities are causing large, abrupt, and enduring changes in the structure and function of ecosystems, also known as regime shifts (Scheffer & Carpenter 2003). Generally, habitats that have undergone regime shifts support less biodiversity and provide fewer ecosystem services (Folke et al. 2004). While the ecological theory of regime shifts is becoming more refined, ways to empirically measure regime shifts remain elusive (Quinlan et al. 2016). To do so in a real-world context, it is necessary not only to identify meaningful variables to quantify, but also to develop a measurement system that can obtain this information at appropriate spatial and temporal scales at low cost. Developing and implementing

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such methods would improve the management and conservation of systems on the brink, especially if they also provide insights into the drivers of regime shifts (Carpenter et al. 2011, Anderson 2018).

Soundscapes (sensu Pijanowski et al. 2011a,b) are emerging as a potential stream of information from which we can measure habitat condition and potentially also regime shifts (Rossi et al. 2017). Soundscape ecology originated in the terrestrial realm (Pijanowski et al. 2011b), but holds particular promise for surveying freshwater (Gottesman et al. 2020) and marine ecosystems (Miksis-Olds et al. 2018), which can be impractical to access regularly. While most marine monitoring programs perform biodiversity surveys once or twice per year, passive acoustic recorders can collect soundscape data continuously for months or years (Staaterman et al. 2014). This fine-scale temporal resolution improves the assessment of rare and cryptic species (Wade et al. 2006, Staaterman et al. 2017), understanding temporal dynamics (McWilliam et al. 2018), and evaluation of disturbance impacts (Locascio & Mann 2005, Biggs et al. 2018).

In this study, we tested whether soundscape recording and analysis could indicate the condition of kelp forests off the coast of California, USA, in the Channel Islands National Park. Kelp forests (Order: Laminariales) are structurally complex, highly productive, and biologically diverse ecosystems that form on rocky marine coastlines in temperate and sub-arctic regions (Steneck et al. 2002). However, stressors such as overharvesting, pollution, and disease can trigger regime shifts in kelp forests; these degraded states generally support less biodiversity, sequester less carbon, and provide scant ecosystem services (Krumhansl et al. 2016, Miller et al. 2018). One driver of regime shifts in kelp forests is the removal of apex predators. When predators become scarce, populations of prey species, like sea urchins, increase rapidly. At high densities, sea urchins can exhaust their normal food supply and start consuming kelp holdfasts, which causes entire plants to drift away (Kriegisch et al. 2019). In a short period of time, urchins can destroy large tracts of kelp forest, at which point the system shifts into an urchin-dominated barren from which it is difficult to recover.

Regional drivers rather than global forces dictate the direction and magnitude of recent changes to kelp forest systems (Krumhansl et al. 2016). No-take marine reserves have increased the density, diversity, and size of targeted fauna (such as California spiny lobster *Panulirus interruptus* and California sheephead *Semicossyphus pulcher*), decreased urchin density, and increased kelp cover by correcting the trophic imbalance that results from overharvesting (Caselle et al. 2015). Given the impact of local stressors and management decisions on kelp forest condition, developing ways to assess kelp forest and regime shift drivers at local to regional scales could improve conservation outcomes. Diver surveys are instrumental for this reason, but they are costly and limited across spatial and temporal scales (Dayton et al. 1998). Satellite remote sensing can measure kelp extent and biomass across entire coastlines, although it only detects kelp near the surface and provides limited information on the mechanisms dictating kelp dynamics (Nijland et al. 2019). A remote sensing approach that measures relevant ecological factors at scale would fill the gap between these 2 existing approaches.

1.1. Soundscapes as indicators of biodiversity and ecosystem health

Numerous taxa within the kelp forest community produce sound during their everyday lives, providing an opportunity to evaluate the status of regime shifts in a non-invasive manner (see Section S1 in Supplement 1 at www.int-res.com/articles/suppl/m654p035_supp1.pdf for review of soniferous taxa in this kelp forest system).

Several recent studies have demonstrated strong positive relationships between soundscapes and marine habitat condition (Bertucci et al. 2016, Coquereau et al. 2017, Gordon et al. 2018), fish diversity (Harris et al. 2016), and fish abundance (Rowell et al. 2017). One emerging pattern is that the low and high portions of the soundscape contain information on different ecological dimensions. Fish generally vocalize in the low-frequency portion of the soundscape (<1000 Hz; Staaterman et al. 2017, Lindseth & Lobel 2018). Acoustic metrics calculated on the low-frequency portion have correlated with fish diversity and density in coral reefs in Panama (Kennedy et al. 2010), Hawaii (Kaplan et al. 2015, Freeman & Freeman 2016), and French Polynesia (Bertucci et al. 2016), as well as on rocky reefs in New Zealand (Harris et al. 2016) and France (Desiderà et al. 2019). Measurements of the high-frequency portion of the soundscape (>1000 Hz), in which many invertebrates produce sound (Bohnenstiehl et al. 2016), have correlated with invertebrate richness and abundance in maerl beds off the coast of France (Coquereau et al. 2017) and invertebrate density in Panama (Kennedy et al. 2010).

Beyond indexing taxonomic diversity, low- and high-frequency portions of the soundscape have also indicated habitat condition, including coral cover (Kennedy et al. 2010, Bertucci et al. 2016, Freeman & Freeman 2016), degradation level (Lillis et al. 2014, Rossi et al. 2017, Gordon et al. 2018), habitat type (Radford et al. 2010), and ecosystem functions (Elise et al. 2019). However, other studies that have employed similar measurements in similar ecosystems have found no such correlations between soundscapes and these dimensions of biodiversity and habitat condition. For example, Freeman & Freeman (2016) found a negative relationship between habitat condition and the intensity of high-frequency sound levels. Additionally, anthropogenic noise can obfuscate these soundscape–ecological relationships by influencing soundscape metrics, especially in areas with high shipping traffic. Therefore, there are still sizeable knowledge gaps regarding (1) the relationships between soundscape and ecological variables, (2) the consistency of these relationships under different anthropogenic noise conditions, and (3) the mechanisms underlying these relationships. Our study sought to address these gaps by identifying soundscape–ecological relationships associated with regime shifts in kelp forests and the relevant mechanisms. To date, few studies have explored soundscape indicators of regime shifts in marine or terrestrial systems (but see Rossi et al. 2017 and Gordon et al. 2018).

1.2. Research questions

In this study, we addressed 2 principal questions: (1) Do soundscape features correlate with ecological drivers of regime shift in kelp forests? (2) Do soundscapes differ inside and outside of marine protected areas, where there is a known difference in habitat condition? We were most interested in identifying acoustic features that linked with fish diversity, urchin abundance, and kelp cover, as this information may provide information on the dynamics of regime shift drivers. We hypothesized that the intensity and dynamics of the low- and high-frequency portions of the soundscape would be positively correlated with fish, invertebrates, and kelp cover and negatively with urchin density due to increased abundance of soniferous fish and invertebrate species in more forested areas. In this way, we predicted that marine protected areas (MPAs) would have more intense and more temporally dynamic low- and high-frequency portions of the soundscape than unprotected areas.

2. MATERIALS AND METHODS

2.1. Study area

This study was carried out in Channel Islands National Park (CINP), which is located off the coast of southern California. The park encompasses the 5 northernmost of the 8 California Channel Islands (Fig. 1). The boundary of CINP extends ~1.6 km (1 mile) from the shores of the islands. As of 1968, CINP contained 1/3 of California's kelp forests (Davies 1968), and aerial surveys from 1989–2016 show that this ratio is still accurate (Shuman 2018). More than 1000 species of macro-flora and -fauna depend on these forests for food, shelter, and substrate (Davis et al. 1996). The high biodiversity of the Channel Islands is due to their oceanographic location at the confluence of 2 major currents, in a region of persistent upwelling of cool, nutrient-rich water. However, decades of overfishing and harvesting have led to a steep decline in targeted fish and invertebrate species and, as a result, habitat degradation. In 2003, in response to the observed steady degradation of kelp forests and fish populations within the park, a network of 13 MPAs was established by the State of California (Gleason et al. 2010). Research based on diver surveys has shown that these reserves increased the biomass and diversity of targeted fish and invertebrate species (Caselle et al. 2015), increased kelp cover, and reduced urchin density, and ultimately improved the resilience and recovery of these kelp forests (Caselle et al. 2018).

2.2. Biodiversity data collection

Biodiversity data were collected as part of the Channel Islands Kelp Forest Monitoring Program (KFMP), one of the oldest ongoing marine monitoring programs in the USA, which initially started in 1982–1985 with 16 sites (Davis et al. 1996). The KFMP was expanded following the establishment of the Channel Islands MPAs in 2003 to 33 sites. The KFMP monitors each site once every summer by conducting diver surveys along 100 m permanent transects. The 5 acoustic recorders were deployed at 5 of the 33 sites, adjacent to the 100 m permanent transects. We utilized 5 different survey methods to assess the diversity and abundance of fish, invertebrate, and kelp species. Kelp abundances (percent cover) were acquired via the KFMP random point contact survey (Kushner & Sprague 2018). Urchin densities were acquired from the KFMP 1 m quadrat survey and KFMP band transect survey following

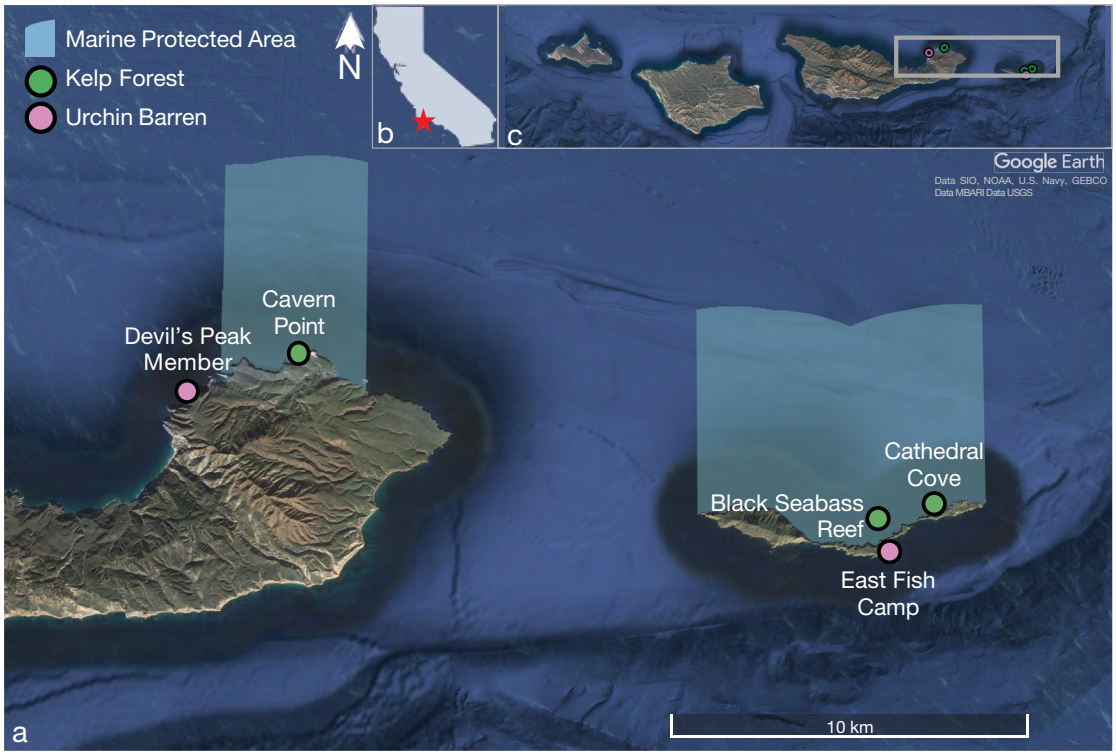

Fig. 1. (a) Five study sites in Channel Islands National Park, California (USA): Cathedral Cove, Cavern Point, Black Seabass Reef, Devil's Peak Member, and East Fish Camp. (b) Location of the Channel Islands in California. (c) Four of the 5 southern Channel Islands

the procedures of Kushner & Sprague (2018). Invertebrate abundances were acquired through integrating the KFMP 1 m quadrat survey, KFMP 5 m quadrat survey, and KFMP band transect survey (Kushner & Sprague 2018). Fish species abundances were acquired via the KFMP visual roving diver fish counts (Kushner et al. 2013). We utilized surveys from 2016 to 2018 to reduce any biasing effects of spatiotemporal sampling differences between survey years so that the biodiversity data were more robust representations of recent kelp forest condition. We aggregated species-specific count data to generate the following 6 biodiversity metrics that summarized taxonomic groups of interest: kelp cover, urchin density, invertebrate density, invertebrate species richness, fish abundance, and fish species richness. For density and count values, we computed the means over these 3 years. For fish and invertebrate species richness, we pooled values across years, and calculated the total number of fish and invertebrate species identified during this period.

2.3. Acoustic data collection

We collected acoustic recordings over a 42 d period from 12 May to 23 June 2018 at 5 sites: 2 on Santa Cruz Island and 3 on Anacapa Island. Both islands have MPAs on their northern coasts that were established in 2003. One site, Cathedral Cove, had been protected since 1978. Recorders were deployed inside and adjacent to these MPAs (Table 1). Recorders were a minimum distance of 1.5 km from other recorders and 1.0 km from MPA boundaries, except for East Fish Camp, an unprotected site that was acousti-

Table 1. Information on the 5 study sites in Channel Islands National Park, California (USA), including their locations, whether or not they occurred within a marine protected area (MPA), and the year in which the MPA was established. NA: not applicable

Site	Island	Lat. (°N)	Long. (°W)	Depth (m)	MPA	Year protected
Cathedral Cove	Anacapa	34.016	119.372	8	Inside	1978
Cavern Point	Santa Cruz	34.054	119.567	12	Inside	2003
Black Seabass Reef	Anacapa	34.013	119.389	16	Inside	2003
Devil's Peak Member	Santa Cruz	34.045	119.601	12	Outside	NA
East Fish Camp	Anacapa	34.005	119.386	12	Outside	NA

cally buffered from other recorders and MPAs because it was the only recorder on the south side of the island chain. We selected sites with similar bathymetry (rocky reef complex), biogeography, and depth (Table 2) in order to better measure the ecological differences caused by habitat condition and protection status. Recordings were collected with SoundTrap 300 STD (Ocean Instruments NZ) underwater sound recorders, which had a working frequency range from 20 Hz–60 kHz. Four of the 5 units had 256 GB of storage and an external battery pack. They recorded 5 min every 15 min, with a sampling rate of 48 kHz, a bit depth of 16 bits, and a gain setting of 'high.' These recordings were cropped to the first minute. The fifth unit that was deployed at Cathedral Cove had 128 GB of storage with no external battery pack. This unit recorded 1 min every 15 min, with a sampling rate of 96 kHz, which was selected in order to assess the prevalence of ultrasonic sounds, and was down-sampled to 48 kHz prior to this analysis. The shorter time recording interval was to compensate for the smaller storage capacity and lack of external battery pack, which limited the amount of data that this unit could record. It had the same bit depth and gain settings as the other recorders. Recorders were enclosed in a PVC housing, fastened to a lead block, and installed on the seafloor or on top of rocks with the hydrophone approximately 15 cm above the substrate (Fig. 2), although at some sites, the recorders were placed on top of a large rock. While we considered other deployment designs in which the hydrophone was suspended at least 1 m above the substrate, installing the unit closer to the seafloor was preferable due to the dynamic and high-energy wave conditions in these shallow-water habitats.

2.4. Soundscape analysis

To assess kelp forest soundscapes, we calculated 9 soundscape variables using 3 complimentary acoustic analyses that measured different dimensions of biological sounds within these sites, including (1) shrimp snaps (2–20 kHz), (2) low-frequency (20–80 Hz; 50–750 Hz) and high-frequency (2–24 kHz) sound levels, and (3) diel dynamics of these soundscape variables. Our dataset consisted of 20 160 recordings that were 56 s in length (96 recordings per day × 42 d × 5 sites). Prior to analysis, we visually and aurally reviewed the recordings and removed 851 files that contained noise from nearby boats (4 % of dataset). East Fish Camp had 318 files containing boat noise, followed by Cathedral Cove (272), Black Seabass Reef (107), Devil's Peak Member (85), and Cavern Point (69). Example spectrograms of files containing boat noise are shown in Fig. S1 in Supplement 1. We linearly interpolated these missing values using the function 'na.interpolation' in the R package 'imputeTS' v.3.0 (Moritz & Bartz-Beielstein 2017), because a subsequent analysis required complete time series and because there were negligible differences on soundscape metrics between interpolating and leaving missing values as 'NA.'

2.4.1. Shrimp snaps

We detected the number of shrimp snaps in the recordings by employing a shrimp snap detector following the methods of Bohnenstiehl et al. (2016). Prior to analysis, we band-pass filtered recordings from 2–20 kHz and trimmed them to the first 30 s. We then performed a shrimp snap detector function that correlated windowed selections of the time-series with the stereotypical shape of a snapping shrimp snap that was generated in Matlab (Bohnenstiehl et al. 2016). Correlations above 0.75 were considered successful detections. We visually verified the accuracy of this detector by inspecting spectrograms and oscillograms annotated with snap detections. To measure shrimp snaps only produced within approximately 100 m of the hydrophones and the biodiver-

Table 2. Six biodiversity variables obtained from Kelp Forest Monitoring Program surveys conducted from 2016 to 2018. MPA: marine protected area (year of establishment given in parentheses)

Site	Fish abundance (n)	Fish species richness (n)	Kelp cover (%)	Urchin density (m^{-2})	Invertebrate density (m^{-2})	Invertebrate richness (n)
Cathedral Cove (MPA 1978)	1285	30	34.8	0.4	1.6	11
Cavern Point (MPA 2003)	1132	31	23.5	2.3	1.4	14
Black Seabass Reef (MPA 2003)	1195	27	7.7	4	1.2	12
Devil's Peak Member (Unprotected)	1244	33	0	10.5	3.6	13
East Fish Camp (Unprotected)	620	20	0.1	26.8	2.6	15

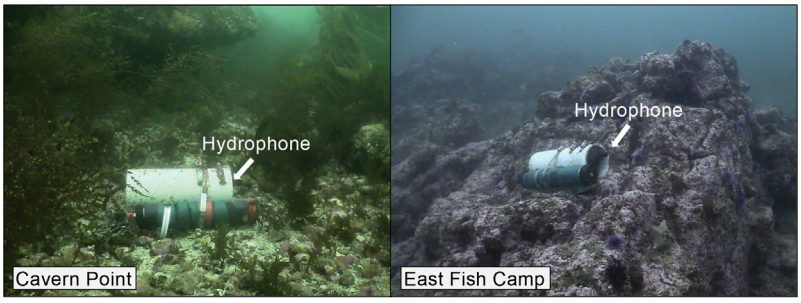

Fig. 2. SoundTrap recorder with external battery pack deployed at Cavern Point at Santa Cruz Island (protected kelp forest site) and East Fish Camp at Anacapa Island (unprotected urchin barren site). White arrows point to the hydrophone element of each recorder

sity transects, we retained snaps that had a root mean squared sound pressure level (SPL_{rms}) of at least 130 dB re 1 µPa^2 (2–20 kHz). We determined this threshold by modeling the propagation of these sounds based on the estimated source level of shrimp snaps and how sound spreads in this shallow water habitat. The source level (SPL_{rms}) of shrimp snaps was determined to be approximately 150 dB re 1 µPa^2 (the 99th percentile SPL_{rms} from 2–20 kHz for detected snaps was 150.3 dB re 1 µPa^2 in the 2–20 kHz frequency band). We used the cylindrical geometric spreading model that is commonly applied in coastal ocean acoustics (Urick 1983, Lillis et al. 2014). We applied the equation $SL - 10 \times \log_{10}(d) = RL$, where SL is the snap source level (150 dB), d is the distance between the sound source and the receiver (100 m), and RL (also SPL_{rms}) is the received level of a snap that was produced at 100 m. The received level threshold of 130 dB also exceeded the ambient noise floor (mean SPL_{rms} from 2–20 kHz = 116.2 dB) by approximately 14 dB. In addition to calculating the number of snaps min^{-1}, we also measured the peak frequency of each snap to try to better understand the biological and environmental effects that could cause differences in snapping shrimp activity across these 5 sites.

2.4.2. Low- and high-frequency sound levels

To measure the intensity of low- and high-frequency sound levels, we calculated SPLs (dB re 1 µPa^2) across 3 different frequency bands. After aurally and visually reviewing recordings and their spectrograms, as well as inspecting long-term spectrograms, we selected 3 frequency bands (20–80 Hz, 50–750 Hz and 2–24 kHz) which contained most biological sounds and partitioned them into broad groups containing different sound producers. The low-frequency bands (20–80 and 50–750 Hz) contained sounds from fish, marine mammals, and invertebrates. We measured both of these bands because the 50–750 Hz band was dominated at some sites by the plainfin midshipman *Porichthys notatus*, which had a fundamental frequency of approximately 100 Hz and strong harmonics to approximately 700 Hz. The 20–80 Hz frequency band contained sounds from larger-bodied fish and organisms that produced low-frequency sounds associated with body movement against substrate. The high-frequency band (2–24 kHz) contained sounds from snapping shrimp, echolocating dolphins, and potentially other soniferous invertebrates (Lillis et al. 2014, Staaterman et al. 2017).

We calculated calibrated SPLs within these frequency bands using custom scripts written in R 3.5.2 and the hydrophone sensitivities provided by SoundTrap for each hydrophone (R Core Team 2018; see Section S3 in Supplement 1 for how to access computer codes used in this study through GitHub). To do so, we first converted recordings into the spectral domain using a discrete Fourier transform with a window length of 8192 samples, 0% overlap, and a Hann window. For each recording and frequency band, we calculated the upper quartile SPL value, which we selected because it measured continuous biological choruses as well as more discrete sound events better than commonly used metrics such as root mean square or median amplitude. Root mean square amplitude was overly sensitive to short-duration, high-amplitude sounds (some over 150 dB) that confounded the measurement of all other biological patterns. The median amplitude was more reflective of ambient soundscape levels, which were influenced by the noise from far away ships. More details of the selection procedure are provided in Section S4 in Supplement 1, and in Fig. S2 we provide visualizations to illustrate the utility of the upper quartile SPL value for measuring biological components of these kelp forest soundscapes.

2.4.3. Diel dynamics of soundscape variables

We measured the daily variation of snap rates and the low-and high-frequency sound levels, since the magnitude of diel soundscape patterns was correlated with fish density (low-frequency diel pattern) and coral cover (high-frequency diel pattern) in pre-

vious studies (Kaplan et al. 2018). Peak frequency was omitted, as we did not expect its diel dynamics to yield meaningful information pertaining to our research questions. To measure the magnitude of the diel trends in these soundscapes, we first utilized the 'decompose' function in the R package 'stats' to decompose the time series of 4 of the 5 soundscape variables (excluding peak snap frequency) into their seasonal (e.g. diel) trend, and irregular components (R Core Team 2018). We extracted the diel component, smoothed it with a 4-point moving average to indicate hourly levels, and cropped it to 1 d length (96 values). To quantify the 'magnitude' of the daily variation, we plotted the diel pattern, and calculated the area above and below its mean using the 'AUC' function from the 'DescTools' package in R, with the assumption that more dynamic sites would have a greater area under the curve (AUC) measurement (Kaplan et al. 2018). AUC values in this study are unitless and should be interpreted relative to values from other sites.

2.4.4. Long-term dynamics of soundscape variables

To better visualize and understand the biological sounds that influenced the soundscape metrics, we generated long-term spectrograms. We did so by calculating the power spectral density (PSD) of each recording using a window length of 8192, a Hann window, and 0% overlap. For each recording, we calculated the 75th percentile PSD value. We then stitched together these PSD values using custom scripts in R to create a long-term spectrogram for each site.

2.5. Statistical analysis

2.5.1. Correlation between soundscapes and drivers of kelp forest regime shifts

We conducted correlation tests between soundscape variables (n = 9) and biological variables (n = 6) associated with kelp forest regime shifts to test our predictions that the intensity and dynamics of the low- and high-frequency portions of the soundscape would be positively correlated with fish, invertebrate, and kelp cover diversity and negatively correlated with urchin density (see Fig. 6 for list of soundscape and biological variables). Instead of testing all possible combinations between these variables, to avoid generating spurious results, we only computed tests for combinations for which we predicted a relationship would exist *a priori*. We predicted that fish density and abundance would be positively correlated with the 4 low-frequency sound variables. We also predicted that kelp cover, invertebrate density, and invertebrate richness would be positively correlated with high-frequency variables (including shrimp-derived metrics), while urchin density would be negatively correlated with high-frequency variables. To prepare data for these correlation tests, we calculated the mean values of the band-level SPLs, shrimp snap rates, and shrimp peak frequency values (4032 values per variable), to obtain 1 value for each site. We conducted Pearson correlation tests for variable combinations that met assumptions. We conducted Shapiro-Wilk tests for normality, Breusch-Pagan tests for heteroscedasticity (though with only 5 points, checking for homogeneous variance was challenging), and visually checked for linearity. Of the 28 variable combinations, 10 did not pass the linearity assumption, and so we did not report on these results. To satisfy the assumptions, some variables first required transformation. 'Fish abundance' first needed to be squared in order to meet the normality assumption. 'Urchin density' needed to be $\log_{10}(x)$ transformed to meet the linearity assumption. We considered correlations significant at $p < 0.1$ and the correlation coefficient $(r) > 0.85$ in order to discuss these potentially important soundscape–ecological relationships that appeared strong in this kelp forest system despite the limited sample size (n = 5).

2.5.2. Effect of MPAs on biological and soundscape components

To determine if soundscapes and biological variables differed depending on protection status, we computed linear models in R using the 'lm' function in the 'stats' package (R Core Team 2018). Prior to performing these models, we reduced the dimensionality of the soundscape and biological variables by conducting separate PCAs on the scaled soundscape and biological variables using the 'prcomp' function from the 'stats' package in R (R Core Team 2018). For both the soundscape and biological variables, we retained the first 2 principal components because their eigenvalues were >1.0 and together they captured >80% of the variability. We computed 2 multivariate regression models, one with the 2 biological principal components as the dependent factors and the other with the 2 soundscape principal components as the dependent factors, and time since protection as the independent

factor (Cathedral Cove = 40 yr; Black Seabass Reef and Cavern Point = 15 yr; East Fish Camp and Devil's Peak Member = 0 yr). Model assumptions were confirmed by performing Shapiro-Wilk tests for normality of residuals and visually inspecting plots for homogeneity of variance and linearity, although with only 5 samples it was difficult to definitively ascertain their distributions and linearity.

3. RESULTS

3.1. Ecological patterns

Kelp cover varied greatly between sites (Table 2). Cathedral Cove, which has been protected for 40 yr, had the highest kelp cover (34.8%). The other 2 protected sites, Cavern Point and Black Seabass Reef, had coverages of 23.5 and 7.7%. The 2 unprotected sites, Devil's Peak Member and East Fish Camp, had coverages of 0.0 and 0.05%. Of the 4 kelp species recorded at these sites, the dominant species was giant kelp *Macrocystis pyrifera*, which comprised 57% of the total.

Urchin density was inversely related with kelp cover. From 2016 to 2018, Cathedral Cove had the lowest mean urchin density (0.4 m^{-2}), followed by Cavern Point (2.3 m^{-2}) and Black Seabass Reef (4.0 m^{-2}). As expected, Devil's Peak Member (10.5 m^{-2}) and East Fish Camp (26.8 m^{-2}) had more urchins than the protected sites. Of the 4 urchin species (*Centrostephanus coronatus*, *Lytechinus anamesus*, *Strongylocentrotus franciscanus*, *S. purpuratus*), the species most associated with regime shifts, *S. purpuratus*, comprised 69% of the urchin community (J. Sprague pers. obs.). While East Fish Camp had between 24.0 and 31.8 urchins m^{-2} from 2016–2018, Devil's Peak Member increased drastically with 3.0 m^{-2} in 2016, 3.0 m^{-2} in 2017, and 25.6 m^{-2} in 2018.

Invertebrate density tracked similarly with urchin density. Invertebrate density was lower at protected sites (1.2–1.6 m^{-2}) than the unprotected sites (2.6–3.6 m^{-2}). Invertebrate species richness also peaked at East Fish Camp (15 m^{-2}) and was lowest at Cathedral Cove (11 m^{-2}). Wavy turban snails *Megastraea undosa*, California sea hares *Aplysia californica*, giant keyhole limpets *Megathura crenulata*, and chestnut cowries *Neobernaya spadicea* were more than twice as abundant in the barrens than in the intact forests.

Fish abundance was similar at 4 of the 5 sites, ranging from 1285 fish per transect at Cathedral Cove to 1132 at Cavern Point. The anomalous fifth site, East Fish Camp, only had 620 fish. Its richness was also the lowest, with 7 fewer species than the other 4 sites. The 2 Santa Cruz sites had the highest species richness values, with Devil's Peak Member and Cavern Point having 31 and 33, respectively. The Anacapa sites, Black Seabass Reef and Cathedral Cove, had 27 and 30, respectively. The 5 most abundant fish species were blacksmith *Chromis punctipinnis* (2716), blue-banded goby *Lythrypnus dalli* (749), rock wrasse *Halichoeres semicinctus* (244), kelp bass *Paralabrax clathratus* (236), and señorita *Oxyjulis californica* (192). All fish species at these sites were temperate rocky reef species. More information about the trophic status of fish species and their abundances can be found in Supplement 2 at www.int-res.com/articles/suppl/m654p035_supp2.xlsx.

3.2. Soundscape patterns

3.2.1. Snapping shrimp snaps

The 3 protected sites had fewer snaps per minute (220–803) and higher peak snap frequencies (3.8–4.4 kHz) than the unprotected sites, where snapping rates ranged from 889–1071 and peak frequencies ranged from 3.4–3.8 kHz (Fig. 3). Snaps per minute were greatest at East Fish Camp (1071) and lowest at Cathedral Cove (220; Table 3). Peak snap frequency exhibited the opposite trend with regards to protection status, as the highest snap frequency was at Cathedral Cove (4.4 kHz) and the lowest was at East Fish Camp (3.4 kHz).

Snap rates were generally high at night, peaked around dawn, and decreased over the course of the day until just before dusk, upon which time rates increased again (Fig. 4). Four of the 5 sites displayed pronounced peaks at dawn, while at Cathedral Cove there was a dip in snap rates. While Black Seabass Reef had the largest diel dynamics (AUC = 10 635), East Fish Camp had the steepest crepuscular peak and the second highest AUC (8991). Cathedral Cove had discernible day–night patterns in snapping shrimp dynamics, but had the second lowest AUC for shrimp snaps (4687), likely because it had the lowest overall snap rate and we did not rescale values prior to this analysis.

3.2.2. Low-frequency sound levels

East Fish Camp had the lowest SPLs for both the 20–80 and 50–750 Hz frequency bands. Fish chorusing events, as shown in the long-term spectrograms,

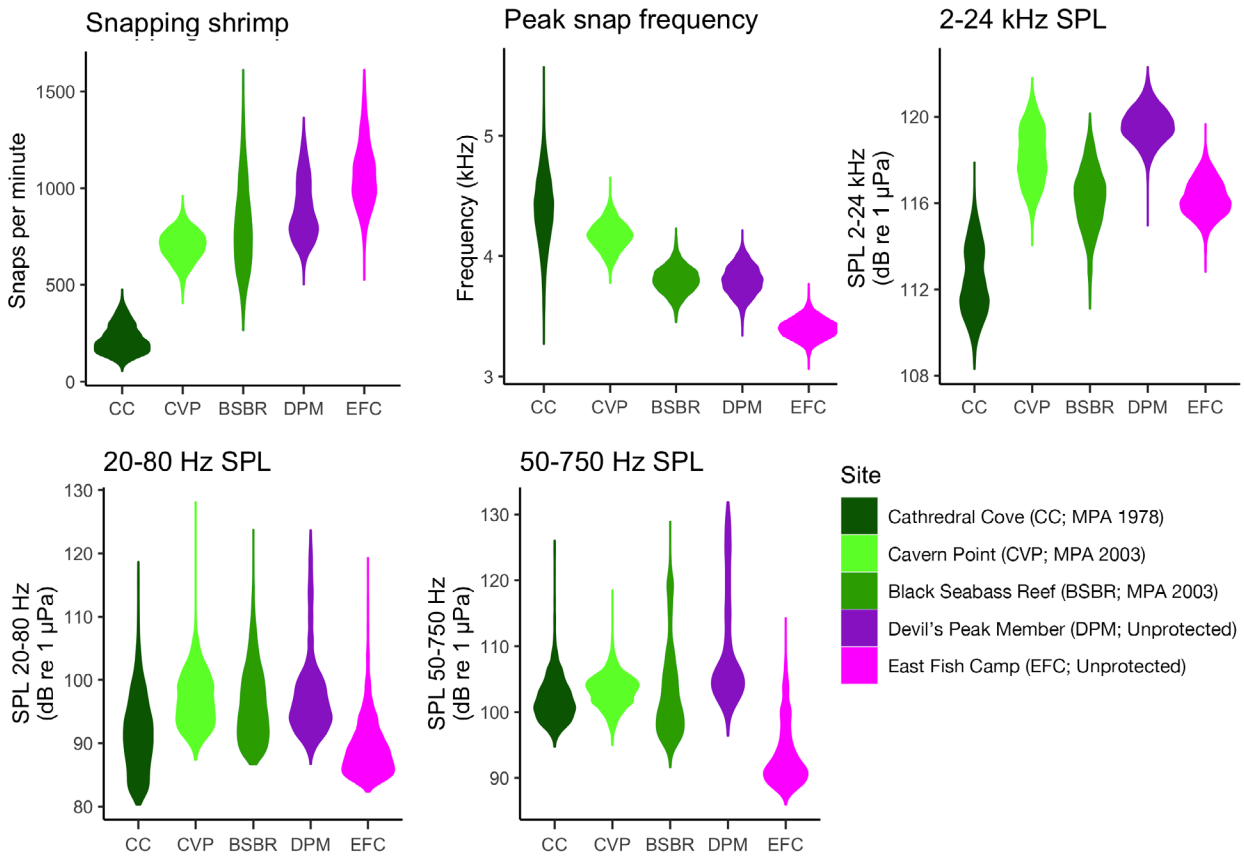

Fig. 3. Five measured soundscape variables. Green shading denotes kelp forest sites (year in which the marine protected area [MPA] was established is indicated in parentheses), and purple and pink denote urchin barren sites. Violin plots are similar to boxplots, except that they display the kernel probability density of the data at different values instead of showing the median and interquartile range. These plots were calculated with the ggplot2 function 'geom_violin' using default parameters in R. SPL: sound pressure level

were also less intense at this site compared to the other 4 sites, which could indicate that the chorusing fish were far from the hydrophone, and potentially outside of this urchin barren. Devil's Peak Member had the highest SPLs for both 20–80 and 50–750 Hz frequency bands due to nightly fish choruses from multiple species, but especially the plainfin midshipman. The long, wide tails on the 50–750 Hz violin plots for Devil's Peak Member, East Fish Camp, and Black Seabass Reef (Fig. 3) were due to regular plainfin midshipman choruses at these sites. The wider distribution of values at Cathedral Cove and Black Seabass Reef were the result of low-frequency fish choruses (<80 Hz), possibly from white seabass *Atractoscion nobilis* and giant black seabass *Stereolepis gigas*, and also high-amplitude sounds that appeared to be produced by body movement against the substrate.

Table 3. Mean ± SD for 5 of the 9 soundscape variables. SPL: sound pressure level

Site	20–80 Hz SPL	50–750 Hz SPL	2–24 kHz SPL	Shrimp snaps min^{-1}	Snap peak frequency (kHz)
Cathedral Cove	91.5 ± 6.1	102.0 ± 3.5	112.4 ± 1.6	220 ± 73	4.4 ± 0.3
Cavern Point	96.9 ± 4.2	103.2 ± 2.5	118.2 ± 1.3	702 ± 80	4.2 ± 0.1
Black Seabass Reef	96.2 ± 5.9	102.8 ± 6.6	116.2 ± 1.4	803 ± 222	3.8 ± 0.1
Devil's Peak Member	97.6 ± 6.5	109.0 ± 8.2	119.6 ± 0.8	888 ± 156	3.8 ± 0.1
East Fish Camp	89.3 ± 4.4	93.3 ± 4.5	116.2 ± 0.9	1071 ± 167	3.4 ± 0.1

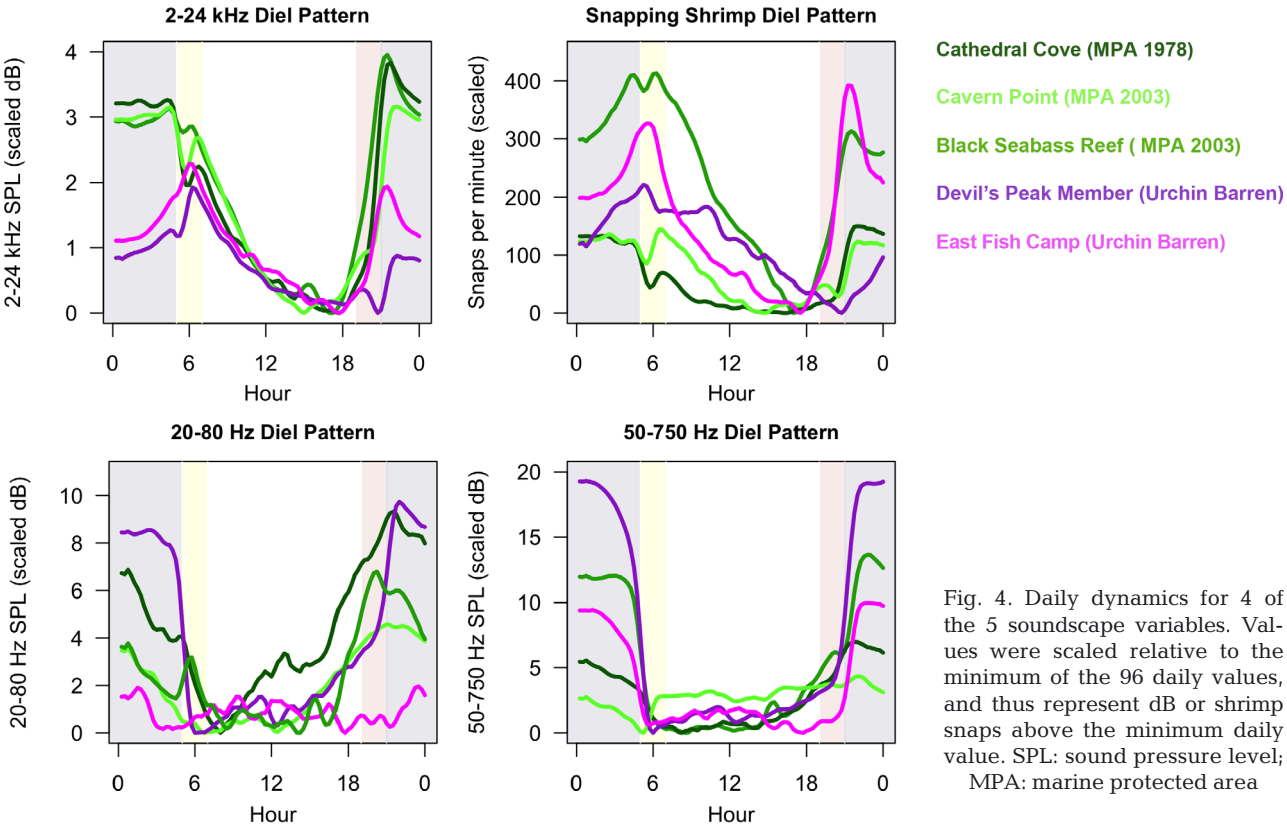

Fig. 4. Daily dynamics for 4 of the 5 soundscape variables. Values were scaled relative to the minimum of the 96 daily values, and thus represent dB or shrimp snaps above the minimum daily value. SPL: sound pressure level; MPA: marine protected area

In general, the 20–80 Hz frequency band was lowest during the day, peaked around sunset, and sustained moderately high levels throughout the night. At Black Seabass Reef, there were crepuscular peaks that coincided with activity of species that produced high-amplitude, low-frequency sounds. Starting just before dawn and subsiding in late morning, these sounds often exceeded 150 dB re 1 µPa, occurred every 5–15 s, and had durations spanning 0.25–5 s. We could not identify the producer but suspect that sounds were produced via body movement against the substrate. The peak at dusk was caused by chorusing fish. While 4 of the sites had strong daily dynamics in this band (AUC = 144–303), dynamics were negligible at East Fish Camp (AUC = 39).

The 50–750 Hz band peaked at night at all sites. The general shape of this diel pattern was associated with fish chorusing activity, and the magnitude of the pattern depended mainly on the prevalence of the plainfin midshipman. Devil's Peak Member had the most intense and consistent chorusing from this fish species and had the highest AUC (549). At Cathedral Cove (164) and Cavern Point (84), plainfin midshipman contributions were relatively faint and infrequent, so these sites had the lowest AUC values. Cavern Point was also the only site where levels increased during the daytime. This increase could be due to wave action elevating background noise within this frequency band (Hildebrand 2009).

3.2.3. High-frequency sound levels

High-frequency SPLs at Cathedral Cove (mean ± SD = 112.4 ± 1.6 dB) were 4–7 dB lower than at the other 4 sites. The 2 Santa Cruz sites, Devil's Peak Member and Cavern Point, had the highest high-frequency SPLs of 118.2 ± 1.3 and 119.6 ± 0.8 dB, respectively. Protected sites had a wider distribution of high-frequency SPLs than the unprotected sites. Standard deviation of these SPLs ranged from 1.3–1.6 in protected and 0.81–0.85 in unprotected areas. The shapes of the 2–24 kHz violin plots reflect this pattern (Fig. 3).

The 2–24 kHz sound levels were lowest during the daytime. There were pronounced peaks at dusk at 4 of the 5 sites. The 2 urchin barren sites also had slight peaks at dawn. The biggest difference between the protected and unprotected sites was that sound levels increased considerably at night at the protected sites (+2.3 dB) but only minimally at the urchin barren habitats (+0.7 dB). This difference in day–night

dynamics was reflected in the AUC values, which ranged from 95–110 in protected habitats and from 39–52 in unprotected habitats.

3.4. Longer-term dynamics in soundscape variables

Over the 42 d sampling period, sites exhibited different longer-term soundscape patterns. Most apparent were the plainfin midshipman choruses at Devil's Peak Member, Black Seabass Reef, East Fish Camp, and Cathedral Cove, which occurred at night from 21:30–04:00 h, and peaked from 22:00–01:45 h. While the production of the plainfin midshipman was consistent across days during this time period, other fish choruses were more variable, with multi-day upticks in activity (i.e. 17–19 May for Devil's Peak Member, Black Seabass Reef and 26–27 May for Cavern Point). Fig. 5 also illustrates the relative lack of low-frequency

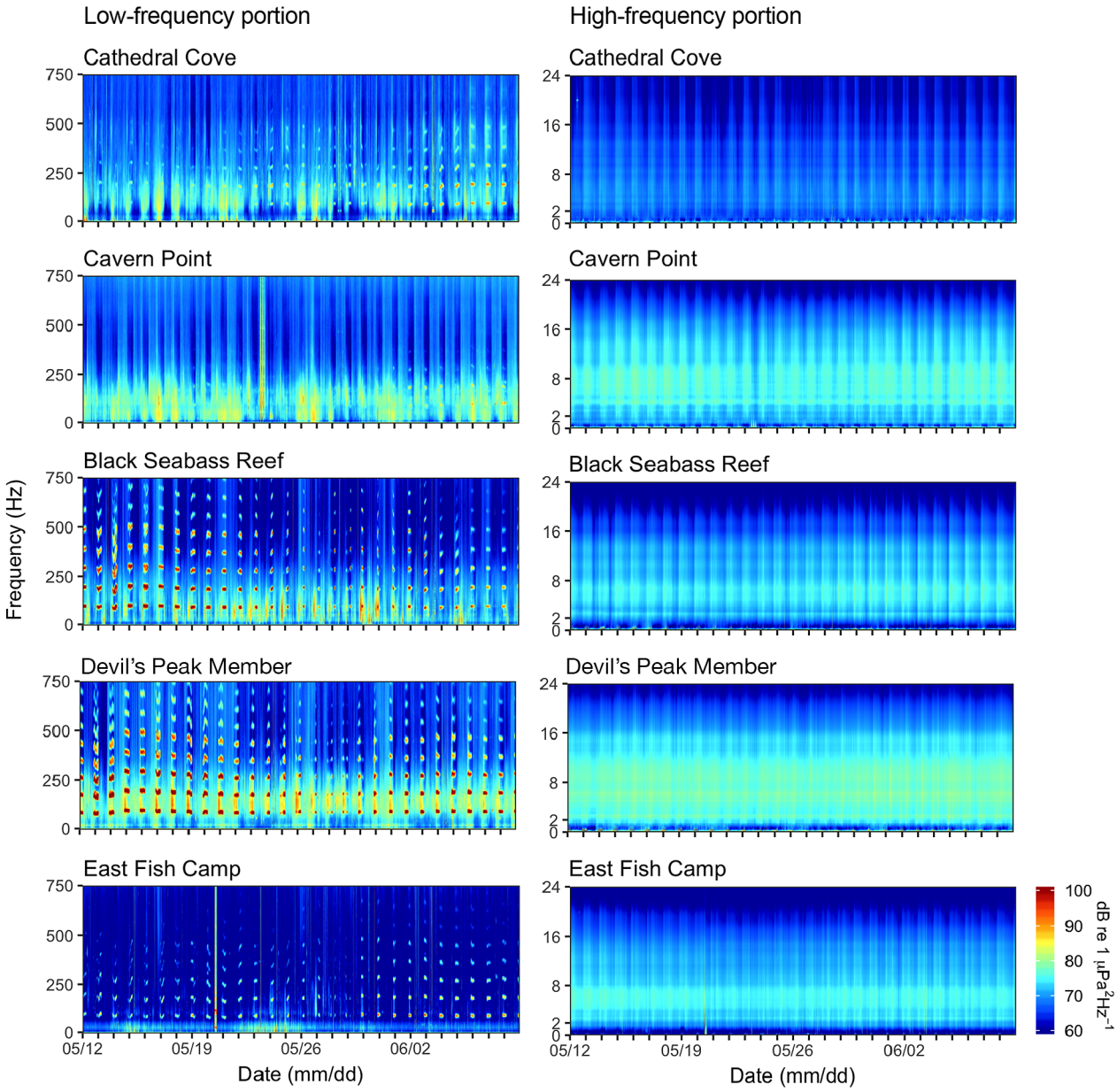

Fig. 5. Long-term power spectral density (PSD) plots depicting the low-frequency (0–750 Hz; left column) and high-frequency (0–24 kHz; right column) portions of the soundscape from 12 May to 9 June 2018. Warmer colors indicate more intense sounds. For each recording, PSD values were derived from a single-sided power spectrum, which we calculated by employing a discrete Fourier transform (8192-point window length; Hann window; 0 % overlap), and then calculating the upper quantile value for each of the 4096 frequency bins in the power spectrum. PSD values from each recording were stitched together to create these visualizations

intensity and dynamics at East Fish Camp. While individual fish pulses at East Fish Camp were quite common, the lower levels here likely reflected the dearth of chorusing fish near the hydrophone at this site.

3.5. Correlation between soundscapes and ecological drivers of kelp forest regime shifts

Three main drivers of regime shifts in kelp forests, i.e. the density of kelp, the density of urchins, and the diversity and abundance of fish, significantly related to different soundscape variables (Fig. 6). Invertebrate density was also significantly related to soundscape variables as well.

Kelp cover negatively correlated (r_3 = –0.93, p = 0.022) with the number of snapping shrimp snaps per minute and positively correlated with the peak frequency of snaps (r_3 = 0.93, p = 0.023). Kelp cover was also negatively correlated with high-frequency SPLs (r_3 = –0.85, p = 0.070).

Sea urchin density positively correlated (r_3 = 0.98, p = 0.004) with the number of snapping shrimp snaps per minute and negatively correlated with the peak frequency of snaps (r_3 = –0.96, p = 0.010). While it was not significantly correlated with high-frequency SPLs, sea urchin density was negatively correlated with high-frequency SPL diel dynamics (r_3 = –0.87, p = 0.058).

Invertebrate density was negatively correlated with the diel trend of the 2–24 kHz frequency band (r_3 = –0.92, p = 0.027). Invertebrate richness was not significantly correlated with the number of snaps per minute (r_3 = 0.79, p = 0.109).

Fish species richness (r_3 = 0.94, p = 0.017) and fish abundance (r_3 = 0.86, p = 0.065) positively correlated with sound levels from 50–750 Hz, but not the daily dynamics within this frequency band. Conversely, fish species richness (r_3 = 0.87, p = 0.054) and fish abundance (r_3 = 0.88, p = 0.047) were highly correlated with the daily dynamics of the 20–80 Hz band, but not with its sound levels.

3.6. Effect of MPAs on biological and soundscape components

While time since protection was not significant for either PCA axis representing the biological variables, there was a significant positive relationship between this variable and the first soundscape PCA axis (adj. R^2 = 0.81, $F_{1,3}$ = 17.8, p = 0.024). The soundscape variables that contributed most to this axis were peak snap frequency (0.50), number of snaps (–0.49), and diel dynamics in the high-frequency band (0.41). This model suggests that the longer a kelp forest site is protected, there will be fewer

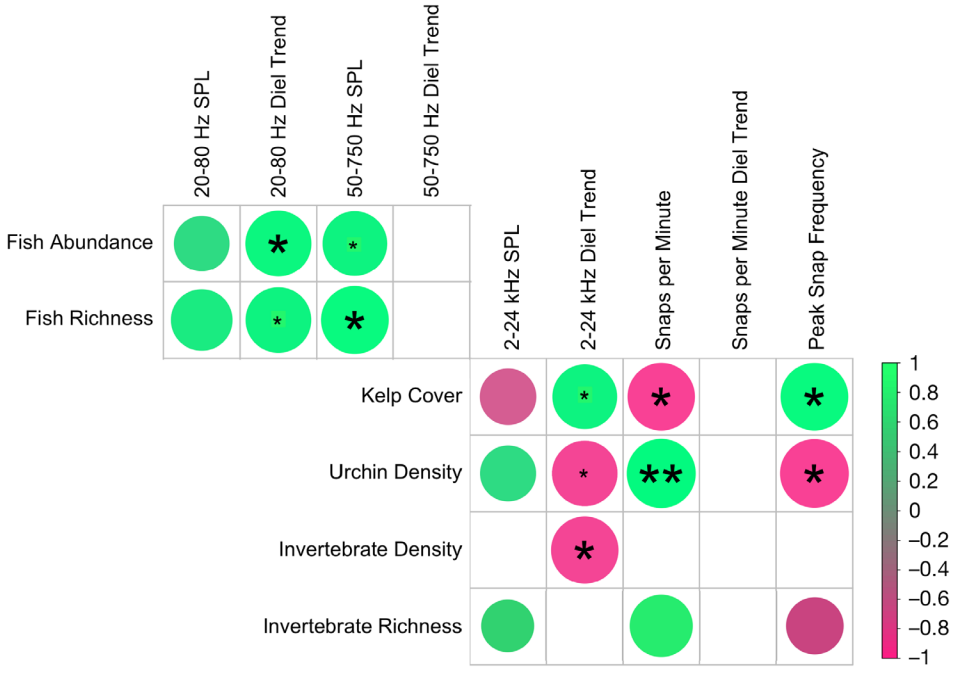

Fig. 6. Correlation plot between soundscape and biological variables. p < 0.1 (•), p < 0.05 (*) and p < 0.01 (**). The colors of the circles reflect the direction of the correlation, while the sizes of the circles indicate the magnitude of the correlation. Variable combinations that did not satisfy the linearity assumption are blank

snaps, these snaps will have a higher peak snap frequency, and there will be greater high-frequency diel dynamics. Regarding the biological variables, only kelp cover and urchin density exhibited monotonic responses to time since protection. Other biological variables varied in ways that could reflect MPA effects. Invertebrate density was more than doubled in unprotected habitats (B. Gottesman unpubl. data). At East Fish Camp, the site with the highest urchin density and lowest kelp cover, fish abundance was approximately half as high as the other 4 sites, and fish species richness was 40% lower.

4. DISCUSSION

This study demonstrates that marine soundscapes can indicate the condition of kelp forests, which are increasingly vulnerable to destruction from sea urchin overgrazing, and we infer a corollary that changes from soundscape baselines will imply changes in ecological condition. Soundscapes also indicated the ecological legacy of these 5 sites, with time since protection significantly related to soundscape variables. A main finding of this study, that degraded sites exhibited increased snapping shrimp activity and to a lesser degree, increased high-frequency sound levels, runs counter to our hypothesis, but harmonizes with a previous study that also found significantly higher shrimp snap rates in urchin-dominated habitats compared to nearby kelp forest patches (Radford et al. 2010). Another main finding is that heavily-fished urchin barrens had flatter diel soundscape dynamics than forested sites, suggesting that shifts in predator abundance may mediate daily rhythms in the soundscape, and that the strength of diel dynamics may signify habitat condition.

This study demonstrates how certain forms of habitat degradation may actually increase sound production from dominant soniferous taxa (snapping shrimp), possibly causing an associated increase in sound levels. Thus far, in almost all soundscape studies that have reported significant relationships between ecological variables (species abundance, species richness, and habitat condition) and soundscape variables (SPLs, soundscape complexity, sound type diversity), these relationships have been positive (Pieretti et al. 2011, Pekin et al. 2013, Butler et al. 2016, Harris et al. 2016, Buxton et al. 2018; but see Freeman & Freeman 2016). Here, we see that a regime shift caused by overfishing was associated with an increase in sounds from snapping shrimp (and potentially other invertebrates) and elevated high-frequency sound levels. Shrimp snapping rates at the 2 urchin barren habitats were 4 times greater than at Cathedral Cove, which has been protected since 1978. The 2 sites that have been protected since 2003 had intermediate snapping rates. Similarly, Cathedral Cove also had high-frequency sound levels (SPL 2–24 kHz) that were 4–7 dB lower than the other 4 sites.

The ecological explanation for why snapping shrimp activity was higher in the urchin barrens is that the removal of apex predators in unprotected habitats resulted in an increase in invertebrates, including sea urchins, mollusks, and potentially snapping shrimp. At the 2 urchin-dominated habitats, invertebrate density was 220% greater than at the protected sites. While snapping shrimp abundance was not directly measured in these surveys, the overall increase in invertebrates suggests that shrimp density could be greater in regime-shifted habitats due to the lack of predators. Bolstering this suggestion, we observed a positive but non-significant correlation between snapping shrimp snaps and invertebrate richness (see Fig. 6). In addition to an increase in invertebrate density, there also could be accompanying changes in invertebrate behavior resulting in soundscape alteration. For example, in healthy kelp forests, urchins usually stay hidden and protected in reef crevices during the day to avoid predation (Kenner 1992, Ling et al. 2015). However, if predator abundance declines substantially, sea urchins become active during the daytime and drastically increase their locomotion in search of kelp, which could lead to a corresponding increase of sounds associated with these activities and a flattening of the diel dynamics. At the urchin barren sites, we did observe the dissolution of day–night patterns in the high-frequency band, which could indicate behavior change from other invertebrate species including shrimp in these degraded, predator-scarce habitats (Fig. 7). In general, for species that produce sound at night and crepuscular periods to avoid detection by predators, it is unclear how their patterns might change when predators are removed. This study produced results consistent with the hypothesis that soundscapes can encode behavioral changes induced by the removal or reintroduction of apex predators. Rather than impoverishing soundscapes, the removal of apex predators appears to have resulted in an influx of snapping shrimp activity and a flattening of the diel soundscape dynamics.

Increased snapping shrimp activity in degraded sites could also be explained by differences in sound propagation. In kelp forests, sound at certain fre-

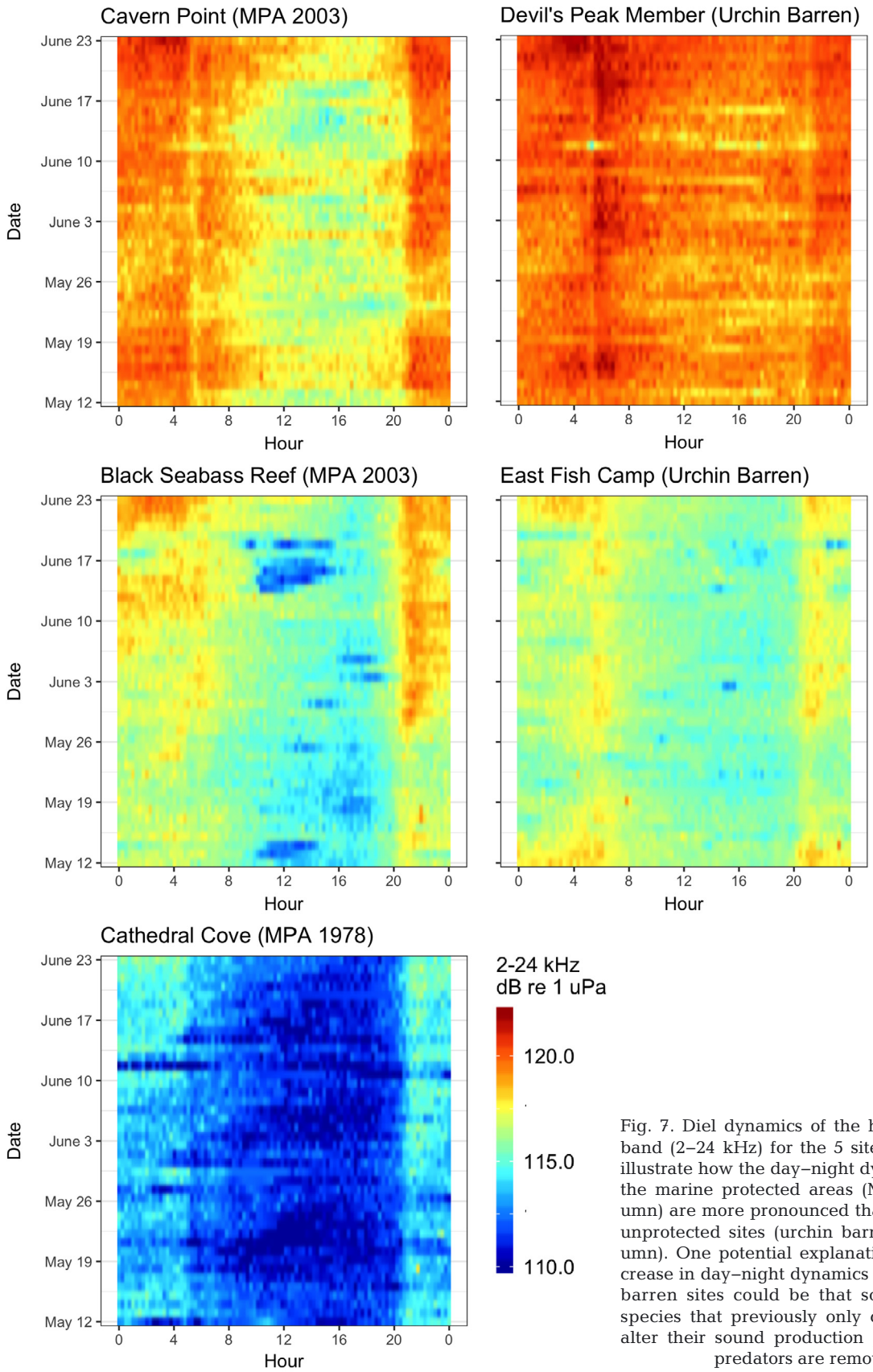

Fig. 7. Diel dynamics of the high-frequency band (2–24 kHz) for the 5 sites. These plots illustrate how the day–night dynamics within the marine protected areas (MPAs; left column) are more pronounced than those in the unprotected sites (urchin barrens; right column). One potential explanation for the decrease in day–night dynamics in the 2 urchin barren sites could be that soniferous prey species that previously only called at night alter their sound production patterns when predators are removed

quencies attenuates more quickly, particularly in the summer months when kelp plants are dense and have high leaf areas (Wilson 2011). Some kelp species have air bladders that can impact sound transmission (Wilson 2011). Therefore, we would expect healthy kelp forests to have an environmental quieting effect that would result in decreased sound levels. This environmental explanation is potentially supported by the strong relationship between kelp cover and peak snap frequency, which could result if kelp attenuates sound waves between 2 and 4 kHz more than sound waves between 4 and 6 kHz, but additional research is needed to determine the nature and extent of how kelp density impacts biological sound transmission. Furthermore, work is needed to characterize any sound production by the kelp plants themselves, as the acoustic signature for marine algae on coral reefs was recently described (Freeman et al. 2018). In ecosystems like kelp forests, where regime shifts also trigger major changes in habitat structure and therefore the propagation environment, assessing biodiversity changes through soundscape analysis is complex because these physical changes need to be taken into account.

The strong negative relationship between snapping shrimp activity and kelp cover contrasts with the results of Rossi et al. (2017), who recorded sounds in healthy kelp forests and adjacent habitats that had shifted into algal turf due to excessive nutrient pollution, rather than urchin predation. They observed that in turf-adjacent kelp forests, shrimp snaps and total sound levels (300–10 000 Hz) declined, likely because habitat simplification reduced niche availability for shrimp. Based on similar observations in macroalgae–seagrass habitats in Italy impacted by acidification (a different regime shift driver), Rossi et al. (2017, p. 239) concluded that 'modified cues of shifted ecosystems are similar regardless of spatial scale and type of environmental driver.' While this is a thought-provoking hypothesis, our study illustrates that different pathways toward kelp forest degradation may result in dissimilar soundscape impacts. Shrimp density may decline in a kelp forest degraded through nutrient pollution (because of fewer niches) but may increase in a kelp forest degraded through overfishing (due to fewer predators). Indeed, when Radford et al. (2010) compared soundscapes in urchin barren and kelp forest habitats off the coast of New Zealand, snapping shrimp activity at dusk was more than 2 times greater at the urchin sites than at macroalgal sites. Our study provides further evidence that kelp forest degradation into an urchin barren state can lead to an increase in shrimp snapping rates and potentially also high-frequency sound levels. The contrasting results between our study and that of Rossi et al. (2017) is important because it shows that different disturbance types may have characteristic, even divergent, soundscape impacts, even if the degree of alteration or ecosystem is similar.

Another unexpected result of our study was the lack of discernible urchin sounds in the urchin barren habitats. Urchin species produce sounds associated with movement and feeding; reported frequency ranges for these sounds have included 0.4–4.0 kHz (Radford et al. 2008a), 0.8–2.5 kHz (Radford et al. 2010), 3.0–6.0 kHz (Coquereau et al. 2016), and ultrasonic components including an initial broadband transient at 37–49 kHz (Coquereau et al. 2016). Urchins in rocky coastal reefs in northern New Zealand generated a 100-fold increase in the intensity of ambient sound at dusk (20 dB re 1 $\mu Pa^2\ Hz^{-1}$ primarily between 0.7 and 2.0 Hz; Radford et al. 2008b). In our study, no comparable increase in sound levels in this frequency range was evident at dusk when we visually inspected long-term spectrograms. One potential reason for this lack of urchin sounds is that soon after a habitat shifts into an urchin barren, urchins quickly exhaust the food supply, presumably decreasing feeding rates and reducing activity. This inactivity could result in minimal sound production during this period in areas with no macroalgae. We did detect repeated scrape-like sounds that occurred mostly at the barren sites, but an expert in urchin bioacoustics thought that they were produced too rapidly to be from a feeding urchin, and were likely produced by a turban snail (Family: Turbinidae) or similar mollusk (N. Soars pers. comm.). Therefore, soundscape monitoring could potentially play a role in detecting the onset of urchin overgrazing, but after a forest has transformed into a barren, the sounds from urchins may not be a usable indicator of their presence, although further studies are needed to verify this claim.

While our study does illustrate the strong relationships between soundscape components and kelp forest condition at these sites, it is important to regard the results in proper context. With only 5 sites surveyed, it is difficult to know for certain whether our results are generalizable to other habitats within the Channel Islands and similar kelp forest systems. While we selected sites with similar environmental and biogeographical characteristics, it is possible that some external factors could have contributed to differences in these soundscapes. For example, East Fish Camp, which had 50–750 Hz sound levels at least 9 dB less than the other sites, was also the only site on the south side of the island chain. Therefore, it

could have been buffered from the Santa Barbara Channel shipping lanes approximately 10–20 km north of Santa Cruz and Anacapa, thus reducing ambient low-frequency sound levels (McKenna et al. 2012). It is possible that distant low-frequency anthropogenic sounds can mask biological sounds or bias soundscape metrics. However, despite the anomalous location of East Fish Camp and the presence of different sources of anthropogenic noise, we are confident that the low-frequency differences between East Fish Camp and the other sites were largely influenced by reduced biological sound production. The other 4 sites had more frequent and intense fish choruses and 20–80 Hz daily dynamics that were 3–8 times greater than at East Fish Camp. The nocturnal peaks in low-frequency sound levels did not correspond to the daytime peaks in commercial fishing activity or the noon and midnight peaks in commercial shipping on the Santa Barbara Channel found by McKenna et al. (2009), though their recorder was deployed at a different location within the Santa Barbara Channel and so daily shipping dynamics were likely different at this location.

In addition to the biasing effects of anthropogenic noise, another confounding factor could have been the acoustic activity of whale species that inhabit the waters surrounding the Channel Islands, including blue whales *Balaenoptera musculus*, fin whales *B. physalus*, and humpback whales *Megaptera novaeangliae*. However, the daily and seasonal patterns of these species do not cleanly match the patterns of low-frequency sound observed in this study (Oleson et al. 2007, Širović et al. 2015).

While the methods employed here measure the main soundscape components, including shrimp snaps, fish choruses, and to a lesser extent pulsed fish and invertebrate sounds, these measurements likely unlock only a fraction of the informational content encoded in marine soundscapes. In order to advance our understanding of soundscape patterns and ecological relationships, it is important to (1) continue to develop automated sound-type based measurements, (2) identify the species producing these different sound types, and (3) understand the environmental and physical conditions that influence these measures. In addition to these sound-type based measurements, this study illustrates that the magnitude of diel patterns is also an ecologically relevant component of soundscapes.

To conclude, this study demonstrates that marine soundscapes can indicate the condition of kelp forests. Several ecological variables associated with regime shifts in kelp forests, including urchin (and invertebrate) density, kelp cover, and fish richness and abundance correlated with measurable soundscape components. However, some of these relationships, such as the inverse relationship between kelp cover and snapping shrimp activity, were unexpected, and illustrate that different disturbance pathways can yield distinct soundscape alterations. Based on this finding, it seems that not all ecological disturbance types result in a decrease in soundscape levels. The fact that ecological degradation is demonstrably coupled with changes to the soundscape, at statistically and ecologically significant levels, provides scientists and managers of MPAs with a new and intriguing way to detect regime shifts and perturbations in marine ecosystems. Passive acoustic recorders work at night, during storms, and for long durations, and they collect data about the marine ecosystem that are not easily obtainable from traditional diver surveys. Soundscape assessments via the deployment of these recorders provide temporal richness and granularity to ecosystem assessments that are complementary to more traditional diving surveys. Therefore, soundscape recording and analysis may assist in the detection of incipient regime changes when indicators are likely to be subtle, but at a point in time when specific human actions to blunt or reverse these changes may be most effective.

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LITERATURE CITED

Anderson CB (2018) Biodiversity monitoring, earth observations and the ecology of scale. Ecol Lett 21:1572–1585

Bertucci F, Parmentier E, Lecellier G, Hawkins AD, Lecchini D (2016) Acoustic indices provide information on the status of coral reefs: an example from Moorea Island in the South Pacific. Sci Rep 6:33326

Biggs CR, Lowerre-Barbieri SK, Erisman B (2018) Reproductive resilience of an estuarine fish in the eye of a hurricane. Biol Lett 14:20180579

Bohnenstiehl DR, Lillis A, Eggleston DB (2016) The curious acoustic behavior of estuarine snapping shrimp: temporal patterns of snapping shrimp sound in sub-tidal oyster reef habitat. PLOS ONE 11:e0143691

Butler J, Stanley JA, Butler MJ IV (2016) Underwater soundscapes in near-shore tropical habitats and the effects of environmental degradation and habitat restoration. J Exp Mar Biol Ecol 479:89–96
Buxton RT, McKenna MF, Clapp M, Meyer E and others (2018) Efficacy of extracting indices from large-scale acoustic recordings to monitor biodiversity. Conserv Biol 32:1174–1184
Carpenter SR, Cole JJ, Pace ML, Batt R and others (2011) Early warnings of regime shifts: a whole-ecosystem experiment. Science 332:1079–1082
Caselle JE, Rassweiler A, Hamilton SL, Warner RR (2015) Recovery trajectories of kelp forest animals are rapid yet spatially variable across a network of temperate marine protected areas. Sci Rep 5:14102
Caselle JE, Davis K, Marks LM (2018) Marine management affects the invasion success of a non-native species in a temperate reef system in California, USA. Ecol Lett 21:43–53
Coquereau L, Grall J, Chauvaud L, Gervaise C, Clavier J, Jolivet A, Iorio LD (2016) Sound production and associated behaviours of benthic invertebrates from a coastal habitat in the north-east Atlantic. Mar Biol 163:127
Coquereau L, Lossent J, Grall J, Chauvaud L (2017) Marine soundscape shaped by fishing activity. R Soc Open Sci 4: 160606
Davies DH (1968) Statistical analysis of the relation between kelp harvesting and sportfishing in the California kelp beds. California Department of Fish and Game, Sacramento, CA
Davis GE, Richards DV, Kushner D (1996) Kelp forest monitoring design review. Tech Rep CHIS-96-01. Channel Islands National Park, Ventura, CA
Dayton PK, Tegner MJ, Edwards PB, Riser KL (1998) Sliding baselines, ghosts, and reduced expectations in kelp forest communities. Ecol Appl 8:309–322
Desiderà E, Guidetti P, Panzalis P, Navone A and others (2019) Acoustic fish communities: sound diversity of rocky habitats reflects fish species diversity. Mar Ecol Prog Ser 608:183–197
Elise S, Urbina-Barreto I, Pinel R, Mahamadaly V and others (2019) Assessing key ecosystem functions through soundscapes: a new perspective from coral reefs. Ecol Indic 107:105623
Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS (2004) Regime shifts, resilience, and biodiversity in ecosystem management. Annu Rev Ecol Evol Syst 35:557–581
Freeman LA, Freeman SE (2016) Rapidly obtained ecosystem indicators from coral reef soundscapes. Mar Ecol Prog Ser 561:69–82
Freeman SE, Freeman LA, Giorli G, Haas AF (2018) Photosynthesis by marine algae produces sound, contributing to the daytime soundscape on coral reefs. PLOS ONE 13:e0201766
Gleason M, McCreary S, Miller-Henson M, Ugoretz J and others (2010) Science-based and stakeholder-driven marine protected area network planning: a successful case study from north central California. Ocean Coast Manag 53:52–68
Gordon TAC, Harding HR, Wong KE, Merchant ND and others (2018) Habitat degradation negatively affects auditory settlement behavior of coral reef fishes. Proc Natl Acad Sci USA 115:5193–5198
Gottesman BL, Francomano D, Zhao Z, Bellisario K and others (2020) Acoustic monitoring reveals diversity and surprising dynamics in tropical freshwater soundscapes. Freshw Biol 65:117–132
Harris SA, Shears NT, Radford CA (2016) Ecoacoustic indices as proxies for biodiversity on temperate reefs. Methods Ecol Evol 7:713–724
Hildebrand JA (2009) Anthropogenic and natural sources of ambient noise in the ocean. Mar Ecol Prog Ser 395:5–20
Kaplan MB, Mooney TA, Partan JW, Solow AR (2015) Coral reef species assemblages are associated with ambient soundscapes. Mar Ecol Prog Ser 533:93–107
Kaplan MB, Lammers MO, Zang E, Aran Mooney T (2018) Acoustic and biological trends on coral reefs off Maui, Hawaii. Coral Reefs 37:121–133
Kennedy EV, Holderied MW, Mair JM, Guzman HM, Simpson SD (2010) Spatial patterns in reef-generated noise relate to habitats and communities: evidence from a Panamanian case study. J Exp Mar Biol Ecol 395:85–92
Kenner MC (1992) Population dynamics of the sea urchin *Strongylocentrotus purpuratus* in a Central California kelp forest: recruitment, mortality, growth, and diet. Mar Biol 112:107–118
Kriegisch N, Reeves SE, Flukes EB, Johnson CR, Ling SD (2019) Drift-kelp suppresses foraging movement of overgrazing sea urchins. Oecologia 190:665–677
Krumhansl KA, Okamoto DK, Rassweiler A, Novak M and others (2016) Global patterns of kelp forest change over the past half-century. Proc Natl Acad Sci USA 113: 13785–13790
Kushner D, Sprague J (2018) Channel Islands National Park kelp forest monitoring handbook. Channel Islands National Park, Ventura, CA
Kushner DJ, Rassweiler A, McLaughlin JP, Lafferty KD (2013) A multi-decade time series of kelp forest community structure at the California Channel Islands. Ecology 94:2655
Lillis A, Eggleston DB, Bohnenstiehl DR (2014) Estuarine soundscapes: distinct acoustic characteristics of oyster reefs compared to soft-bottom habitats. Mar Ecol Prog Ser 505:1–17
Lindseth A, Lobel P (2018) Underwater soundscape monitoring and fish bioacoustics: a review. Fishes 3:36
Ling SD, Scheibling RE, Rassweiler A, Johnson CR and others (2015) Global regime shift dynamics of catastrophic sea urchin overgrazing. Philos Trans R Soc B 370:20130269
Locascio JV, Mann DA (2005) Effects of Hurricane Charley on fish chorusing. Biol Lett 1:362–365
McKenna MF, Soldevilla M, Oleson E, Wiggins S, Hildebrand JA (2009) Increased underwater noise levels in the Santa Barbara Channel from commercial ship traffic and the potential impact on blue whales (*Balaenoptera musculus*). In: Damiani CC, Garcelon DK (eds) Proceedings of the 7th California Islands Symposium. Institute for Wildlife Studies, Arcata, CA, p 141–149
McKenna MF, Ross D, Wiggins SM, Hildebrand JA (2012) Underwater radiated noise from modern commercial ships. J Acoust Soc Am 131:92–103
McWilliam JN, McCauley RD, Erbe C, Parsons MJG (2018) Soundscape diversity in the Great Barrier Reef: Lizard Island, a case study. Bioacoustics 27:295–311
Miksis-Olds J, Martin B, Tyack P (2018) Exploring the ocean through soundscapes. Acoust Today 14:26–34
Miller RJ, Lafferty KD, Lamy T, Kui L, Rassweiler A, Reed DC (2018) Giant kelp, *Macrocystis pyrifera*, increases faunal diversity through physical engineering. Proc R Soc B 285:20172571

Moritz S, Bartz-Beielstein T (2017) imputeTS: time series missing value imputation in R. The R Journal 9:207–218
Nijland W, Reshitnyk L, Rubidge E (2019) Satellite remote sensing of canopy-forming kelp on a complex coastline: a novel procedure using the Landsat image archive. Remote Sens Environ 220:41–50
Oleson EM, Wiggins SM, Hildebrand JA (2007) Temporal separation of blue whale call types on a southern California feeding ground. Anim Behav 74:881–894
Pieretti N, Farina A, Morri D (2011) A new methodology to infer the singing activity of an avian community: the acoustic complexity index (ACI). Ecol Indic 11: 868–873
Pijanowski BC, Farina A, Gage SH, Dumyahn SL, Krause BL (2011a) What is soundscape ecology? An introduction and overview of an emerging new science. Landsc Ecol 26:1213–1232
Pijanowski BC, Villanueva-Rivera LJ, Dumyahn SL, Farina A and others (2011b) Soundscape ecology: the science of sound in the landscape. Bioscience 61:203–216
Quinlan AE, Berbés-Blázquez M, Haider LJ, Peterson GD (2016) Measuring and assessing resilience: broadening understanding through multiple disciplinary perspectives. J Appl Ecol 53:677–687
R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
Radford C, Jeffs A, Tindle C, Montgomery JC (2008a) Resonating sea urchin skeletons create coastal choruses. Mar Ecol Prog Ser 362:37–43
Radford CA, Jeffs AG, Tindle CT, Montgomery JC (2008b) Temporal patterns in ambient noise of biological origin from a shallow water temperate reef. Oecologia 156: 921–929
Radford C, Stanley J, Tindle CT, Montgomery JC, Jeffs AG (2010) Localised coastal habitats have distinct underwater sound signatures. Mar Ecol Prog Ser 401:21–29
Rossi T, Connell SD, Nagelkerken I (2017) The sounds of silence: regime shifts impoverish marine soundscapes. Landsc Ecol 32:239–248
Rowell TJ, Demer DA, Aburto-Oropeza O, Cota-Nieto JJ, Hyde JR, Erisman BE (2017) Estimating fish abundance at spawning aggregations from courtship sound levels. Sci Rep 7:3340
Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol Evol 18:648–656
Shuman C (2018) Kelp extent for California Region 7. California Department of Fish and Wildlife, Monterey, CA. https://wildlife.ca.gov/Conservation/Marine/Kelp/Aerial-Kelp-Surveys
Širović A, Rice A, Chou E, Hildebrand JA, Wiggins SM, Roch MA (2015) Seven years of blue and fin whale call abundance in the Southern California Bight. Endang Species Res 28:61–76
Staaterman E, Paris CB, DeFerrari HA, Mann DA, Rice AN, D'Alessandro EK (2014) Celestial patterns in marine soundscapes. Mar Ecol Prog Ser 508:17–32
Staaterman E, Ogburn MB, Altieri AH, Brandl SJ and others (2017) Bioacoustic measurements complement visual biodiversity surveys: preliminary evidence from four shallow marine habitats. Mar Ecol Prog Ser 575: 207–215
Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ Conserv 29:436–459
Urick RJ (1983) Principles of underwater sound. Peninsula Publishing, Westport, CT
Wade P, Heide-Jørgensen MP, Shelden K, Barlow J and others (2006) Acoustic detection and satellite-tracking leads to discovery of rare concentration of endangered North Pacific right whales. Biol Lett 2:417–419
Wilson CJ (2011) The acoustic ecology of submerged macrophytes. PhD dissertation, University of Texas, Austin, TX

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