RESEARCH ARTICLE

# Whale entanglements disentangled through the lens of cumulative habitat compression

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## Abstract

Ten years following a marine heatwave event, whale entanglements continue to challenge ecosystem-based fishery and protected species management in the California Current Large Marine Ecosystem (CCLME). Although new fishing regulations combined with environmental changes resulted in a decline in humpback whale (*Megaptera novaeangliae)* entanglements from the peak during a prolonged heatwave, reports continue at a higher rate than prior to 2014. The entanglement record is imperfect because many entanglements go unobserved and those that are observed may not correspond to where the entanglement occurred. Thus it remains a challenge to understand when and where entanglements are most likely to occur and under what environmental conditions. Monitoring spatial changes in compression of cool thermal habitat and forage species availability previously permitted detection of ecosystem conditions that result in shoreward shifts in whales that overlapped with fixed gear fisheries. Following the heatwave (2015–2016), a surge in anchovy populations and increased variability of krill abundance, has led to increased concentrations of prey nearshore, fueling whale populations as they continue to recover from historical whaling. We reapply the habitat compression index to examine the association among annual humpback whale entanglement reports, population abundance and cumulative changes in thermal habitat availability throughout the CCLME. Using a two-step analysis, we document that reported entanglements, alone and adjusted for population growth, are highest during years of low thermal habitat area. We discuss how this relationship can be used to inform fishery management decisions through application of short-term forecasts of habitat compression, and how it can benefit whale entanglement mitigation.

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## Introduction

With post-whaling recovery and spatio-temporal shifts in both whales and fisheries, whale entanglements are increasing in many ecosystems globally [1,2,3,4,5,6]. The application of ecosystem assessments and risk mitigation planning are increasingly critical tools to both protect whales and to ensure sustainable fisheries is an emerging priority [7,8,9]. This challenge is increasingly difficult because some proportion of entanglements go unobserved, and when observed, events are spread out across a large geographic area and do not necessarily correspond with the specific location and timing of the entanglement event [5]. Reported entanglements within the California Current Large Marine Ecosystem (CCLME) have increased markedly over past decades with an unprecedented record number during a persistent multi-year marine heatwave ([5,9]; Fig 1). The record number of reported entanglements for humpback whales (*Megaptera novaeangliae*) was attributed to several inter-connected changes in environmental and socio-economic factors, ranging from a sustained harmful algal bloom, fishery season delays, increases in whale populations, and compression of thermal habitat that corresponded with changes in forage species consumed by whales, resulting in greater overlap of whales and commercial fishing gear in coastal waters [9].

Following the heatwave (2015–2016; [10]), new regulations were implemented on the California commercial Dungeness crab (*Metacarcinus magister*) fishery to actively monitor and reduce risk of whale entanglement, including delayed season openings and earlier season closures, fishing gear allotment and depth restrictions [11]. These resulted in the reduction of reported entanglements since 2016. However, despite intensive intervention to fishing practices, whale entanglements continue to be reported at levels greater than before the marine heatwave period, posing significant challenges with respect to balancing the needs of fisheries with those of protected species. To meet the mandates of the Marine Mammal Protection Act (16 U.S.C. 1387(f)(6)(A)(i)) and Endangered Species Act (16 U.S.C. 1539), additional management interventions are likely necessary, including a Take Reduction Team (TRT). The mandate of a TRT is to evaluate scientific information available, and develop a plan to achieve a significant decrease in the risk of mortality and serious injury of whales ([12], McDonald et al. 2016). In the case of West Coast humpback whales the primary risk is associated with entanglement in several fixed-gear fisheries within the CCLME (e.g., Dungeness crab; [5]). To that end, understanding the seasonal occurrence and foraging ecology of migratory humpback whales within the CCLME is critical for evaluating potential mitigation strategies. Briefly, although the timing, arrival and departure of humpback whales can vary annually [13,14], they are typically present from early spring through early winter, and primarily feed on krill and coastal pelagic fish species (e.g., anchovy) and exhibit prey-switching behavior depending on prey species availability ([15,9]; [16]).

The science of whale entanglement is impeded by the ability to detect, collect and record as much information as possible on any reported entanglement [1,3,4,5], and as such, this can be considered a data-limited scientific problem [17]. In the CCLME, the majority of reported whale entanglements are associated with coastal human

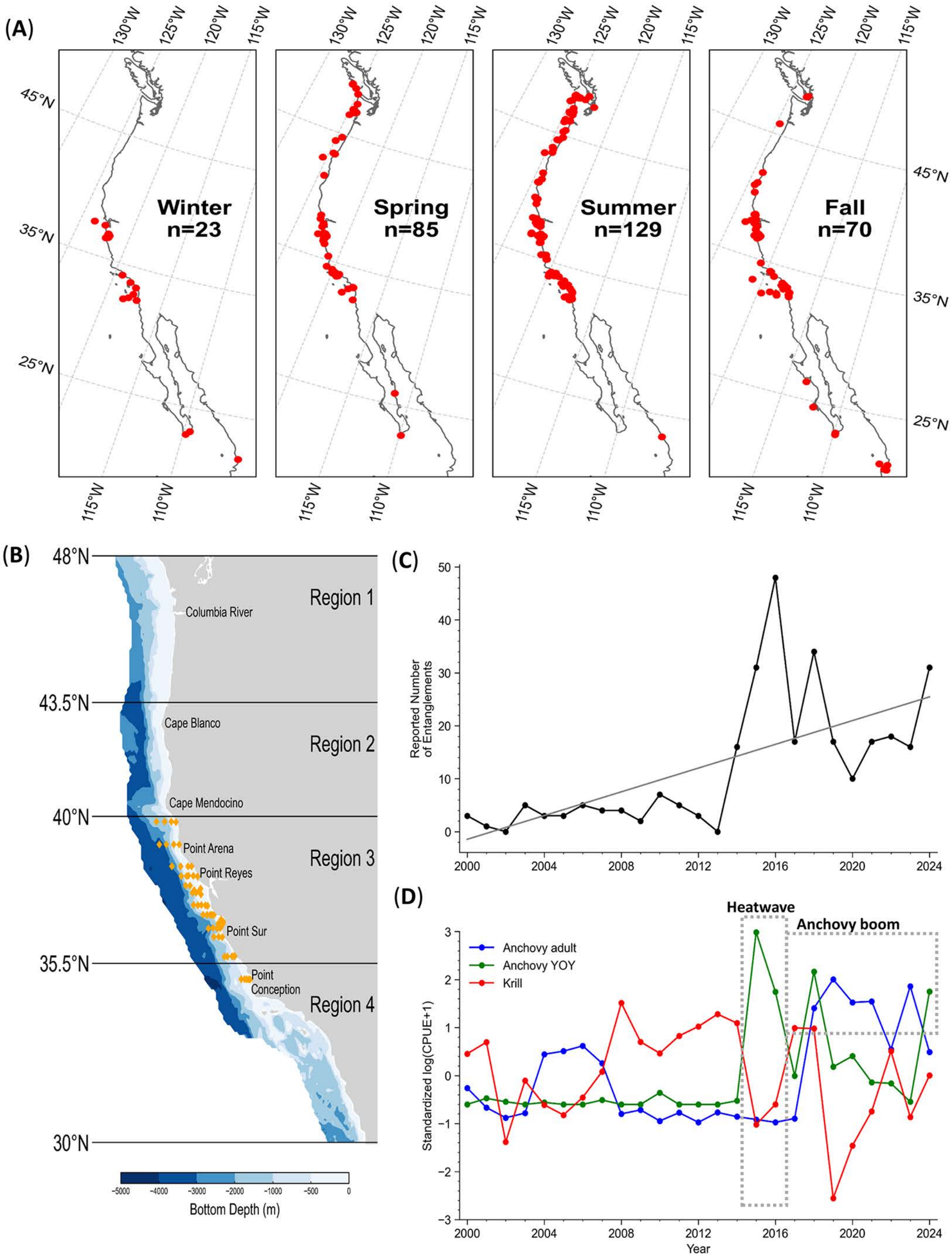


**Fig 1. An integrated view of reported whale entanglements and ecosystem conditions in the California Current Large Marine Ecosystem (CCLME). (A)** Geographic distribution and seasonal summary (JFM, AMJ, JAS, OND) of reported humpback whale entanglements (red dots) in the CCLME and those found off Mexico with that were confirmed to be entangled in the California Current, 2000-2024 (note reports occur throughout the CCLME, **(B)** Biogeographic regions showing extent of continental shelf and slope habitat where habitat compression is monitored in the CCLME; orange dots are sampling stations for forage indices. **(C)** Update of the whale entanglement temporal record for the confirmed number of Humpback whale entanglements reported over 2000 to 2024. The grey line is a long-term trend (trend = 1.11*year-2226.0), with a slope that is approximately 1 whale per year. **(D)** Standardized relative abundance of northern anchovy (adult and Young-of-the-Year; YOY) and total krill abundance collected from the Rockfish Recruitment and Ecosystem Assessment Survey (stations shown in **(B)**), which samples forage species during April-June throughout 32°N-42°N, provides a generally reflective index for conditions within the CCLME; dashed boxes indicate heatwave and post anchovy boom.

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population centers, where there are generally more eyes on the water. While the time series of reported whale entanglements represents an incomplete and imperfect record, it is the best available information used to assess the impact of fishing gear on stocks of marine mammals [18–20]. For example, a reported entanglement does not always indicate where and when the entanglement occurred, even when the origin and type of the fishing gear is identified, unless it can be linked to a specific time and place of gear deployment or loss. This means that most entanglements cannot be linked to a particular location or date, month or year, as some entanglements can be detected outside the fishery season, or in migratory and overwintering habitats used by whales ([5]; Fig 1). Also, the reported entanglement record has not previously been adjusted or scaled to account for likely impacts that are not observed or documented. The inability to know or estimate the total level of serious injury or mortality remains a significant challenge to management of fisheries and whale interactions, as the true number of entanglements remains difficult to estimate [18]. Further, humpback whale populations have steadily increased in the CCLME over the past 50 years [20], which leads to more potential for interactions with fishing gear, and may increase the likelihood of entanglements, with or without the direct impact of climate and ecosystem change. Therefore, establishing connections between the observed entanglement record and the ocean ecosystem and fishing activity is beneficial to developing a more comprehensive understanding on the types of ocean conditions that increase the likelihood of whale entanglements, and what may be done to minimize the frequency of entanglements given this knowledge.

The Habitat Compression Index (HCI) was developed to monitor thermal habitat conditions to identify short-term (monthly to seasonal) ecosystem shifts related to changes in the distribution and abundance of forage species, to better understand the shoreward (or offshore) shifts in whales and their co-occurrence with fishing gear [9]. The development and application of the index and related knowledge was done in partnership with fishermen, fishery managers, conservationists and scientists, particularly those involved with the Dungeness crab fishery, and the index is now routinely monitored and included in risk assessments that inform the management of the crab fishery. The HCI is a monthly adjusted metric that quantifies the spatial extent of cool thermal habitat. The CCLME, like other Eastern Boundary Upwelling Ecosystems (EBUE), has cooler coastal waters due to the upwelling cooler/nutrient rich waters along the coast, and high interannual variability corresponding to years of anomalously cool and warm sea surface temperatures (SST) linked to the influence of North Pacific climate and equatorial teleconnections involving El Niño Southern Oscillation [21]. Previously, we have shown how the HCI related to a decline in krill and increase of anchovy abundance, and an increase in reported whale entanglements off California during the marine heatwave [9]. We then standardized and extended the utility of the HCI within 4 biogeographic regions throughout the CCLME and established its connection with a variety of changes in ocean climate indices and pelagic biodiversity [22,23]. Here we examine the utility of the HCI as an indicator to inform the rate at which thermal habitat changes annually and to assess whether such changes are associated with the reported whale entanglement record.

Herein, we describe how the HCI can improve understanding of the humpback whale entanglement reports over 2.5 decades (2000-present), covering the before, during and aftermath of a large marine heatwave, when whale safe fishing regulations were enacted and there was a boom in northern anchovy (*Engraulis mordax*) populations. Specifically, we review the annual entanglement record and examine correlations with the cumulative habitat compression index – a metric which tracks the overall availability of thermal habitat throughout a year. As noted, we do not know exactly when and where many of the humpback whale entanglements reported occurred in the CCLME, so indicators like the HCI are increasingly important to connect entanglements across several U.S. West Coast fixed-gear fisheries (e.g., Dungeness crab, sablefish *Anoplpoma fimbria* and spot prawn *Pandalus platyceros*). Our overarching hypothesis is that the annual humpback whale entanglement record is related to cumulative changes in available thermal habitat that govern and structure the shared habitat used by whales and fisheries. Furthermore, we examine the trends in both entanglements and a representative humpback whale population abundance estimate by conducting a residual analysis to evaluate whether the increase in reported entanglements may be explained by or attributed primarily to population growth or if climate driven changes in thermal habitat availability may be a leading cause. Therefore, we evaluate the connection between habitat compression with annual variation in reported entanglements since the dramatic increase in 2014–2016, along with a density-dependent perspective involving the long-term recovery and population increase of humpback whales in the CCLME. We review and discuss important ecosystem considerations that may influence the risk of entanglements and their detections, including how a major fishery changed due to regulations to protect whales, the surge in anchovy populations, recovery of derelict gear, and the closing of major salmon fishing seasons during recent years (2023–2024). Finally, building on recent work to forecast habitat compression [24], we highlight forecasts of 2024 and discuss the applicability of short-term forecasts of habitat compression, and how operationalizing the cumulative HCI as a strategic tool may support risk assessments aimed at mitigating whale entanglement.

## Materials and methods

### Whale entanglement records

The confirmed reports of humpback whale (and other whales) entanglement data in the U.S. West Coast Region are summarized annually and publicly available: https://oceanview.pfeg.noaa.gov/cciea-table/?opentab=1&report=whale_entanglement. Additional metadata for the source data for all humpback whale entanglements are also available: https://www.fisheries.noaa.gov/s3//2025-07/2024-whale-entanglements-report-updated-508.pdf. No permits are required for tabulating the annual entanglement record. In brief, all entanglement reports are scrutinized by a team that compares all descriptions, photos and video recordings of individuals (humpback whales have distinct markings and body patterns) [25,5] to ensure that individual reports are not double counted. When possible, if gear marking is present and identifiable, such as numbers on a buoy or a Dungeness crab buoy tag, then it may be assigned to the report. However, the fishing gear for many entanglements are not assignable [5], although best practices documents are available to assist in the identification of fishing gear that has been found on entangled whales ([5]; https://www.fisheries.noaa.gov/s3//2024-04/nmfs-gear-guide-march-2024.pdf). Documentation of whale entanglement reports from Canada and Mexico and Central America are confirmed if they have fishing gear that originated from US waters and therefore count for the annual record for the US West Coast.

### Anchovy and krill abundance

Knowledge of humpback whale forage species is important context for understanding populations, foraging distributions and timing of migration. Annually since 1983, the National Oceanic and Atmospheric Administration National Marine Fisheries Service Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) has sampled ocean conditions and forage species, using a mid-water trawl, to inform stock and ecosystem assessments [26,22]. Standardized model-based forage indicators [27] provide information on the status of key forage species used by whales and other protected species [22]. All research permits to conduct trawling that are required are approved and maintained by NOAA Fisheries; no animal experimentation was conducted. The RREAS samples and monitors prey species used by humpback whales, and prey abundance data from the survey have been shown to follow very similar patterns as humpback whale prey as inferred by stable isotope analysis [15]. Therefore, forage indices that reflect the shifting prey community are key to illuminating how changes in whale feeding behavior may relate to entanglements [9]. Updated annual indices (Catch-Per-Unit-Effort; CPUE) through 2024 are applied here to monitor and describe changes in total krill abundance, adult and young-of-the-year (YOY) northern anchovy within the central and southern CCE (from Cape Mendocino ~40°N to Point Conception 34°N; Fig 1; [9]). These indices are informative of the general ecosystem state for the central and southern CCLME [28] and overlap with the California Dungeness Crab fishery, where many entanglements are reported [5]. The RREAS trawl data is publicly available: https://oceanview.pfeg.noaa.gov/erddap/tabledap/FED_Rockfish_Catch.html.

### Habitat compression, entanglements and population relationships

Habitat compression indices were developed and derived from Santora et al. [9] and Schroeder et al. [23]. Thermal habitat compression is an area-based index that describes the spatial extent of cool sea surface temperature (SST) within coastal upwelling ecosystems, adjusted monthly, that relates to distribution and abundance shifts of forage species, and shoreward concentration of whales with increased likelihood of aggregation. To monitor the availability of thermal habitat and the rate at which it changes on a monthly to annual basis, we monitor the cumulative HCI (cHCI; [23]). The cHCI indicates the rate of change in accumulated thermal habitat and is monitored within four biogeographic regions of the CCLME (S1 Fig). Each year (1980–2024) has a unique cumulative curve and is constructed by the cumulative sum over the twelve months of the year. The cumulative index approach allows for monitoring the rate of change of cool thermal habitat and provides information on habitat changes from winter to spring (preconditioning effects on ecosystem). An important concept underlying the cumulative habitat compression approach is that the index is tracking thermal habitat accumulation over the year and monthly estimates are not independent, except for January. Thermal habitat accumulation from one month to the next is the sum of the previous months in the calendar year. This is an important aspect and feature because the index accounts for how thermal habitat evolves on an annual basis by incorporating autocorrelation. However, cHCI time series on an annual basis are independent (i.e., a January time series is different from a June series). This distinction is important for our analysis of annual reported entanglements. Since the precise timing and location of most entanglement events are unknown, we correlate annual reported entanglements with monthly cHCI indices to identify potential seasonal predictors. Given the index's cumulative design, we anticipate that significant correlations with entanglement rates will be consistent across adjacent months (e.g., a signal in February is likely to persist into March). We also utilize habitat compression forecasts developed by Brodie et al. [24] to document reductions in thermal habitat availability (relative to long-term mean) at a variety of monthly lead times. Previously, these forecasts were skillful at predicting habitat compression during the large marine heatwave (2015–2016) at 6–12 months in advance. We also extend the forecast example by documenting how short-term forecasts involving prediction of spring conditions from the previous December may benefit strategic planning of springtime fisheries when whales are migrating back to CCLME waters. The HCI forecasts and models are reviewed by Brodie et al. [24] and are reapplied here for demonstration and discussion purposes.

The primary objective of this analysis is to identify relationships and patterns between time series of reported entanglements and habitat compression, so that relationships can be examined in future risk and simulation studies to improve estimation of whale mortality and serious injury and mitigation strategies of trap-based fisheries. For comparisons with cHCI, the humpback whale entanglement time series was log-transformed and detrended. The entanglement record has a long-term trend (approx. 1.11 whale per year, trend = 1.11*year-2226.0; Figs 1C and 2) and the cHCI also has a trend (cumulative, by design), so trends were removed to allow unbiased (time-independence) correlations with compression indices. Trends were removed using least squares linear regression, calculating the difference between observed and predicted values. Given the unknown aspects of when and where the majority of reported entanglements occurred [5], the long-term trend in the reported whale entanglement record and broad distribution of reports occurring throughout the CCLME and in all seasons (Fig 1A), we used Spearman rank correlations (*rho*) to assess relationship and patterns between the annual entanglement record and the monthly cHCI (both detrended), by biogeographic region (2000–2024; N = 25 years of overlapping data). We used a Moving Block Bootstrap procedure to estimate robust 95% confidence intervals (CIs) for the Spearman rank correlation coefficients (*rho*). We used a block size of b = 2 years (determined by the $N^{1/3}$ heuristic) to preserve the internal temporal structure of the data. For each of the 48 environmental variables, we generated 10,000 simulated datasets by resampling 2-year blocks of paired entanglement reports and cHCI data with replacement. The 95% CI was derived from the 2.5th and 97.5th percentiles of the bootstrapped correlation distribution. Correlations were considered significant if the 95% CI excluded zero [29].

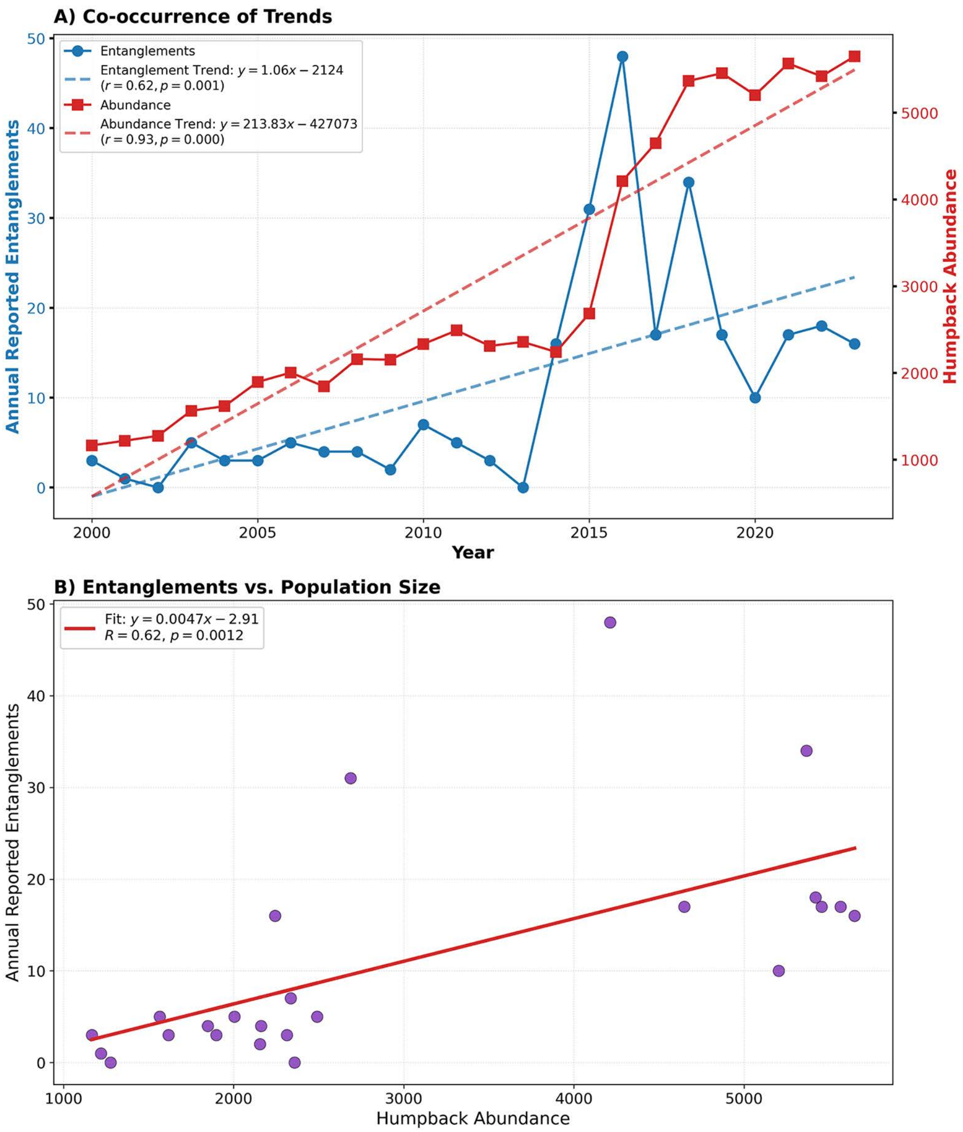


**Fig 2. Comparison of reported humpback whales whale entanglements and population trends. (A)** Trends in reported entanglements and a representative population abundance of humpback whales within the California Current, 2000–2023; (B) relationship between entanglements and humpback whale abundance; residuals were derived from this relationship to evaluate a density-dependent control of entanglements through changes in habitat compression. Note that the residuals reflect the 'excess entanglements'.

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Our second analysis involved assessing trends of reported entanglements and humpback population growth in order to evaluate whether increases in entanglement reports could primarily be attributed to or explained as a result of population recovery. Previous studies have documented potential links between humpback population growth and migration timing may be related to environmental variability [30,31]. In short, this analysis examines the question of whether the increase in reported entanglements is a consequence of increased population size of whales [20,32,14] or a consequence of climate-driven changes in the CCE, which are reflected in amount of thermal habitat that the cHCI tracks. To distinguish between density-dependent factors (population growth) and environmental drivers (habitat compression), we applied a two-stage analytical approach using N = 24 years of overlapping data (2000–2023; no estimate for 2024). For illustrating the overall change in humpback whale population size, we used the reported abundance time series from [32] which is informed by a mark-recapture analysis of photo identification [14] and builds on previous stock assessment research [20]. Importantly, it is worth noting that the humpback whale abundance time series represents the number of whales in the California and Oregon region and is applied here as a representative time series or population growth. There is considerable ongoing research on developing model-based time series of humpback whale abundance [32,14], so the numbers are routinely considered a placeholder for when new estimates are available (i.e., due to mark-recapture research design, counts are likely to change when new identifications are considered in models). Overall, it is the trend in population size that we were interested in relating to the increase in reported entanglements, so the example population time series is of value for our investigation. First, we assessed the relationship between annual humpback whale abundance estimates and total confirmed entanglements using linear regression. To isolate environmental drivers from this population signal, we calculated the entanglement residuals for each year. These residuals represent excess entanglement reports; deviations in the observed rate that cannot be explained by population size alone. We then correlated these entanglement residuals with the 48 monthly, region-specific cHCI time series using the same Moving Block Bootstrap procedure to estimate 95% confidence intervals (CIs) for the Spearman rank correlation coefficients (rho).

## Results and discussion

### Whale entanglement record

A byproduct of the successful protection and recovery of whale populations in the CCLME is the increase in negative interactions between humans and whales, hampering sustainable management of fisheries and protected species, (e.g., fishery entanglements and ship strikes; [18,20,13,33]). Here we briefly review an update for the reported humpback whale entanglement record for the US West Coast from 2000-2024. Co-occurring with humpback whale population recovery [20] is a stark trend in the increase in reported entanglements (Figs 1C, and 2A–B), most notably an order of magnitude increase due to the short-term ecosystem shift coinciding with the prolonged marine heatwave of 2015–2016 (Fig 1C). Prior to 2014, the number of reported humpback whale entanglements were below ten per year.

As a result of the increased number of entanglement reports that began in 2014, substantial changes to the California Dungeness crab fishery were implemented in 2019 to reduce whale entanglement risk, resulting in delayed fishing season opening and early closures (e.g., shifts to late December or January opening and closures in April or earlier; [11]) that are triggered by whale concentrations that are routinely monitored by vessel and aerial surveys, and the recent entanglement record. Additionally, by 2020, new measures had been implemented in the Oregon and Washington Dungeness crab fisheries to reduce entanglement risk (among a number of measures) which included seasonal reductions in the number of crab traps that may be fished (in both Oregon and Washington), and seasonal depth restrictions (in Oregon). Since then, reported entanglements remain higher than pre-heatwave years, with years totaling more than 20 becoming more common. In 2024, entanglements rose to 31, coinciding with another warmer ocean condition year (El Niño) and persistent compressed thermal habitat nearshore throughout summer and autumn (Figs 1C and 3).

Disentangling the record of whale entanglements as related to ocean ecosystem conditions requires an appreciation and accounting for the trend in reported entanglements and whale abundance (Figs 1C and 2). Since entanglement reports are opportunistically rather than systematically detected, the whale entanglement record will always represent an underestimate of the true number of entanglements. However, an assessment of the entanglement reports relative to estimates of habitat compression may help us better understand when we may anticipate increases or decreases in detecting entanglements, and should improve the ability to estimate unobserved entanglements. Our following assessment addresses whether more entanglements are being reported due to there being more humpback whales in the CCLME or whether environmental changes play a role in exacerbating entanglement risk and reporting. Indeed, there exists a significant relationship between reported entanglements and the long-term increase in population abundance of humpback whales (2000–2023; Fig 2).

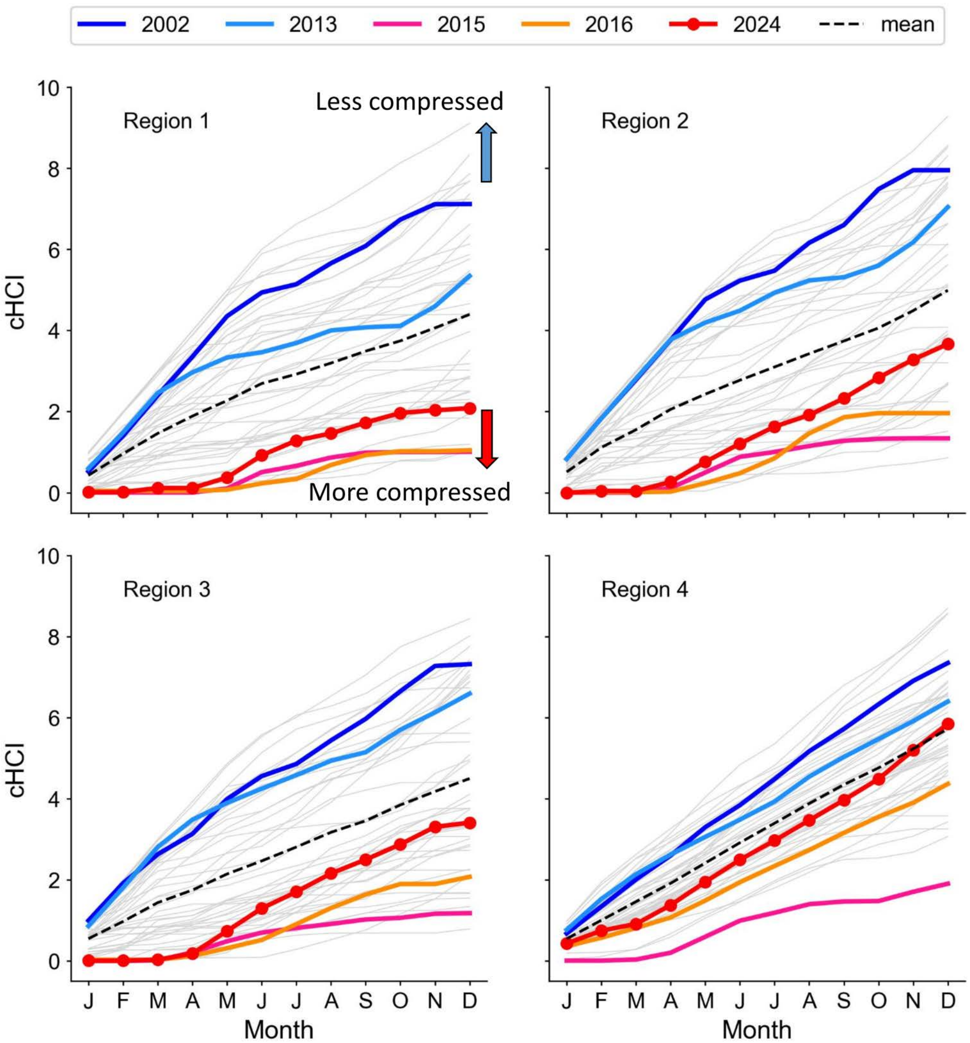


**Fig 3. Cumulative habitat compression index – a method for tracking annual evolution of thermal habitat in the California Current Large Marine Ecosystem per biogeographic region that highlights years above and below when thermal habitat was enhanced or truncated.** Cumulative HCI (cHCI) curves for all years starting from 1980. The cHCI curve for a given year is calculated by doing the cumulative sum of monthly value over the year starting in January. All cHCI curves are plotted in gray, with the long-term mean plotted with the black-dashed curve. Select years of low (2002, 2013; blue lines) and high (2015, 2016; orange and pink lines) coastwide humpback whale entanglement annual averages are highlighted with colored curves. The most recent year 2024 is shown in red, which is similar to 2015 and 2016 in most regions. See Fig 1 for regional biogeographic boundaries.

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## A role for cumulative habitat compression

The area, availability, and persistence of cool thermal habitat in upwelling ecosystems is related to the production of foraging habitat used by whales. When thermal habitat is compressed shoreward, whale foraging behavior is likely to shift shoreward as a response to the availability of the forage species that they may target. The cHCI allows us to document how available thermal habitat is changing throughout the year relative to long-term averages, and permits the rapid identification and comparison per biogeographic region (1980-present; Fig 3).

To illustrate the benefits of the cHCI and approach to entanglement records, we offer guiding questions: What is the extent of cool thermal habitat within the coastal domain in a year? At what rate did cool thermal habitat evolve in a given year (e.g., fast, slow, delayed then fast), and how does that rate compare to other years? How does availability of thermal habitat change during a marine heatwave or ENSO event? Can we disentangle whether there are now more reported entanglements due to increased whale population growth or if climate variability impacts on thermal habitat is a key driver of this record?

Our results show that the answers to these questions can be informed by inspecting the patterns in thermal habitat across several decades to appreciate the full envelope of annual thermal habitat in the CCLME by biogeographic region (Fig 3). The dashed lines in Fig 3 represents the long-term average of how thermal habitat evolves in the CCLME. Trajectories above the mean depict years when thermal habitat developed rapidly and was less compressed; those below the mean are sluggish years where development of thermal habitat was slow to start (notably in the winter through early spring), indicating the system experienced significant overall habitat compression. Thermal habitat was reduced and compressed during the 2015–16 heatwave coinciding with the spike in entanglement reports, although similar years occurred in the past. Following the 2019 heatwave, 2020 followed an average year pattern, while 2021–2023 were above average (less compression; not shown), and in 2024 (a moderate El Niño), the thermal habitat was reduced in all regions except in southern California (Region 4; Fig 2). To facilitate further development of habitat compression as an indicator of potential short-term ecosystem shifts, regional seasonal time series of cHCI are provided (S1 Fig).

### Relating habitat compression and entanglements

It is infeasible to align the spatial and temporal scales of the marine environment to any one entanglement report due to limited reporting. That is, given the dynamic nature of the ocean, the spatial extent of the CCLME, and how whales respond to spatially variable foraging opportunities [15,9,16], alignment of entanglements along with concurrent ocean conditions is problematic. Instead, we conducted an assessment of the total number of entanglements in a calendar year relative to the extent of available thermal habitat throughout the same calendar year. Our 2-step analysis assesses the statistical association of entanglements with the cHCI, as well as evaluating the density-dependent process involving increased population abundance of humpbacks through calculating residuals between the entanglement records and whale abundance time series, and then correlating residuals (i.e., the excess entanglements) with cHCI time series.

First, since there is a trend in the humpback whale entanglement record (Figs 1C and 2A), we examined correlations between regional monthly detrended cHCI and detrended entanglement time series (48 time series; 12 months by 4 regions). This yielded a strong negative relationship (e.g., rho = -0.81, $p < 0.01$, February Region 3; Fig 4A), indicating that deviations in thermal habitat availability are tightly coupled with deviations in reported entanglements. All correlations were negative, significant and robust ($p < 0.01$; Fig 4; see S1 Table and S1 Text for randomizations and confidence intervals), indicating an increase in whale entanglement reports during years of lower-than-average cool thermal habitat area in the CCLME, across all regions (Figs 3 and 4; S1 Table and S1 Text). Correlations ranged from -0.65 to -0.81, and correlations were coherent among biogeographic regions, although slightly weaker in Region 4, where the cHCI is comparatively less variable (Figs 3 and 4). The correlations between annual entanglement reports and cHCI in Regions 1–3 are strongest because those regions contain the most continental shelf habitat (Fig 1B) and more intensive effort within fixed-gear fisheries, and consequently a large extent of risk for entanglements [34,5].

Second, there is a significant positive correlation (r = 0.62, $p < 0.01$) between annual humpback whale abundance and total reported entanglements (2000–2023; Fig 2). This suggests that population recovery may drive the long-term baseline increase in entanglement reports. However, population growth alone failed to account for the extreme inter-annual variability, particularly the spikes observed in 2015–2016 (Fig 2). To explicitly control for density-dependent effects, we calculated the residuals of the entanglement-abundance regression (Fig 2B) and correlated them with detrended cHCI. These residuals or 'excess entanglements' remained strongly correlated with cHCI (e.g., rho = -0.73, $p < 0.01$, February Region 3; Fig 4B; see S2 Table and S2 Text for randomizations and confidence intervals). This strongly suggests that habitat compression exacerbates reported entanglements significantly beyond what is expected from changes in population abundance alone.

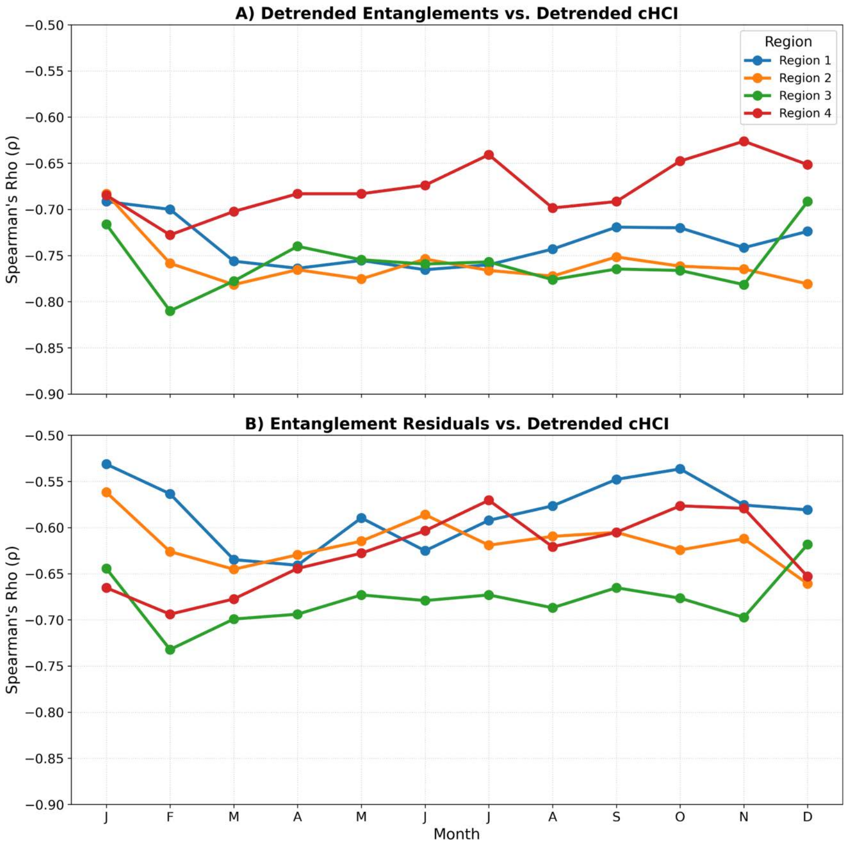


**Fig 4. Correlations between reported whale entanglements and habitat compression. (A)** Spearman correlations between monthly cumulative HCI (cHCI) and the annual humpback whale entanglement record (detrended). **(B)** Spearman correlations between monthly cHCI and residuals derived from the entanglement and population abundance time series (see Fig 2). Negative correlations indicate more entanglements during periods of low cHCI. All correlations are significant, $p < 0.001$ (see S1 and S2 Tables and S1 Text and S2 Text for bootstrapping results). See Fig 1 for regional biogeographic boundaries.

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Overall, the significant correlations between cHCI and reported humpback whale entanglements across all regions suggests greater likelihood of entanglements (both becoming entangled and detecting an entanglement) during years of truncated thermal habitat (Fig 5). Given that entanglements may occur any time of the year and region, during both open and closed fishery periods (e.g., due to lost gear), the significant correlations with cHCI could provide the basis for development of a probability function parameter for an integrated strategic risk model. Although this study is observational, this finding is significant and could be incorporated into risk assessment and mitigation models involving fishing activity (i.e., tracking fishing distribution; [34]) and humpback whale density distribution. Based on our results, not accounting for the relationship between habitat compression and entanglement reports in an integrated fishing and whale risk model may hamper short-term (1–6 months) risk forecast effectiveness. Including a relationship between the observed entanglement record and habitat compression will benefit risk assessments, especially when strategic management is needed when the environment is forecast to include a period of lower availability of thermal habitat (see Fig 6). We recommend that the observed patterns documented here be considered in the future development of a mechanistic and simulation modeling approach to improve the entanglement record (e.g., resolve unknown detection probabilities) and potential risk assessments.

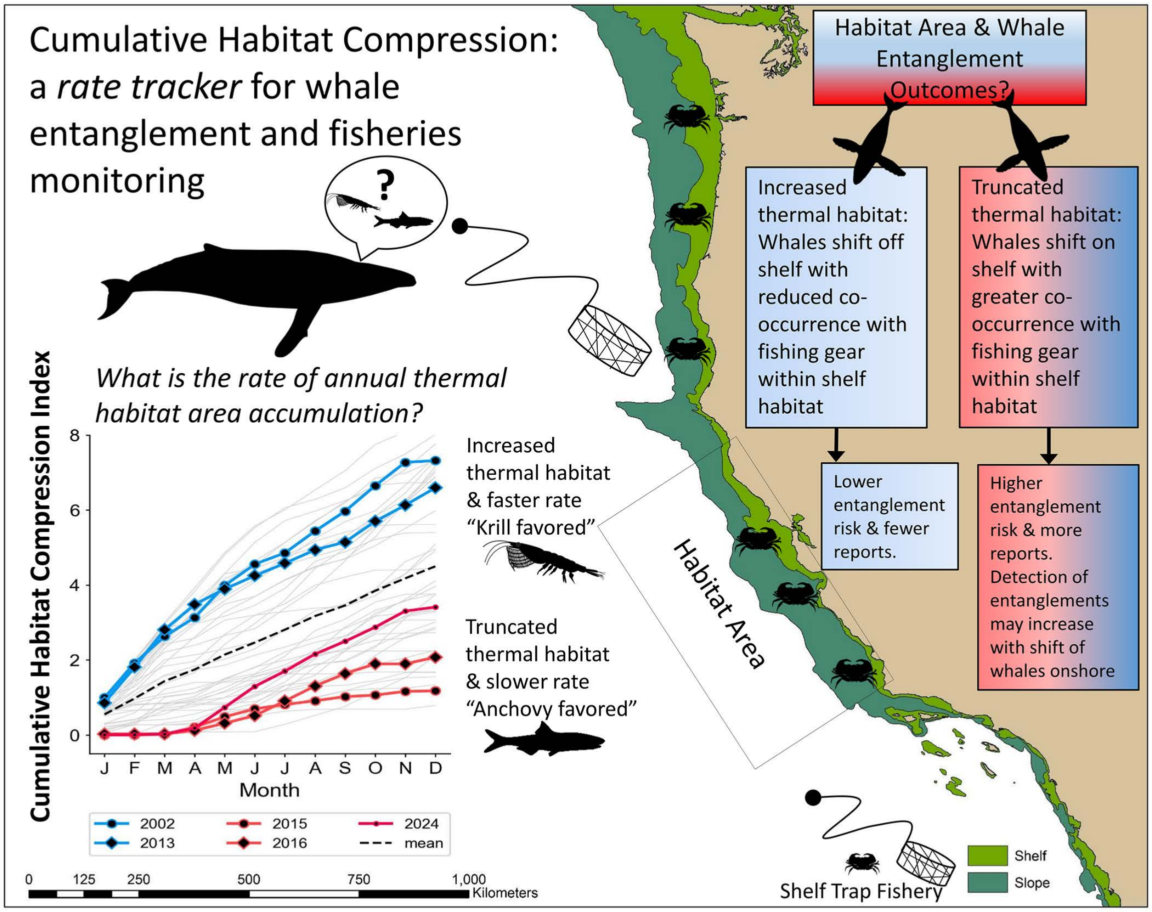


**Fig 5. Conceptual summary on the utility of the cumulative Habitat Compression Index as an rate tracker of thermal habitat availability pertaining to ecosystem shifts (involving humpback whales and their prey in slope and shelf coastal habitats) to inform whale entanglement mitigation science strategies in the central CCLME (e.g., tactical and strategic ecosystem-based fishery management).** In this example, the cHCI in Region 3 (inset; central California coast) shows the outcomes of years with increased and truncated thermal habitat on whale entanglements. Over 2000-2024, this study found a higher number of whale entanglement reports during years of truncated thermal habitat and highlights the role of the recent anchovy population boom (Fig 1), and potential for increased detection of entanglements when whales are closer to shore. The utilization of short-term seasonal forecasts (at January and July; 6 months out) of habitat compression could improve tactical decisional support for dynamic ocean management (e.g., dynamic versus static fisheries closures).

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## Return of the anchovy and other fishery changes

Underlying the recent spikes of reported entanglements and increased population size are signs that whales are responding to distribution of their prey (Fig 1D). Anchovy population cycles remain difficult to predict, although their habitat occurrence and effects on food web/predator responses to their population wax and wane may be generalizable, their impact on ecosystem function is beyond doubt [35,36]. Off California, our previous assessment of the 2015–2016 spikes in reported humpback whale entanglements and habitat compression pointed to a shift in forage species (humpbacks prey-switch) involving a decline in krill abundance and patch distribution, and a slight increase in anchovy (*Engraulis mordax*) abundance (Fig 1D). Following 2017, the central and southern CCLME experienced the largest increase in northern anchovy biomass since the 1970s [37]. Anchovy abundance is negatively related to habitat compression (more anchovy during reduced thermal habitat; [23]), which may have facilitated their recent boom following the record compression

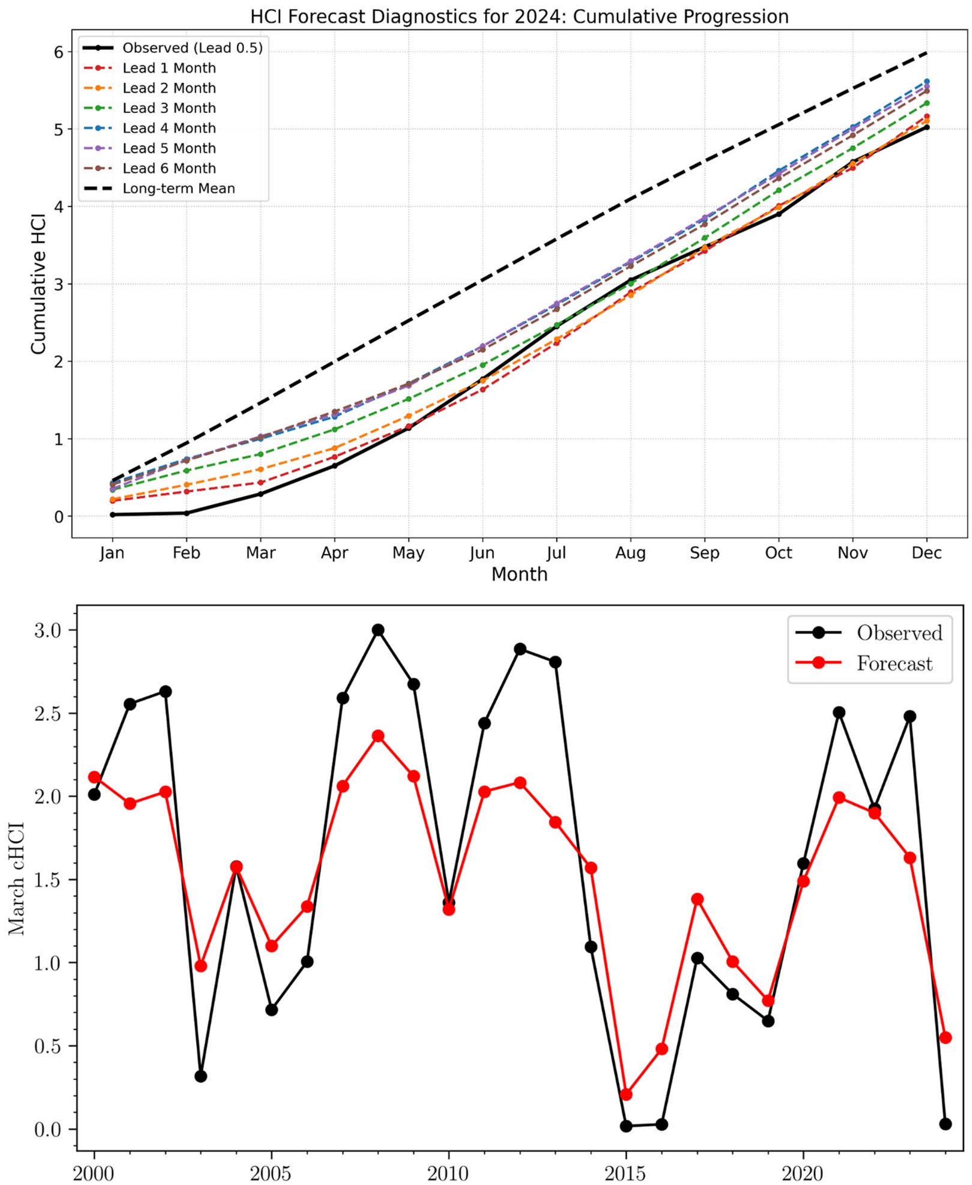


**Fig 6. Forecasts and observations of habitat compression for 2024 for Region 3 (central California).** (top) The rate of thermal habitat accumulation (cHCI) was forecast below average (dashed line; see Fig 3c) for 2024 and demonstrates skill in forecast at 1-6 months leads. (bottom) Strategic example of how the forecast of cHCI can be implemented to inform changes in spring through applying a forecast from December to March. This is the March cHCI values for every year (2000-2024) for forecasts starting the previous December 14 (i.e., Jan = 0.5, Feb = 1.5, Mar = 2.5 etc…). For example, this strategic short-term forecast of the cHCI can inform the status of habitat compression during a critical time period when humpback whales are migrating back to California waters and when the spring Dungeness Crab fishery is operating and decisions are being made about the length of the season.

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observed in 2015–2016 [37]. Anchovy biomass increased to over 2 million metric tons by 2021, and has remained high, but variable since that time [37], with dense aggregations found throughout the central and southern CCLME (regions 3 and 4 in Fig 1B), which characterize the forage landscape most intensively used by humpback whales [16]. The increase in anchovy biomass and their aggregations nearshore have resulted in persistent foraging of humpback whales closer to shore, exacerbated by lower availability of krill abundance (Fig 1D; see [9]). Since then, reported entanglements remain higher than pre-heatwave years, and are possibly attributed partially to persistent anchovy biomass nearshore, where whales are more likely to overlap with fixed fishing gear deployed on the continental shelf, and reported entanglement detections are more likely. The increase of more public awareness about the entanglement issue, and more whales close to shore, may have resulted in increased diligence of entanglement reporting [5]. Furthermore, greater opportunities for detecting entangled whales may have ensued as whale-watching operators can increase the number of trips when whales are reliably closer to the ports of operation.

When anchovy biomass declines, as it has in the past, it may be anticipated that humpback whales are likely to alter their foraging behavior. For example, if anchovy abundance declines and they are concentrated nearshore, as has been the historical pattern during "bust" or declining anchovy abundance periods [38], whales are more likely to concentrate nearshore. When very low anchovy abundance has coincided with years of higher abundance of krill offshore, humpback whales have shifted offshore to feed on krill [9]. If food resources are stressed (e.g., 2015–16), with the current humpback population size (recovering and increasing; [20]), there could be starvation events that impact population size [14] and anomalous foraging distributions of whales (e.g., increased nearshore concentrations, remaining longer on foraging grounds during winter). Ensuring further development of methods for detecting entanglements will help continue to identify the potential role of the current anchovy boom on entanglement occurrence and detection estimation.

*Ghosts in the ocean* - the impact of lost and derelict fishing gear can pose significant challenges to ecosystem-based fishery management [39]. During years of truncated thermal habitat, whales may be more likely to interact with all gear, including lost gear, while foraging nearshore. Historically, the Dungeness crab fishery experiences a high gear loss (upwards of 10% per fishing season; https://wildlife.ca.gov/Notices/Regulations/Gear-Retrieval-Expansion), but it is often difficult to discern whether gear loss is related to entanglements rather than potential conflicts with other gear and weather, although there are instances of reported lost gear entangled on whales [5]. Derelict fishing gear continues to pose a challenge; a rare entanglement of a leatherback sea turtle (*Dermochelys coriacea*) was documented during November 2023 to have occurred in the California Dungeness crab fishing gear that had been lost 1–2 years earlier near the Farallon Islands (https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=218045&inline). New efforts to remove lost fishing gear (both in season and out of season) have increased in recent years and with the help of fishermen. The fishery for California central valley Chinook salmon (*Onchorhychus tshawytscha*) is among the largest on the US West Coast, yet this fishery was completely closed during 2023 and 2024, with massive economic impacts to coastal communities. A large fraction of salmon fishermen also participate in the Dungeness crab fishery [40], and in most years the salmon fleet plays a critical role in recovering lost fishing gear (salmon trolling can be snagged on lost gear). Consequently, lost gear recovery is likely reduced when the salmon fishery is closed or limited, exacerbating lost gear challenges and increasing entanglement risk. This is just one example of how changes in one fishery can impact another, thereby requiring a more complete socio-ecological and economic perspective in co-developing plans to reduce whale entanglements while continuing to ensure the sustainability of fishing communities. Further, while it is important to remove all lost gear whenever possible, increased diligence to remove lost gear during low thermal habitat area years could be beneficial for reducing entanglement risk (e.g., incentivizing conservation).

### Benefits for Whale-Fisheries management

The results of our study may benefit a Take Reduction Team (TRT) that aims to reduce the incidental Mortality and Serious Injury (MSI) of humpback whales along the U.S West Coast. The TRT is a consensus building process that requires coordination among individuals committed to reducing MSI [41]. The best available science must be collected and considered to determine pathways involving tactical and strategic management strategies that will result in a reduction of MSI within the potential biological removal framework. In the long-term, a TRT aims to reduce MSI to below 10% of potential biological removal (i.e., a zero-mortality rate goal) while accounting for fishery economics and potential revision of fishery management plans. To support future management efforts, novel analyses that integrate data on whale behavior, distribution and abundance, fishing activity, and ecosystem conditions that inform entanglement risk or predict how whales may interact with fishing gear and become entangled are needed in a timely manner (Fig 5).

Our previous analysis of the factors associated with the sharp increase in reported entanglements during the marine heatwave helped serve the basis for an ecosystem perspective to inform the California Dungeness Crab Risk Assessment and Mitigation Program (RAMP; [9]). At the center of that synthesis, the conceptualization and quantification of habitat compression as an indicator of ecosystem shifts was critical for bringing clarity to the entanglement management issue (Fig 5). Here, we demonstrate that the US West Coast whale entanglement record is correlated to cHCI along the US West Coast, highlighting the role of annual thermal habitat evolution within a large marine ecosystem. This information can help resolve the role of the environment in understanding entanglement risk, it remains a difficult challenge to identify thresholds that can be used at this time to recommend a trigger for fishery management regulation.

To benefit whale entanglement risk assessments, the cHCI should be considered both alongside and within an integrated fishing and whale abundance and distribution modeling framework to further assess its utility and sensitivity as an indicator. For example, the cHCI may be useful as a strategic indicator within a modeling framework [42,7,8], whereby the rate of thermal habitat availability is considered in simulations specific to each fishery; when the cHCI is below average during winter, extending into spring, or stalls, resulting in significantly less thermal habitat, we may anticipate there could be distribution shifts of whales shoreward (or alternatively offshore) and more interactions with fishing gear, increasing entanglement risk. More generally, whale entanglement mitigation science may consider using the cHCI as a strategic monitoring tool to increase survey effort for detecting entanglements during low thermal habitat periods, or use the information to strategically evaluate predictions and observations of entanglement, meeting the short-term and long-term goals of a whale entanglement mitigation science program.

Considering promising short- and long-term forecasting applications [24,43,44], the cHCI is a good candidate for use as a dynamic ocean management tool [45] for mitigating whale entanglement risk, and considering strategic planning (e.g., static versus dynamic closures). Therefore, proactive management measures could be examined to allow fishery operations during years where short-term forecasts indicate an increase in thermal habitat [46], which most likely coincide with more dispersed whale foraging behavior and less-likelihood of interaction with gear (Fig 5). For example, habitat compression forecasts [24], predicted that the accumulation of thermal habitat throughout 2024 was markedly below the long-term mean throughout the year, with concerning low levels during January-April that are similar to 2015 and 2016 (Figs 3 and 6A). The 31 reported entanglements in 2024 (relatively high compared to the record) and overall elevated entanglement risk, likely could have been forewarned by using cHCI forecasts, which was available in January 2024. Furthermore, short-term forecasts of cHCI from December into spring may benefit strategic decision making about changes in habitat compression during a time period when humpback whales are migrating back to California waters and when the spring Dungeness Crab fishery is operating (Fig 6B). In this manner, forecasts of cHCI for March are robust and can provide resource managers with extended outlooks with confidence (Fig 6B). Long-term forecasts (decades) of cHCI could also inform how climate variability may alter phenology in thermal habitat availability, providing a case scenario for evaluating management strategies [44] to mitigate long-term impacts of fisheries and whale populations. We recommend that additional integrated modeling studies are needed to evaluate the potential of the cHCI as a dynamic ocean management tool.

## Limitations, considerations and conclusions

Unfortunately, we may never know the true entanglement record. While the current reported entanglement time series is the best scientific information available for evaluating entanglement risk, improved estimation of unobserved entanglements may be possible by developing connections of entanglement risks to ecosystem conditions (Fig 5). We also need to manage expectations on use of environmental indicators because increased climate variability may result in unstable relationships, and thus requires ongoing evaluation with new observations. A perfect environmental predictor or model-based solution does not currently exist, and solutions should include an active monitoring program to benefit detection and reporting of entanglements to ensure mitigation strategies are effective.

Habitat compression can also potentially inform models of whale population growth. The representative humpback whale abundance time series used in this study (Fig 2) shows a punctuated increase between 2014–2016 (growth>30% per year; [20,32,14]), a rate that exceeds biological plausibility (typically 6–8% per year, though a max 10% is theoretical; [47]). Rather than perceive this as an error, we hypothesize that the extreme habitat compression and forage species shifts of 2015–2016 facilitated a step-change in detections of individuals. The compression events and concentration of prey near coastal areas (e.g., Monterey Bay) may have increased the recapture probability of previously uncatalogued individuals, allowing it to resolve a higher baseline of the population during and after the heatwave era. We hypothesize that habitat compression concentrates whales and enhances detection probabilities, causing short-term inflationary biases in abundance estimates during heatwaves that are balanced by periods of lower detection during dispersed conditions, ultimately leaving the long-term population trend unbiased. Our residual analysis relies on these resolved abundance estimates. By accounting for this high population abundance, we suggest that the elevated entanglement reports observed during and after the heatwave were not merely a function of there being more whales, but that habitat compression led to both the higher overlap of whales with fishing gear and more whales concentrated closer to shore. This 'compression-assisted resolution' hypothesis requires more evaluation and consideration using new population estimates and demographic modeling, and can be extended to other regions globally where evidence suggests other environmental variability (e.g., temperature and sea-ice shifts) may influence abundance counts of humpback whales [30,14,31,48].

The connections established previously on the role of habitat compression and the unprecedented number of reported entanglements during the marine heatwave paved the way forward on how to monitor changes in ocean conditions. Unfortunate as it was, the previous spike in reported entanglements indicates that our current entanglement detection and reporting methods can detect major entanglement issues after they occur [5]. We must continue to improve our entanglement monitoring efforts, both with using novel technology (e.g., photo IDs, drones, reporting applications) and analytically through development of new statistical and probability methods to estimate how many entanglements are likely to occur that are unreported [18]. The connections between habitat compression and the humpback whale entanglement record may offer several new areas of active research. For example, the application of short-term (6–12 months) SST forecasts have enabled forecasts of habitat compression, without the use of a downscaled regional ocean model, and found that the compression during the marine heatwave was predicted skillfully several months before start of the heatwave and throughout the multi-year event [24,49,46]. We now show that ecological forecasts from that research [24] indicated drastic reductions of thermal habitat in 2024, which corresponds to increased reports of entanglements, suggesting predicting spring conditions could be a strategic advantage (Fig 6). We should continue investigating the application of short-term forecasts of habitat compression to improve predictions at shorter scales (monthly), especially in coordination with ongoing fishery risk assessments [50,45] and longer-term planning to support entanglement mitigation strategies, including ongoing tactical management.

The cumulative habitat compression perspective may be considered a *rate tracker* indicator tool (Fig 5) to evaluate the effect and rate of warming on Eastern Boundary Upwelling Ecosystems [51,23]. EBUEs are some of the most productive ecosystems in the world that support large fisheries and fishing communities [52]. Climate change and variability is disrupting marine ecosystems functioning globally ([53]; [54]), and in particular the effect of persistent marine heatwaves has caused drastic changes impacting the socio-ecological and economic sustainability of fisheries [55,56]. Tools are needed to track the rate of global warming on the availability of thermal habitat within these systems [24,49]. We contend that monitoring the cumulative habitat compression is an effective means for assessing the rate at which these systems are changing seasonally and annually, can inform changes in biodiversity and human wildlife conflicts, as well as evaluating impacts of future warming. Future shifting temperature baselines are likely to occur, thus conducting long-term multi-decadal forecasting of SST [49,43] is necessary for charting a course on how marine ecosystem functioning will change compared to present day (i.e., inform SST thresholds in HCI calculations).

### Conclusion

We found evidence for understanding humpback whale reported entanglement patterns through the lens of cumulative habitation compression changes, resulting in 4 primary conclusions. (1) Habitat compression is an underlying driver of humpback whale entanglements. We found strong negative correlations between the amount of cool thermal habitat and the number of reported whale entanglements. Years with low cumulative thermal habitat (high compression) result in the highest number of entanglements across all biogeographic regions of the US West Coast. The cHCI is likely a critical predictor of both entanglement risk and detection of entanglements. (2) Changes in habitat compression matter more than population growth trends. While the recovery of the humpback whale population contributes to the baseline increase in interactions, it does not fully explain the extreme spikes in entanglements (e.g., 2015–2016 and 2024). We controlled for population size by calculating "excess entanglements" (residuals), these residuals were strongly correlated with habitat compression. This suggests that environmental conditions exacerbate risk significantly beyond what is expected from density-dependent factors alone. Furthermore, we suggest a new "compression-assisted resolution" hypothesis that may explain the biologically implausible humpback whale population growth rates (greater than 30% per year) recorded during the 2015–2016 marine heatwave. (3) Ecological forecasting of habitat compression provides an early warning system. We show that the cHCI effectively forecasts ocean conditions 6–12 months in advance. For example, forecasts available in January 2024 correctly predicted the low thermal habitat conditions observed later that year, which coincided with a rise in entanglements (31 reports). (4) The collective evidence of habitat compression and whale entanglements suggest that operationalizing the cumulative habitat compression as a "rate tracker" will benefit fisheries and protected resources management. We recommend integrating the cHCI into regional risk assessments (like the RAMP) and at the scale of the U.S. West Coast as a "rate tracker" and evaluating management scenarios where by entanglement risk could be mitigated. By monitoring the rate at which thermal habitat accumulates during winter and spring, managers can make strategic decisions regarding seasonal fishing activity and improve both detection and mitigation of whale entanglements.

### Data availability

The data and analysis files for the cumulative habitat compression index and whale entanglements are included as a Supplemental file (S1 Data).

## Supporting information

**S1 Table. Spearman rank correlations between detrended humpback whale entanglements and cHCI (monthly by region), and randomization results for confidence intervals (2000–2024).**
(CSV)

**S2 Table. Spearman rank correlations between humpback whale entanglement residuals (excess entanglements) and detrended cHCI (monthly by region), and randomization results for confidence intervals (2000–2023).**
(CSV)

**S1 Fig. Cumulative HCI (cHCI) time series for January (top), June (middle), and December (bottom).**
(TIF)

**S1 Text. Results of all bootstrap randomization tests, distributions and confidence intervals for Spearman rank correlations between detrended humpback whale entanglements and cHCI (monthly by region).**
(PDF)

**S2 Text. Results of all bootstrap randomization tests, distributions and confidence intervals for Spearman rank correlations between humpback whale entanglement residuals (excess entanglements) and detrended cHCI (monthly by region).**
(PDF)

**S1 Data. Data.**
(XLSX)


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