Message in a Bottle: Archived DNA Reveals Marine Heatwave-Associated Shifts in Fish Assemblages

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Summary: Novel quantitative abundance estimates from archived DNA reveals marine heatwave-associated shifts in fish assemblages.

**Abstract**

Marine heatwaves can drive large-scale shifts in marine ecosystems, but studying their impacts from a species assemblage perspective can be difficult. Here, we leverage the taxonomic breadth and resolution of DNA sequences derived from the ethanol of a 23-year longitudinal sample collection, combining these with microscopy-derived ichthyoplankton identification to yield higher-resolution species-specific quantitative abundance estimates of fish assemblages in the California Current Large Marine Ecosystem during and after the 2014-16 Pacific marine heatwave. This integrated dataset reveals patterns of tropicalization with increases in southern, mesopelagic species associated and declines in important temperate fisheries targets (e.g. North Pacific Hake (*Merluccius productus*) and Pacific Sardine (*Sardinops sagax*)). We observed novel assemblages of southern, mesopelagic fishes and temperate species (e.g. Northern Anchovy, *Engraulis mordax*) even after the return to average water temperatures. Our novel modeling approach opens the door to reconstructing the historical dynamics of assemblages from modern and archived samples worldwide.

**Introduction**

Climate-induced marine heatwaves (MHWs) are increasing in frequency and severity with far-reaching consequences in marine ecosystems (*1*) ranging from severe organismal stress to cascading ecosystem effects (*2*). Notable recent examples include repeated bleaching events across the Great Barrier Reef (2016, 2017, 2020) (*3*) and near-total kelp deforestation in Northern California, USA (2016-19)(*4*). These marine heatwaves precipitated drastic, unprecedented changes in dominant foundational species across hundreds of thousands of square kilometers of shallow, coastal ecosystems.

The impacts of such large environmentally driven disturbances on coastal marine ecosystems have been ecologically and economically significant (*5*–*7*). In the 1940s, the dramatic collapse of Pacific Sardine (*Sardinops sagax*) disrupted marine foodwebs, causing broad-scale, negative socio-economic impacts across the Northeast Pacific (*8*–*10*). To better understand the processes driving these complex marine ecosystem dynamics and to avert similar fisheries collapses within the California Current Large Marine Ecosystem (CCLME), the California Cooperative Oceanic Fisheries Investigations (CalCOFI) was formed in 1949. CalCOFI has continuously conducted systematic fisheries-independent surveys of the southern CCLME from 1951 until present (*11*, *12*), focusing on monitoring larval fish assemblages, as larval fish dynamics are a key predictor of ecosystem health and function (*5*, *12*, *13*).

Larval fish abundances help to characterize the state of marine ecosystems as they track spawning-stock biomass (*14*). Over 70 years of CalCOFI research has documented decadal and annual changes in fish assemblages in response to environmental conditions, identifying major shifts in response to Pacific Decadal Oscillations and El Niño Southern Oscillations (*12*, *15*–*17*). These decadal and annual changes in ichthyoplankton dynamics are superimposed over the strong biogeographic assemblage associations with distinct water mass characteristics within the Southern California Bight (*17*). Ichthyoplankton assemblages differ among the colder and fresher California Current, warmer and saltier California Counter Current and Central Pacific water mass, and in upwelling conditions across the continental shelf (*11*, *13*, *18*, *19*). Importantly, periods of elevated temperatures were historically associated with higher abundances of southern, mesopelagic species and Pacific Sardine while colder periods were associated with higher abundances of northern, mesopelagics and Northern Anchovy (*Engraulis mordax*) (*10*, *20*). These insights into forage fish community dynamics across decadal climatic regime shifts are vital to understanding the effects of climate change on the CCLME (*9*, *11*, *19*).

Despite the value of previous CalCOFI ichthyoplankton efforts, such traditional manual identification of larvae is labor-intensive, and taxonomic resolution is often limited by a lack of discernible morphological characteristics (*21*). Here, we reconstruct ichthyoplankton assemblages over 23 years, applying genetic metabarcoding (amplicon sequencing) to the ethanol surrounding preserved CalCOFI plankton samples. We pair these data with morphological count observations in a joint Bayesian model to estimate species-specific larval abundance.

We model taxon sequence-read counts from metabarcoding as an outcome of the PCR process, wherein each taxon has a different amplification efficiency for the primer set used (see Materials and Methods). We link the sequencing data to morphological ichthyoplankton counts to constrain the species-specific starting concentrations of DNA in the ethanol jars. The resulting integrated model leverages the taxonomic breadth and resolution (*22*, *23*) of amplicon sequencing, combining these with the power of morphological counts to yield species-specific quantitative abundance estimates. By jointly interpreting these datasets, we can track changes in abundance for a broad diversity of larval fish species, yielding a much higher-resolution picture of these assemblages.

The resulting estimates capture major and sometimes highly unexpected changes to the fish assemblages during and after the 2014–2016 Pacific Marine Heatwave (MHW), the warmest 3-year period in the North Pacific over 100 years of recorded history (*24*). We directly examine the responses of ichthyoplankton assemblages to sea surface temperature (SST) as an abiotic proxy for the MHW as a whole, recognizing that a suite of environmental variables including upwelling strength and location, dissolved oxygen, and salinity, among other environmental covariates, changed dramatically during the climate change influenced MHW (*25*–*28*). Complementary analyses using mean water-column temperature – rather than SST – yielded similar results (See Supplement S1).

**Results**

Metabarcoding with MiFish *12S* (*29*) generated a total of 59.9 million sequence reads across 84 jars representing 90 unique DNA extractions and 262 unique PCR technical replicates. All sequence data were processed using the *Anacapa Toolkit* (*30*). After quality control, sequence-variant (ASV) dereplication, and decontamination processes (*22*, *30*, *31*), we retained a total of 54.5 million reads (See Supplement 1 Methods). From these data, we classified 130 unique taxa including 103 species-level assignments (79%), 15 genus-level assignments (12%), 11 family-level assignments (8.5%), and 1 class-level assignment. We identified two distinct morphologically indistinguishable lineages of the Northern Lanternfish (*Stennobrachius leucopsarus*). The two lanternfish lineages exhibited dramatically different ecological patterns across the samples and were therefore treated separately.

Independent microscopy-count data from paired, matching formalin-preserved samples consisted of 9,610 larvae sorted across 84 jars. From these data, we classified a total of 92 unique taxa including 76 species-level assignments (83%) and 16 genus-level assignments (17%).

For our integrated Bayesian model, we focused on the 56 species that had sufficient representation across the metabarcoding data set to achieve model convergence (observed in >10 technical PCR replicates) and thus provided reliable quantitative estimates (Figures S3-S5). Model fits yielded station-, species-, and year-specific larval abundances for 56 fish species spanning a 23-year period.

*Displacement of Target Fish Species and Tropicalization of Fish Assemblages Associated with the Marine Heatwave*

We observed a transformation of marine ichthyoplankton assemblages during the 2014–2016 MHW where southern, mesopelagic species increased while several temperate species of critical ecological and economic importance declined. Such synchronous changes in the marine ichthyoplankton assemblages occurred during the MHW despite the hundreds of kilometers between stations and unique biogeographic characteristics associated with each sampled geographic location (See Supplement 1 results). For example, the mesopelagic Mexican Lampfish (*Triphoturus mexicanus*) was at peak abundance during the MHW, and extended its typical range both poleward and into coastal shelf waters (Figures 1a & c, S6-10).

Shifts were observed throughout the ichthyoplankton assemblages of the study region (Figures 2-3). On the one hand, subtropical, mesopelagic species uniformly increased in association with elevated sea-surface temperatures. On the other hand, many coastal species typically seen in the region tended to decrease (Figure 2, S6-26). In particular, the abundances of northern, mesopelagic species and fisheries targets such as Pacific Sardine (*Sardinops sagax*) and North Pacific Hake (*Merluccius productus*) were significantly correlated with colder sea surface temperatures and displayed negative co-occurrence patterns with warm associated southern, mesopelagic taxa (Figure 3, S27-28).

Graphical user interface, application

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**Figure 1. Temperature-Occurrence Associations in Fish Species**

Changes in species occurrence patterns associated with SST, with southern, mesopelagic species increasing in prevalence with elevated temperature (A). T statistic (slope coefficient / standard error) from a generalized binomial mixed model was calculated for each species across all stations. Only 23 out of 56 total species with significant slopes (95% CI that exclude zero) are plotted. Importantly, metabarcoding identified cold-associated variants of the Northern Lanternfish (*Stennobrachius leucopsarus*) that cannot be morphologically identified (B) as well as common warm-associated species such as the Mexican Lampfish (*Triphoturus mexicanus*) (C).

Diagram

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**Figure 2. Increased Abundance of Southern Oceanic Species Drive Fish Community Shifts**

Changes in species abundance in response to SST ˚C, with southern, mesopelagic species increasing in abundance with elevated sea surface temperature (A). As in Fig 1, significant T statistics from generalized linear models are plotted. Southern mesopelagic fishes were associated with increased temperature as indicated by summarizing species-specific slopes from generalized linear models (B) and by the aggregated abundance relationship (C; each point is the mean posterior estimate of abundance for all southern, mesopelagic species in a single year). In contrast, abundances of benthic species and coastal pelagic species such as Northern Hake and Pacific Sardine abundances, were associated with cooler temperatures.

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**Figure 3. Novel Marine Heatwave Assemblages**

Shifts in species abundances before the MHW (1996-2013) compared to during and after the MHW (2014-2019). Synchronous increases in southern, mesopelagics and Northern Anchovy were observed across all stations. Here, stations are shown in rows, species in columns, and the change in abundance between the two ecological phases shown as the response variable. Fisheries targets including Pacific Sardine and North Pacific Hake, as well as many other benthic and coastal species, had concurrent negative associations. Significant differences during and after the MHW are marked with + or -.

*Biomass Changes in Forage Fishes*

Both because of their own commercial value and because they are prey for other high-value fishery species, sardine and anchovy fluctuations have been a major focus of fisheries research since the 1950s (*9*). Our model estimates are consistent with other studies (*20*, *32*) that documented a decline in both sardines and anchovy beginning in 2005. This period of time was followed by high abundances of anchovy, but continued low abundances of sardine in the wake of the MHW, 2015-2019 (Figure 4). Although anchovy larvae abundance was low in spring during the 2014-2016 MHW, anchovy recruitment was high in summer 2015 (*33*). Anchovy mature in approximately one to two years (*32*, *34*) and thus the 2015 class likely began spawning in mid-2016 (*20*), leading to high anchovy spawning stock biomass and larval abundances by 2016 and lasting into 2019 and 2020 (*35*).

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**Figure 4. Synchronous Increase in Anchovy Abundance During and After Marine Heatwave**

Posterior estimates for larval fish abundances (counts/10m2) over time at each of the four sampled stations. Joint modeling of metabarcoding and morphological counts reconstructed increases in Northern Anchovy (*Engraulis mordax*) [blue] during the recent Pacific Marine Heatwave and low spawning of Pacific Sardine (*Sardinops* sagax) [red] over the past decade (points are means and error bars are 95% credible intervals; shaded region is during and after the MHW). SST is plotted above the Northern Anchovy and Pacific Sardine abundances, for reference.

**Discussion**

*Displacement of Target Fish Species and Tropicalization of Fish Assemblages Associated with the Marine Heatwave*

Recent studies demonstrate the tropicalization of terrestrial and marine ecosystems in response to climate change (*40*, *41*). These shifts can induce novel species interactions, catalyzing changes in ecosystem function (*2*, *25*). For example, we observe the combination of high abundances of both Northern Anchovy and southern, mesopelagics (*5*, *38*) – a pattern otherwise undocumented in the previous >70-year CalCOFI dataset (*16*, *20*). Furthermore, our results suggest multiple coastal pelagic fisheries targets may continue to be scarce as environmental conditions that are similar to the 2014-2016 MHW become more common (*5*, *38*, *39*). Although the ecological implications of these novel assemblages are, by definition, unpredictable, our results suggest that if future assemblages resemble those seen in the MHW, increases in Northern Anchovy and southern, mesopelagic fishes are likely to be associated with decreases in Pacific Sardine and North Pacific Hake in the Southern CCLME (*40*, *41*); these shifts have fundamentally changed ecosystems and fisheries relative to the recent past (*20*).

*Biomass Changes in Forage Fishes*

The rise in anchovy and continued low abundances of sardine during the MHW is an ecological surprise. Correlative analyses between basin-scale environmental indices such as the Pacific Decadal Oscillation indicate that, for the latter half of the 20th century, anchovy thrived under cooler conditions and sardine under warmer conditions (*10*). However, our findings and others (*5*, *9*, *38*, *42*) suggest that the mechanisms that govern the population dynamics of these species are not a mere function of temperature, but that more complex factors drive recruitment dynamics of these species (*20*). For example, despite largely synchronous responses of fish assemblages to the marine heatwave, sardine declines were not consistent across the CCLME, with refugia of localized abundance in nearshore waters potentially driven by distinct, favorable conditions (*9*, *20*, *32*).

Further improving our mechanistic understanding of drivers of fish assemblage dynamics will better inform ecological predictions in the face of extreme ocean events such as MHWs which are likely to increase in frequency and duration under climate change (*43*). As we demonstrate, a combination of metabarcoding and visual surveys can characterize species across trophic levels (*44*) and this has the potential to reveal ecological mechanisms. Here, we used metabarcoding to accurately characterize the composition of larval fishes in CalCOFI plankton samples. Future efforts could focus on documenting the phytoplankton and zooplankton assemblages that comprise both larval prey and predators. Several major hypotheses seeking to explain recruitment variability are underpinned by the capacity of young larvae to consume appropriate prey that facilitates faster growth (*45*). Unfortunately, accurately characterizing the larval prey field has traditionally been difficult as prey are generally too small to be accurately sampled by nets (*46*). Metabarcoding of water samples from the same locations where larvae are collected, however, can characterize the larval prey field at an unprecedentedly high level of detail. In addition, metabarcoding of the stomachs of larval fishes can then identify actual prey items that were consumed by larvae. Evaluating the larval prey field and gut contents through metabarcoding will help us to finally understand the drivers of recruitment volatility in coastal pelagic and other fishes (*5*, *32*, *47*–*51*).

The described unexpected rise in anchovy during the 2014-16 MHW resonated throughout the CCLME (*39*). For example, California sea lion pups grew at anomalously high rates after their mothers consumed copious anchovy forage and produced ample milk (*40*). High rates of almost exclusively anchovy consumption also seemingly induced thiamine deficiency in adult salmon resulting in poor condition of recruits (*52*). Birds capable of feeding on anchovy thrived (*38*) while those unable to consume anchovy perished (*41*). Given that conditions comparable to the 2014–2016 MHW are predicted to be more common in the CCLME in the future (*1*), our results suggest that continued biological responses to both anchovy-dominated forage-fish assemblages and MHW-associated ocean warming conditions are likely to be without modern analog (*20*).

*Novel Insights from Legacy Collections*

Molecular tools differentiated variants and species that were not morphologically identifiable in the ichthyoplankton (*21*).For example, metabarcoding identified unique cold-associated variants of the Northern Lampfish (*Stennobrachius leucopsarus*) that are morphologically indistinguishable and combined as a complex are only weakly associated with cooler temperatures. By illuminating such unseen variation, molecular methods reveal ecological dynamics otherwise hidden by shared larval morphology.

Ultimately, our approach to studying historical fluctuations in ichthyoplankton assemblages reveals climate-associated biological changes in the CCLME, and suggests ways in which these changes could alter the function and socio-economic benefits derived from marine ecosystems. Importantly, this novel approach provides quantitative estimates by non-destructively sampling legacy collections via metabarcoding, and at the same time provides a mechanistic framework for determining absolute abundance estimates from compositional amplicon sequencing data (*53*–*56*). Here we relied on morphological counts to ground compositional metabarcoding data, but our framework suggests that any estimate of abundance (e.g. qPCR) or amplification efficiency (e.g. derived from mock communities) can achieve similar results (See Supplement 2) (*55*, *56*). Unlocking such quantitative metabarcoding approaches expands the potential for linking ecological assemblages to environmental processes beyond just presence-absence analyses (*57*–*59*). Such quantitative approaches may prove critical in modeling and predicting future ecosystem change, although directly linking assemblage dynamic responses to climate-driven forces remains inherently challenging. While the CalCOFI samples are specific to ichthyoplankton from the CCLME, bulk collection of community samples is commonly used to survey plankton, insects, pollen, gut contents, and microbiomes, among many other targets (*60*). As such, here we provide broadly applicable methodology with which to efficiently understand modern and historical changes in ecological communities.

**Materials and Methods**

*Study Design*

To investigate decadal changes in the ichthyoplankton assemblages in the California Current vicinity, we identified ichthyoplankton from four distinct stations during spring months. Archived spring ichthyoplankton samples were collected across four biogeographically dissimilar stations with variable water properties (*61*) over 2 decades (1996,1998-2019; Figure S1; See Supplement 1 methods)(*5*, *38*). Decades of research within the study region (*16*, *17*, *20*, *62*) indicate the majority of species spawn in spring and closely track adult biomass (*63*). Hence, we expect the spring ichthyoplankton to reflect underlying changes in the local fish assemblages.

At each station, oblique bongo net tows were conducted from 210 m depth to the surface using standard CalCOFI methods (*15*, *64*–*66*). Cod end contents of both bongo nets were preserved at sea. The starboard side was preserved in sodium borate-buffered 2% formaldehyde and the port side was preserved in Tris-buffered 95% ethanol. Microscopy was conducted to identify species abundance from formaldehyde-preserved samples following standardized CalCOFI techniques (*61*). DNA metabarcoding was conducted on the ethanol in which port side samples were preserved using the MiFish Universal Teleost (*67*) PCR primer set targeting the *12S* rRNA mitochondrial gene region. See Supplement 1 methods for full description.

*Estimating Abundance*

We estimated the abundance of ichthyoplankton in each jar using a novel joint Bayesian hierarchical model described in detail in Supplement 2. In brief, we estimate that the number of sequenced amplicons, for any species *i,* is proportional to the species-specific fraction of DNA in the PCR template (*53*, *55*, *56*). The amplicons produced during a PCR reaction are dictated by the amplicon efficiency parameter , which is characteristic of the interaction between the particular primer set and each species being amplified. Thus, for any species *i*, the number of amplicons should be directly related to the efficiency of amplification and the starting concentration of DNA template such that

(1)

where is amplicon abundance, is the true number of DNA copies in the reaction attributable to species *i*, is the species-specific amplification efficiency (bounded on (0,1)), and is the number of PCR cycles used in the reaction (*68*).

However, not all molecules of DNA are transferred through each molecular step (*69*, *70*), changing what in eq. 1 appears to be a single-species process – each species being amplified independently – into a multi-species process; the number of amplicons observed for species *i* will depend upon both the amplicons produced for species *i* = 1 and the amplicons produced for species *i* = 2, 3, ..., *I* in the same reaction. Observations of amplicons are thus compositional data, meaning they are the proportions of the sample amplicon reads and convey relative quantitative information of the observed species and therefore need to be analyzed as such (*54*).

To retain the data-generating structure from eq.1 as much as possible, we develop a model for a single sample with many species. As above, if we let *I* index species with *I* = 1, 2, ..., *I*, then we can write a deterministic equation for the number of amplicons observed in log-space as

(2)

where the only new term is η, representing the proportion of reads observed from a given sampling run (See supplement 2 for details). Note that in this formulation η is a single value shared across all species and serves to scale the number of amplicons observed. Additionally, we can rewrite the number of DNA copies in terms of proportional number of counts, log() = log() − log() . Note that the second term in this equation is a sum of the counts across all species, and so is a single shared value for all species. As such it can be integrated into the value η that scales the overall abundance for each species *i*,

(3)

This equation is appealing because it provides a process-oriented description of the biology of interest (the βs), a term for how PCR modifies our amplicon sequence count observation of the true abundance ( , and a term for how subsampling of DNA reads will adjust the number of amplicons observed (log(η)).

However, in the absence of additional information, it is not possible to estimate the β and *a* parameters from metabarcoding data alone. Including morphological count data enables us to estimate the confounded parameters from metabarcoding data. For each sampled station, we have two independent sets of observed data: 1) counts of larval/juvenile fishes for each taxon from the formaldehyde jars and 2) counts of amplicons for each taxon from ethanol jars. These observed data arise from a common (but unobserved) biomass for each species at each station-year combination, and thus we can model them jointly (*71*).

Microscopy counts were modeled as Poisson-distributed given their relatively small absolute values and low variance (*64*), and amplicon sequence data were modeled using a Negative Binomial distribution given their relatively high absolute values and high variability among replicates (Figure S2-S4). These statistical distributions are commonly used in models of amplicon and count data, respectively (*35*–*37*). A full description of model implementation and assumptions are provided in Supplement 2.

*Data Analysis*

After model estimation, we calculated mean abundance estimates (larvae counts per standardized volume towed) per species per station per year. To explore species-specific sea surface temperature (SST) relationships, we fit a Bayesian generalized linear model using log (abundance) as the response variable and SST (˚C) as a continuous predictor variable. Models were implemented for each species using Stan as implemented in R (*75*, *76*). We then summarized the affinity between each species and SST by calculating a T-statistic based on each species' estimated coefficients (mean slope/standard deviation). We further plotted the estimated slope for each “species grouping” by habitat associations derived from previous CalCOFI research (See Supplement 1 methods)(*63*). We summed total log (abundance) per habitat association per station per year and fit a Bayesian generalized linear model using log (total abundance) as the response variable and SST (˚C) as a continuous predictor variable.

We repeated the above analyses using a Bayesian binomial model using presence as the response variable and SST (˚C) as a continuous predictor variable across the data set to explore occurrence relationships with temperature and identify warm- and cool- associated taxa. We set a threshold of presence/absence based on the model using a threshold of < 0.01 larvae per standardized volume to be considered absent within a station.

We further explored species occurrence and abundance relationships with SST by fitting the above Bayesian generalized linear models with station as a random effect (See Supplement 1 results).

We visualized anchovy and sardine abundance over time by calculating the mean log (abundance) of each species per station per year. We then plotted the mean log (abundance) of each of the four stations while error bars represent the 95% confidence intervals observed for a given species at a given station in that year.

To evaluate the effect of the marine heatwave (MHW) on CCLME fishes we compared estimated species abundances before the MHW (1996-2013), to both during and after the MHW (2014-2019), at each station respectively. We first calculated the mean abundance for each species at each station for each model run. We then subtracted the means for each model run to evaluate changes in MHW abundance per species per station per model run. We then calculated a 95% CI of change in MHW abundance per species to identify which species were significantly different before vs. during and after the MHW at each station.

All data and code to conduct analyses and generate all figures are available on GitHub (https://github.com/zjgold/CalCOFI\_eDNA) and associated Google Drive link (https://drive.google.com/drive/folders/12cU9mY\_CWoro-x6Hgh\_pgv\_66zZEzm1h?usp=sharing) [will be replaced with a Dryad repository upon acceptance].

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* Conceptualization: ZG, DK, KDG, ART, LRT, PHB
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*Competing Interests*

The authors declare no competing interests.

*Data and Materials Availability*

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. All data and code to conduct analyses and generate all figures are available on GitHub (https://github.com/zjgold/CalCOFI\_eDNA) and associated Google Drive link (https://drive.google.com/drive/folders/12cU9mY\_CWoro-x6Hgh\_pgv\_66zZEzm1h?usp=sharing) [will be replaced with a Dryad repository upon acceptance].

**References**

1. E. C. J. Oliver, S. E. Perkins-Kirkpatrick, N. J. Holbrook, N. L. Bindoff, 9. Anthropogenic and natural influences on record 2016 marine heat waves. *Bull. Am. Meteorol. Soc.* **99**, S44–S48 (2018).

2. T. L. Frölicher, C. Laufkötter, Emerging risks from marine heat waves. *Nat. Commun.* **9** (2018), pp. 1–4.

3. T. P. Hughes, J. T. Kerry, A. H. Baird, S. R. Connolly, A. Dietzel, C. M. Eakin, S. F. Heron, A. S. Hoey, M. O. Hoogenboom, G. Liu, M. J. McWilliam, R. J. Pears, M. S. Pratchett, W. J. Skirving, J. S. Stella, G. Torda, Global warming transforms coral reef assemblages. *Nature*. **556**, 492–496 (2018).

4. L. Rogers-Bennett, C. A. Catton, Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. *Sci. Rep.* **9**, 1–9 (2019).

5. J. M. Nielsen, L. A. Rogers, R. D. Brodeur, A. R. Thompson, T. D. Auth, A. L. Deary, J. T. Duffy-Anderson, M. Galbraith, J. A. Koslow, R. I. Perry, Responses of ichthyoplankton assemblages to the recent marine heatwave and previous climate fluctuations in several Northeast Pacific marine ecosystems. *Glob. Chang. Biol.* **27**, 506–520 (2021).

6. W. W. L. Cheung, T. L. Frölicher, Marine heatwaves exacerbate climate change impacts for fisheries in the northeast Pacific. *Sci. Rep.* **10**, 1–10 (2020).

7. M. L. Pinsky, R. L. Selden, Z. J. Kitchel, Climate-Driven Shifts in Marine Species Ranges: Scaling from Organisms to Communities. *Ann. Rev. Mar. Sci.* **12**, 153–179 (2020).

8. E. A. Becker, K. A. Forney, J. V. Redfern, J. Barlow, M. G. Jacox, J. J. Roberts, D. M. Palacios, Predicting cetacean abundance and distribution in a changing climate. *Divers. Distrib.* **25**, 626–643 (2019).

9. D. M. Checkley, R. G. Asch, R. R. Rykaczewski, Climate, Anchovy, and Sardine. *Ann. Rev. Mar. Sci.* **9**, 469–493 (2017).

10. F. P. Chavez, J. Ryan, S. E. Lluch-Cota, C. M. Ñiquen, Climate: From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. *Science (80-. ).* **299**, 217–221 (2003).

11. M. Lindegren, D. M. Checkley, T. Rouyer, A. D. MacCall, N. C. Stenseth, Climate, fishing, and fluctuations of sardine and anchovy in the California Current. *Proc. Natl. Acad. Sci. U. S. A.* **110**, 13672–13677 (2013).

12. N. D. , E. Drenkard, A. R. Thompson, E. D. Weber, D. Wilson-Vandenberg, S. McClatchie, J. A. Koslow, B. X. Semmens, Bridging From Monitoring to Solutions-Based Thinking: Lessons From CalCOFI for Understanding and Adapting to Marine Climate Change Impacts. *Front. Mar. Sci.* **6**, 695 (2019).

13. P. E. Smith, H. G. Moser, Long-term trends and variability in the larvae of Pacific sardine and associated fish species of the California Current region. *Deep. Res. Part II Top. Stud. Oceanogr.* **50**, 2519–2536 (2003).

14. C. H. Hsieh, C. S. Reiss, J. R. Hunter, J. R. Beddington, R. M. May, G. Sugihara, Fishing elevates variability in the abundance of exploited species. *Nature*. **443**, 859–862 (2006).

15. A. R. Thompson, W. Watson, S. McClatchie, E. D. Weber, Multi-scale sampling to evaluate assemblage dynamics in an oceanic marine reserve. *PLoS One*. **7**, e33131 (2012).

16. H. G. Moser P.E. Smith, and L.E. Eber, Larval fish assemblages in the California Current region, 1954-1960, a period of dynamic environmental change. *CalCOFI Rep.* **28**, 97–127 (1987).

17. H. Moser, R. Charter, P. Smith, D. Ambrose, W. Watson, S. Charter, E. Sandknop, Distributional atlas of fish larvae and eggs in the Southern California Bight region: 1951-1998. *Calif. Coop. Ocean. Fish. Investig. Atlas*. **34**, 1–166 (2001).

18. M. A. Snyder, L. C. Sloan, N. S. Diffenbaugh, J. L. Bell, Future climate change and upwelling in the California Current. *Geophys. Res. Lett.* **30**, 1823 (2003).

19. R. G. Asch, Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. *Proc. Natl. Acad. Sci. U. S. A.* **112**, E4065–E4074 (2015).

20. A. R. Thompson, N. J. Ben-Aderet, N. M. Bowlin, D. Kacev, R. Swalethorp, W. Watson, Putting the Pacific marine heatwave into perspective: The response of larval fish off southern California to unprecedented warming in 2014–2016 relative to the previous 65 years. *Glob. Chang. Biol.* **28**, 1766–1785 (2022).

21. A. R. Thompson, D. C. Chen, L. W. Guo, J. R. Hyde, W. Watson, Larval abundances of rockfishes that were historically targeted by fishing increased over 16 years in association with a large marine protected area. *R. Soc. Open Sci.* **4**, 170639 (2017).

22. Z. Gold, E. E. Curd, K. D. Goodwin, E. S. Choi, B. W. Frable, A. R. Thompson, H. J. Walker, R. S. Burton, D. Kacev, L. D. Martz, P. H. Barber, Improving metabarcoding taxonomic assignment: A case study of fishes in a large marine ecosystem. *Mol. Ecol. Resour.* **21**, 2546–2564 (2021).

23. M. Miya, R. O. Gotoh, T. Sado, MiFish metabarcoding: a high-throughput approach for simultaneous detection of multiple fish species from environmental DNA and other samples. *Fish. Sci.* **86**, 939–970 (2020).

24. M. G. Jacox, M. A. Alexander, N. J. Mantua, J. D. Scott, G. Hervieux, R. S. Webb, F. E. Werner, 6. Forcing of multiyear extreme ocean temperatures that impacted California current living marine resources in 2016. *Bull. Am. Meteorol. Soc.* **99**, S27–S33 (2018).

25. C. A. Morgan, B. R. Beckman, L. A. Weitkamp, K. L. Fresh, Recent Ecosystem Disturbance in the Northern California Current. *Fisheries*. **44**, 465–474 (2019).

26. C. L. Gentemann, M. R. Fewings, M. García-Reyes, Satellite sea surface temperatures along the West Coast of the United States during the 2014–2016 northeast Pacific marine heat wave. *Geophys. Res. Lett.* **44**, 312–319 (2017).

27. A. S. Ren, D. L. Rudnick, Temperature and salinity extremes from 2014-2019 in the California Current System and its source waters. *Commun. Earth Environ.* **2**, 1–9 (2021).

28. I. D. Schroeder, J. A. Santora, S. J. Bograd, E. L. Hazen, K. M. Sakuma, A. M. Moore, C. A. Edwards, B. K. Wells, J. C. Field, Source water variability as a driver of rockfish recruitment in the California Current Ecosystem: implications for climate change and fisheries management. *Can. J. Fish. Aquat. Sci.* **76**, 950–960 (2019).

29. M. Miya, Y. Sato, T. Fukunaga, T. Sado, J. Y. Poulsen, K. Sato, T. Minamoto, S. Yamamoto, H. Yamanaka, H. Araki, M. Kondoh, W. Iwasaki, MiFish, a set of universal PCR primers for metabarcoding environmental DNA from fishes: Detection of more than 230 subtropical marine species. *R. Soc. Open Sci.* **2**, 150088 (2015).

30. E. E. Curd, Z. Gold, G. S. Kandlikar, J. Gomer, M. Ogden, T. O’Connell, L. Pipes, T. M. Schweizer, L. Rabichow, M. Lin, B. Shi, P. H. Barber, N. Kraft, R. Wayne, R. S. Meyer, Anacapa Toolkit: An environmental DNA toolkit for processing multilocus metabarcode datasets. *Methods Ecol. Evol.* **10**, 1469–1475 (2019).

31. R. Gallego, E. Jacobs-Palmer, K. Cribari, R. P. Kelly, Environmental DNA metabarcoding reveals winners and losers of global change in coastal waters: EDNA and climate change. *Proc. R. Soc. B Biol. Sci.* **287**, 20202424 (2020).

32. W. J. Sydeman, S. Dedman, M. García-Reyes, S. A. Thompson, J. A. Thayer, A. Bakun, A. D. MacCall, Sixty-five years of northern anchovy population studies in the southern California Current: A review and suggestion for sensible management. *ICES J. Mar. Sci.* **77**, 486–499 (2020).

33. A. R. Thompson, I. D. Schroeder, S. J. Bograd, E. L. Hazen, M. G. Jacox, A. Leising, B. K. Wells, J. L. Largier, J. L. Fisher, K. C. Jacobson, S. M. Zeman, E. P. Bjorktedt, R. R. Robertson, M. Kahru, R. Goericke, C. E. Peabody, T. Baumgartner, B. E. Lavaniegos, L. E. Miranda, E. Gómez-Ocampo, J. Gómez-Valdés, T. D. Authy, E. A. Daly, C. A. Morgan, J. B. Burke, J. C. Field, K. Sakuma, E. D. Weber, W. Watson, J. M. Porquez, J. Dolliver, D. E. Lyons, R. A. Orben, J. Zamon, P. Warybok, J. Jahncke, J. A. Santora, S. A. Thompson, B. Hoover, W. J. Sydeman, S. Melin, State of the California current 2018-19 : a novel anchovy regime and a new marine heat wave? *Calif. Coop. Ocean. Fish. Investig. Rep.* **60**, 1–60 (2019).

34. R. H. Parrish, D. L. Mallicoate, R. A. Klingbeil, Age dependent fecundity, number of spawninge per year, sex ratio, and maturation stages in northern anchovy, Engraulis mordax. *Fish. Bull.* **84**, 503–517 (1986).

35. E. D. Weber, T. D. Auth, S. Baumann-Pickering, T. R. Baumgartner, E. P. Bjorkstedt, S. J. Bograd, B. J. Burke, J. L. Cadena-Ramírez, E. A. Daly, M. de la Cruz, State of the California Current 2019–2020: Back to the Future With Marine Heatwaves? *Front. Mar. Sci.*, 1081 (2021).

36. A. Vergés, C. Doropoulos, H. A. Malcolm, M. Skye, M. Garcia-Pizá, E. M. Marzinelli, A. H. Campbell, E. Ballesteros, A. S. Hoey, A. Vila-Concejo, Y. M. Bozec, P. D. Steinberg, Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. *Proc. Natl. Acad. Sci. U. S. A.* **113**, 13791–13796 (2016).

37. C. Chaudhary, A. J. Richardson, D. S. Schoeman, M. J. Costello, Global warming is causing a more pronounced dip in marine species richness around the equator. *Proc. Natl. Acad. Sci. U. S. A.* **118** (2021), doi:10.1073/pnas.2015094118.

38. A. R. Thompson, C. J. Harvey, W. J. Sydeman, C. Barceló, S. J. Bograd, R. D. Brodeur, J. Fiechter, J. C. Field, N. Garfield, T. P. Good, E. L. Hazen, M. E. Hunsicker, K. Jacobson, M. G. Jacox, A. Leising, J. Lindsay, S. R. Melin, J. A. Santora, I. D. Schroeder, J. A. Thayer, B. K. Wells, G. D. Williams, Indicators of pelagic forage community shifts in the California Current Large Marine Ecosystem, 1998–2016. *Ecol. Indic.* **105**, 215–228 (2019).

39. J. A. Santora, N. J. Mantua, I. D. Schroeder, J. C. Field, E. L. Hazen, S. J. Bograd, W. J. Sydeman, B. K. Wells, J. Calambokidis, L. Saez, D. Lawson, K. A. Forney, Habitat compression and ecosystem shifts as potential links between marine heatwave and record whale entanglements. *Nat. Commun.* **11**, 1–12 (2020).

40. H. Robinson, J. Thayer, W. J. Sydeman, M. Weise, Changes in California sea lion diet during a period of substantial climate variability. *Mar. Biol.* **165**, 1–12 (2018).

41. J. F. Piatt, J. K. Parrish, H. M. Renner, S. K. Schoen, T. T. Jones, M. L. Arimitsu, K. J. Kuletz, B. Bodenstein, M. García-Reyes, R. S. Duerr, R. M. Corcoran, R. S. A. Kaler, G. J. McChesney, R. T. Golightly, H. A. Coletti, R. M. Suryan, H. K. Burgess, J. Lindsey, K. Lindquist, P. M. Warzybok, J. Jahncke, J. Roletto, W. J. Sydeman, Extreme mortality and reproductive failure of common murres resulting from the northeast Pacific marine heatwave of 2014-2016. *PLoS One*. **15**, e0226087 (2020).

42. S. McClatchie, Sardine biomass is poorly correlated with the Pacific Decadal Oscillation off California. *Geophys. Res. Lett.* **39** (2012), doi:10.1029/2012GL052140.

43. C. Deutsch, A. Ferrel, B. Seibel, H. O. Pörtner, R. B. Huey, Climate change tightens a metabolic constraint on marine habitats. *Science (80-. ).* **348**, 1132–1135 (2015).

44. K. A. Rose, J. Fiechter, E. N. Curchitser, K. Hedstrom, M. Bernal, S. Creekmore, A. Haynie, S. ichi Ito, S. Lluch-Cota, B. A. Megrey, C. A. Edwards, D. Checkley, T. Koslow, S. McClatchie, F. Werner, A. MacCall, V. Agostini, Demonstration of a fully-coupled end-to-end model for small pelagic fish using sardine and anchovy in the California Current. *Prog. Oceanogr.* **138**, 348–380 (2015).

45. J. A. Hare, The future of fisheries oceanography lies in the pursuit of multiple hypotheses. *ICES J. Mar. Sci.* **71**, 2343–2356 (2014).

46. D. Robert, H. M. Murphy, G. P. Jenkins, L. Fortier, Poor taxonomical knowledge of larval fish prey preference is impeding our ability to assess the existence of a “critical period” driving year-class strength. *ICES J. Mar. Sci.* **71**, 2042–2052 (2014).

47. E. Garcia-Vazquez, O. Georges, S. Fernandez, A. Ardura, eDNA metabarcoding of small plankton samples to detect fish larvae and their preys from Atlantic and Pacific waters. *Sci. Rep.* **11**, 1–13 (2021).

48. K. J. Pitz, J. Guo, S. B. Johnson, T. L. Campbell, H. Zhang, R. C. Vrijenhoek, F. P. Chavez, J. Geller, Zooplankton biogeographic boundaries in the California Current System as determined from metabarcoding. *PLoS One*. **15**, e0235159 (2020).

49. C. Mariac, J. F. Renno, G. Carmen, Y. Vigouroux, E. Mejia, C. Angulo, D. Castro Ruiz, G. Estivals, C. Nolorbe, A. García Vasquez, J. Nuñez, G. Cochonneau, M. Flores, J. Alvarado, J. Vertiz, W. Chota-Macuyama, H. Sánchez, G. Miranda, F. Duponchelle, Species-level ichthyoplankton dynamics for 97 fishes in two major river basins of the Amazon using quantitative metabarcoding. *Mol. Ecol.* (2021), doi:10.1111/mec.15944.

50. M. Barbato, T. Kovacs, M. A. Coleman, M. K. Broadhurst, M. de Bruyn, Metabarcoding for stomach-content analyses of Pygmy devil ray (Mobula kuhlii cf. eregoodootenkee): Comparing tissue and ethanol preservative-derived DNA. *Ecol. Evol.* **9**, 2678–2687 (2019).

51. M. Erdozain, D. G. Thompson, T. M. Porter, K. A. Kidd, D. P. Kreutzweiser, P. K. Sibley, T. Swystun, D. Chartrand, M. Hajibabaei, Metabarcoding of storage ethanol vs. conventional morphometric identification in relation to the use of stream macroinvertebrates as ecological indicators in forest management. *Ecol. Indic.* **101**, 173–184 (2019).

52. H. L. Thalmann, E. A. Daly, R. D. Brodeur, Two Anomalously Warm Years in the Northern California Current: Impacts on Early Marine Steelhead Diet Composition, Morphology, and Potential Survival. *Trans. Am. Fish. Soc.* **149**, 369–382 (2020).

53. R. P. Kelly, A. O. Shelton, R. Gallego, Understanding PCR Processes to Draw Meaningful Conclusions from Environmental DNA Studies. *Sci. Rep.* **9**, 1–14 (2019).

54. G. B. Gloor, J. M. Macklaim, V. Pawlowsky-Glahn, J. J. Egozcue, Microbiome datasets are compositional: And this is not optional. *Front. Microbiol.* **8**, 2224 (2017).

55. M. R. McLaren, A. D. Willis, B. J. Callahan, Consistent and correctable bias in metagenomic sequencing experiments. *Elife*. **8**, e46923 (2019).

56. J. D. Silverman, R. J. Bloom, S. Jiang, H. K. Durand, E. Dallow, S. Mukherjee, L. A. David, Measuring and mitigating PCR bias in microbiota datasets. *PLoS Comput. Biol.* **17**, e1009113 (2021).

57. M. Y. Stoeckle, J. Adolf, Z. Charlop-Powers, K. J. Dunton, G. Hinks, S. M. Vanmorter, Trawl and eDNA assessment of marine fish diversity, seasonality, and relative abundance in coastal New Jersey, USA. *ICES J. Mar. Sci.* **78**, 293–304 (2021).

58. A. Lacoursière-Roussel, G. Côté, V. Leclerc, L. Bernatchez, Quantifying relative fish abundance with eDNA: a promising tool for fisheries management. *J. Appl. Ecol.* **53**, 1148–1157 (2016).

59. M. C. Yates, D. J. Fraser, A. M. Derry, Meta-analysis supports further refinement of eDNA for monitoring aquatic species-specific abundance in nature. *Environ. DNA*. **1**, 5–13 (2019).

60. M. M. Zenker, A. Specht, V. G. Fonseca, Assessing insect biodiversity with automatic light traps in Brazil: Pearls and pitfalls of metabarcoding samples in preservative ethanol. *Ecol. Evol.* **10**, 2352–2366 (2020).

61. S. McClatchie, A. R. Thompson, S. R. Alin, S. Siedlecki, W. Watson, S. J. Bograd, The influence of Pacific Equatorial Water on fish diversity in the southern California Current System. *J. Geophys. Res. Ocean.* **121**, 6121–6136 (2016).

62. H. G. Moser, R. L. Charter, P. E. Smith, D. A. Ambrose, S. R. Charter, C. A. Meyer, E. M. Sandknop, W. Watson, *Distributional atlas of fish larvae and eggs in the California Current region: taxa with 1000 or more total larvae, 1951 through 1984* (Marine Life Research Program, Scripps Institution of Oceanography, 1993), vol. 53.

63. C. H. Hsieh, C. Reiss, W. Watson, M. J. Allen, J. R. Hunter, R. N. Lea, R. H. Rosenblatt, P. E. Smith, G. Sugihara, A comparison of long-term trends and variability in populations of larvae of exploited and unexploited fishes in the Southern California region: A community approach. *Prog. Oceanogr.* **67**, 160–185 (2005).

64. A. R. Thompson, S. McClatchie, E. D. Weber, W. Watson, C. E. Lennert-Cody, Correcting for bias in calcofi ichthyoplankton abundance estimates associated with the 1977 transition from ring to bongo net sampling. *Calif. Coop. Ocean. Fish. Investig. Reports*. **58**, 1–11 (2017).

65. D. Kramer, M. J. Kalin, E. G. Stevens, J. R. Thrailkill, J. . Zweifel, *Collecting and processing data on fish eggs and larvae in the California Current. NOAA Tech. Rep. NMFS Circ., vol. 370.* (US Department of Commerce, National Oceanic and Atmospheric Administration …, 1972), vol. 370.

66. S. McClatchie, *Regional fisheries oceanography of the california current system: The CalCOFI program* (Springer, 2014).

67. M. Miya, Y. Sato, T. Fukunaga, T. Sado, J. Y. Poulsen, K. Sato, T. Minamoto, S. Yamamoto, H. Yamanaka, H. Araki, M. Kondoh, W. Iwasaki, MiFish, a set of universal PCR primers for metabarcoding environmental DNA from fishes: Detection of more than 230 subtropical marine species. *R. Soc. Open Sci.* **2**, 150088 (2015).

68. N. Lalam, Estimation of the reaction efficiency in polymerase chain reaction. *J. Theor. Biol.* **242**, 947–953 (2006).

69. J. D. Silverman, K. Roche, S. Mukherjee, L. A. David, Naught all zeros in sequence count data are the same. *Comput. Struct. Biotechnol. J.* **18**, 2789–2798 (2020).

70. J. J. Jos´, J. Egozcue, J. Graffelman, M. I. Ortego, V. Pawlowsky-Glahn, Some thoughts on counts in sequencing studies. *NAR Genomics Bioinforma.* **2**, 1–10 (2020).

71. N. T. Hobbs, M. B. Hooten, *Bayesian Models: A Statistical Primer for Ecologists. 593 Princeton University Press* (Princeton, 2015).

72. X. Ren, P. F. Kuan, Negative binomial additive model for RNA-Seq data analysis. *BMC Bioinformatics*. **21**, 1–15 (2020).

73. T. Chambert, D. S. Pilliod, C. S. Goldberg, H. Doi, T. Takahara, An analytical framework for estimating aquatic species density from environmental DNA. *Ecol. Evol.* **8**, 3468–3477 (2018).

74. E. Meyer-Gutbrod, L. Kui, R. Miller, M. Nishimoto, L. Snook, M. Love, Moving on up: Vertical distribution shifts in rocky reef fish species during climate-driven decline in dissolved oxygen from 1995 to 2009. *Glob. Chang. Biol.* **27**, 6280–6293 (2021).

75. B. Goodrich, J. Gabry, I. Ali, S. Brilleman, rstanarm: Bayesian applied regression modeling via Stan. *R Packag. version*. **2**, 1758 (2020).

76. Stan Development Team, RStan: the R interface to Stan (2021).

77. J. N. Heine, California Cooperative Oceanic Fisheries Investigations. Reports. **49**, 264 (2008).

78. S. McClatchie, J. Gao, E. J. Drenkard, A. R. Thompson, W. Watson, L. Ciannelli, S. J. Bograd, J. T. Thorson, Interannual and Secular Variability of Larvae of Mesopelagic and Forage Fishes in the Southern California Current System. *J. Geophys. Res. Ocean.* **123**, 6277–6295 (2018).

79. E. Valsecchi, J. Bylemans, S. J. Goodman, R. Lombardi, I. Carr, L. Castellano, A. Galimberti, P. Galli, Novel universal primers for metabarcoding environmental DNA surveys of marine mammals and other marine vertebrates. *Environ. DNA*. **2**, 460–476 (2020).

80. R. A. Collins, G. Trauzzi, K. M. Maltby, T. I. Gibson, F. C. Ratcliffe, J. Hallam, S. Rainbird, J. Maclaine, P. A. Henderson, D. W. Sims, S. Mariani, M. J. Genner, Meta-Fish-Lib: A generalised, dynamic DNA reference library pipeline for metabarcoding of fishes. *J. Fish Biol.* **99**, 1446–1454 (2021).

81. A. Polanco F., E. Richards, B. Flück, A. Valentini, F. Altermatt, S. Brosse, J. C. Walser, D. Eme, V. Marques, S. Manel, C. Albouy, T. Dejean, L. Pellissier, Comparing the performance of 12S mitochondrial primers for fish environmental DNA across ecosystems. *Environ. DNA*. **3**, 1113–1127 (2021).

82. K. Deiner, H. M. Bik, E. Mächler, M. Seymour, A. Lacoursière-Roussel, F. Altermatt, S. Creer, I. Bista, D. M. Lodge, N. de Vere, M. E. Pfrender, L. Bernatchez, Environmental DNA metabarcoding: Transforming how we survey animal and plant communities. *Mol. Ecol.* **26**, 5872–5895 (2017).

83. P. Taberlet, A. Bonin, L. Zinger, E. Coissac, *Environmental DNA: For biodiversity research and monitoring* (Oxford University Press, 2018).

84. R. C. Edgar, Accuracy of taxonomy prediction for 16S rRNA and fungal ITS sequences. *PeerJ*. **2018**, e4652 (2018).

85. M. A. Min, P. H. Barber, Z. Gold, MiSebastes: An eDNA metabarcoding primer set for rockfishes (genus Sebastes). *Conserv. Genet. Resour.* **13**, 447–456 (2021).

86. M. Leray, J. Y. Yang, C. P. Meyer, S. C. Mills, N. Agudelo, V. Ranwez, J. T. Boehm, R. J. Machida, A new versatile primer set targeting a short fragment of the mitochondrial COI region for metabarcoding metazoan diversity: Application for characterizing coral reef fish gut contents. *Front. Zool.* **10**, 34 (2013).

87. P. A. Hastings, R. S. Burton, Establishing a DNA Sequence database for the marine fish fauna of California, 5 (2008).

88. B. E. Deagle, S. N. Jarman, E. Coissac, F. Pompanon, P. Taberlet, DNA metabarcoding and the cytochrome c oxidase subunit I marker: Not a perfect match. *Biol. Lett.* **10**, 20140562 (2014).

89. J. L. O’donnell, R. P. Kelly, N. C. Lowell, J. A. Port, Indexed PCR primers induce template- Specific bias in Large-Scale DNA sequencing studies. *PLoS One*. **11**, e0148698 (2016).

90. D. M. Gohl, P. Vangay, J. Garbe, A. MacLean, A. Hauge, A. Becker, T. J. Gould, J. B. Clayton, T. J. Johnson, R. Hunter, D. Knights, K. B. Beckman, Systematic improvement of amplicon marker gene methods for increased accuracy in microbiome studies. *Nat. Biotechnol.* **34**, 942–949 (2016).

91. K. Bohmann, V. Elbrecht, C. Carøe, I. Bista, F. Leese, M. Bunce, D. W. Yu, M. Seymour, A. J. Dumbrell, S. Creer, Strategies for sample labelling and library preparation in DNA metabarcoding studies. *Mol. Ecol. Resour.* (2021), doi:10.1111/1755-0998.13512.

92. R. P. Kelly, R. Gallego, E. Jacobs-Palme, The effect of tides on nearshore environmental DNA. *PeerJ*. **2018**, e4521 (2018).

93. R. Mendelssohn, rerddapXtracto: Extracts Environmental Data from “ERDDAP” Web Services. R package version 1.0.0 (2020).

94. H. G. Moser, R. L. Charter, W. Watson, D. A. Ambrose, K. T. Hill, P. E. Smith, J. L. Butler, E. M. Sandknop, S. R. Charter, The CalCOFI ichthyoplankton time series: Potential contributions to the management of rocky-shore fishes. *Calif. Coop. Ocean. Fish. Investig. Reports*. **42**, 112–128 (2001).

95. S. Juggins, rioja: Analysis of Quaternary science data, R package version (0.9-9). *Compr. r Arch. Netw.* (2015).

96. A. de Vries, B. D. Ripley, Create Dendrograms and Tree Diagrams Using “ggplot2.” *URL https//github. com/andrie/ggdendro*, 12 (2020).

97. J. Oksanen, F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, O. R.B., G. L. Simpson, P. Solymos, M. H. H. Stevens, H. Wagner, *vegan*: Community ecology package. *R Packag. version 2.3-5* (2016), (available at https://cran.r-project.org/package=vegan).

98. J. Niku, F. K. C. Hui, S. Taskinen, D. I. Warton, gllvm: Fast analysis of multivariate abundance data with generalized linear latent variable models in r. *Methods Ecol. Evol.* **10**, 2173–2182 (2019).

99. A. Kucukelbir, R. Ranganath, A. Gelman, D. Blei, Automatic variational inference in Stan. *Adv. Neural Inf. Process. Syst.* **28** (2015).

100. R. Jiang, W. V. Li, J. J. Li, mbImpute: an accurate and robust imputation method for microbiome data. *Genome Biol.* **22**, 1–27 (2021).

101. M. Leray, N. Knowlton, Random sampling causes the low reproducibility of rare eukaryotic OTUs in Illumina COI metabarcoding. *PeerJ*. **2017**, e3006 (2017).

102. J. A. Royle, W. A. Link, Generalized site occupancy models allowing for false positive and false negative errors. *Ecology*. **87**, 835–841 (2006).