RESEARCH ARTICLE



• WILEY

Deep-pelagic fishes: Demographic instability in a stable environment

Max D. Weber¹ | Travis M. Richards¹ | Tracey T. Sutton² | Joshua E. Carter¹ | Ron I. Eytan^{1,3}

Revised: 10 March 2024

¹Texas A&M University at Galveston, Galveston, Texas, USA

²Nova Southeastern University, Dania Beach Florida USA

³Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana, USA

Correspondence

Ron I. Eytan, Texas A&M University at Galveston, 1001 Texas Clipper Road OCSB Building 3029, Galveston, TX 77554, USA. Email: ron.eytan@gmail.com

Funding information

The Gulf of Mexico Research Initiative: National Oceanic and Atmospheric Administration's RESTORE Science Program, Grant/Award Number: NA19NOS4510193

Abstract

Demographic histories are frequently a product of the environment, as populations expand or contract in response to major environmental changes, often driven by changes in climate. Meso- and bathy-pelagic fishes inhabit some of the most temporally and spatially stable habitats on the planet. The stability of the deep-pelagic could make deep-pelagic fishes resistant to the demographic instability commonly reported in fish species inhabiting other marine habitats, however the demographic histories of deep-pelagic fishes are unknown. We reconstructed the historical demography of 11 species of deep-pelagic fishes using mitochondrial and nuclear DNA sequence data. We uncovered widespread evidence of population expansions in our study species, a counterintuitive result based on the nature of deep-pelagic ecosystems. Frequency-based methods detected potential demographic changes in nine species of fishes, while extended Bayesian skyline plots identified population expansions in four species. These results suggest that despite the relatively stable nature of the deep-pelagic environment, the fishes that reside here have likely been impacted by past changes in climate. Further investigation is necessary to better understand how deep-pelagic fishes, by far Earth's most abundant vertebrates, will respond to future climatic changes.

KEYWORDS

bathypelagic, climate change, mesopelagic, population ecology, population genetics

TAXONOMY CLASSIFICATION Demography, Genetics, Population ecology

| INTRODUCTION 1

The demographic history of a species is strongly influenced by the environment it inhabits (Alheit & Hagen, 1997; Avise, 2000; Grant, 2015). Major changes in the environment can alter the distribution and size of suitable habitat for a species, reducing or

increasing the species' range. Population sizes expand or contract in response to these fluctuations in habitat suitability (Avise, 2000; Nye et al., 2009). Evidence for the environment's control over population dynamics can be seen across taxonomic groups in terrestrial and marine habitats around the world (Almada et al., 2012; Eytan & Hellberg, 2010; Grant, 2015; Robalo et al., 2012).

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Authors. Ecology and Evolution published by John Wiley & Sons Ltd.

Given that changes in environmental conditions strongly influence population size, species inhabiting unstable environments should be characterized by unstable population sizes. On the other hand, species inhabiting temporally stable environments should be less susceptible to frequent population expansions or contractions due to global or regional climatic events. Studies have supported this notion, finding genetic diversity to be greater in species inhabiting more stable environments than closely related species in environments more subject to change (Carnaval et al., 2009; Gugger et al., 2013).

The open ocean mesopelagic (200-1000m depth) and bathypelagic (1000m to approximately 100m above the sea floor) domains (deep-pelagic, cumulatively) are arguably the most temporally and spatially stable environments on the planet. In terms of physical characteristics like temperature, there is a strong latitudinal homogeneity in the environment that increases with depth (Robison, 2009). In comparison to shallower habitats, temperature change occurs slowly and the magnitude of change is less (Abraham et al., 2013; Clark et al., 2006, 2009; Levitus et al., 2012; Mora et al., 2013; Robison, 2009). Regarding age, the deep-pelagic milieu has existed longer than continents; while the latter have shifted position, uplifted, submerged, and fractionated, the former have remained relatively unchanged, inter-ocean connectivity notwithstanding. Based on the age and stability of the environment, as well as our current understanding of the manner in which habitat influences demography, the population sizes of the fishes inhabiting the deep-pelagic would be expected to be stable over time.

If the demographic histories of deep-pelagic fishes include population size fluctuations, it is difficult to predict which physical factors could drive this instability. Molecular analyses are frequently used to reconstruct and infer historical demography, however molecular investigations into the historical demography of deep-sea organisms are few and have focused on deep-benthic species (Etter et al., 2005; Sakuma et al., 2014; Varela et al., 2012). The deep-benthic environment, benthic habitat found below 200m depth, is much more heterogeneous than the deep-pelagic and likely under differing environmental pressures (Sutton et al., 2017; Thurber et al., 2014; Watling et al., 2013). Recent publications based on the fossil record have reported local changes in deep-pelagic fish abundance and community composition (Lin et al., 2023; Salvatteci et al., 2022). These observations could be indicative of range changes and fluctuations in population size. Correlations between climate have been made to these findings, but the precise mechanism driving the phenomenon is not yet known.

The physical factors influencing the historical demography of marine fishes inhabiting the less homogenous coastal and epipelagic (upper 200 m of the ocean water column) zones are better understood. Studies have consistently shown population size changes that correspond with major changes in these environments that would not be expected in the more homogenous, 'sheltered' deep-pelagic domain. A plurality of these studies indicates widespread population expansions in shallow-dwelling fishes following the last glacial maximum (Avise, 2000; Eytan & Hellberg, 2010; Grant, 2015; Robalo et al., 2012). Two factors are frequently cited to explain increases in geographic range and a corresponding increase in population size: an increase in global sea-surface temperatures and sea-level rise that dramatically increased shelf habitats (Avise, 2000; Eytan & Hellberg, 2010; Grant, 2015) During this period of great change for shallow marine habitats, the deep-pelagic experienced far smaller changes in temperature, and the amount of deep-pelagic habitat would have increased negligibly (Abraham et al., 2013; Clark et al., 2006, 2009; Levitus et al., 2012; Robison, 2009).

If the demographic histories of deep-pelagic fishes reveal largescale population fluctuations, it is possible that physical conditions external to the deep-pelagic domain drive these dynamics. One habit shared by many deep-pelagic fishes could be responsible, diel vertical migration.

Most mesopelagic fish species perform diel vertical migrations, a nocturnal migration to the shallower and more variable epipelagic waters and a diurnal return to mesopelagic depths (Barham, 1966; Sutton, 2013). Vertical migrations by bathypelagic fishes, while not unknown are much less common (Cook et al., 2013). An analysis of the distribution of mesopelagic fishes found that the ranges of vertically migrating species were more likely to change in response to large-scale changes in climate than the ranges of species that do not vertically migrate (Hsieh et al., 2009). This could be a result of the greater influence of atmospheric heating on the upper ocean than deep waters. If the changes in surface waters are no longer physiologically tolerable to vertically migrating fishes, then these species would no longer persist in their former range. If vertical migratory behavior alone drives demography in deep-pelagic fishes, vertical migrators should be characterized by population expansions and/ or contractions, while the population sizes of non-vertical migrators should be relatively stable over time.

Given the current lack of knowledge regarding deep-pelagic fish historical demography, we sought to investigate the demographic history of 11 species inhabiting this environment, using two sets of molecular based analyses: frequency-based tests and gene treebased analyses. These tests can infer demographic events such as population expansion and complement one another. Knowledge of the demographic history of deep-pelagic fishes serves two key purposes. First, it will provide insight into the ecological processes driving population dynamics in the world's largest and most environmentally stable ecosystem. These insights provide the basis for an ideal case study to test the hypothesis that a stable environment should in turn lead to stable demographic histories. Second, understanding how deep-pelagic fishes responded to past climatic events will allow us to make predictions about how they will respond to future changes in climate.

2 | METHODS

2.1 | Sampling and sequence generation

We selected 11 deep-pelagic species that span phylogenetic lineages, life histories, and vertical migration behavior (see Table 1). Samples were obtained by trawling with a MOCNESS (Multiple Opening and Closing

3 of 21

species.
study :
r the
lata fo
iomic c
l taxon
s and
/ trait
history
Life
4
BLE
1

TABLE 1 Life history tra	its and taxonomic data	a for the study species.					
Species	Family	Order	Diel vertical migrators	Upper depth of occurrence	Lower depth of occurrence	Total depth range	References
Bathophilus pawneei	Stomiidae	Stomiiformes	Yes	0	1500	1500	McEachran and Fechhelm (1998) and Sutton and Hopkins (1996)
Chauliodus sloani	Stomiidae	Stomiiformes	Yes	0	1800	1800	McEachran and Fechhelm (1998), Clarke (1983) and Sutton and Hopkins (1996)
Cyclothone alba	Gonostomatidae	Stomiiformes	No	300	600	300	McEachran and Fechhelm (1998) and Miya and Nemoto (1986)
Cyclothone pseudopallida	Gonostomatidae	Stomiiformes	oZ	300	006	600	McEachran and Fechhelm (1998) and Miya and Nemoto (1986)
Diplospinus multistriatus	Gempylidae	Perciformes	Yes	100	1000	006	McEachran and Fechhelm (1998) and Clarke and Wagner (1976)
Ditropichthys storeri	Cetomimidae	Stephanoberyciformes	No	650	2150	1500	McEachran and Fechhelm (1998) and Paxton (1989)
Photostomias guernei	Stomiidae	Stomiiformes	Yes	15	800	785	Clarke (1983) and Sutton and Hopkins (1996)
Scopelogadus mizolepis	Melamphaidae	Stephanoberyciformes	Yes	100	1000	006	McEachran and Fechhelm (1998), Clarke (1983) and Clarke and Wagner (1976)
Sigmops elongatus	Gonostomatidae	Stomiiformes	Yes	50	1200	1150	McEachran and Fechhelm (1998) and Lancraft et al. (1988)
Sternoptyx pseudobscura	Sternoptychidae	Stomiiformes	No	800	1500	700	McEachran and Fechhelm (1998)
Stomias affinis	Stomiidae	Stomiiformes	Yes	50	850	800	McEachran and Fechhelm (1998) and Sutton and Hopkins (1996)



FIGURE 1 Map of the sampling locations. Station locations are indicated by the black dots, and depth is indicated according to color.

Net and Environmental Sensing System) in discrete depth zones from the surface to 1500m depth in the northern Gulf of Mexico (GOM) (see Figure 1 for sampling locations). Upon collection and identification of vouchers at sea, a ~1cm strip of lateral muscle tissue was preserved in 95% non-denatured ethanol, stored at ~20°C while at sea, and moved to long-term storage at ~80°C when back on land. Voucher specimens are housed in the Ocean Ecology Lab at Nova Southeastern University pending accession into a permanently curated fish collection.

DNA was extracted from tissues using a Qiagen DNEasy Blood & Tissue extraction kit (Germantown, MD, USA). We generated DNA sequence data from the mitochondrial gene cytochrome oxidase I (COI) as well as three nuclear DNA exons (PLAG, ENC, and MYH). PCR was performed using Promega GoTAQ (Madison, Wisconsin, USA) (see Table A2 for primers used). Following amplification, all PCR products were cleaned using a standard PEG protocol (Glenn, 2019). Amplicons were Sanger-sequenced on an ABI 3730 capillary sequencer at Yale Keck Biotechnology Resource Laboratory. Sequences were cleaned and edited in Sequencher v5.1. Nuclear markers were phased using Phase v2.1 to resolve heterozygous sites (Stephens & Scheet, 2001, 2005). The sequences were then aligned using MAFFT in Geneiousv9.1.8 (Kearse et al., 2012).

2.2 | Frequency-based analyses

We calculated Tajima's D, Fu's F_s , and R^2 for each marker (Fu, 1997; Ramos-Onsins & Rozas, 2002; Tajima, 1989). Comparisons of the statistical power of frequency-based tests have shown that F_s and R^2 are the most capable of detecting population growth (Ramos-Onsins & Rozas, 2002). They complement one another as well, with F_s excelling at population growth detection in large sample sizes, while R^2 performs better with small sample sizes. A significant and large negative F_s value suggests population growth, while a significant and small positive R^2 value indicates population growth. Tajimas's *D* points to population growth and/or a selective sweep when significant and negative.

All of the frequency-based tests were performed in DNAsp v6 (Rozas et al., 2017). Ambiguity codes were replaced with Ns to allow for calculation in DNAsp. Significance of Tajima's *D* results are determined by the test itself. The significance of all three tests was also determined using coalescent simulations with 1000 replicates implemented in DNAsp.

2.3 | Gene tree-based analysis

The second set of tests makes use of the topologies and branch lengths of gene trees to infer changes in population size over time using the coalescent. We performed these analyses in BEAST v2.4.7 (Bouckaert et al., 2014) to generate extended Bayesian skyline plots (EBSPs). EBSPs utilize coalescent theory and a Markov Chain Monte Carlo Algorithm to infer and visualize demographic changes in a dataset. The Bayesian skyline plot is preferable to earlier skyline plot methods as it models both genealogy and demographic history simultaneously, which reduces error rates from uncertainty in estimates of node time (Heled & Drummond, 2008; Ho & Shapiro, 2011).

Nuclear and mitochondrial genes were included in the analysis for each species. The chain length was set to 50,000,000 sampling every 1000. COI rates were fixed, while the nuclear rates were allowed to vary. The partitioning scheme and substitution models were set based on PartitionFinder v2.0 results (Lanfear et al., 2012). A second set of trees was created using the same methodology, with the exception of the selection of substitution models. All partitions were set to the RBS substitution model (Bouckaert et al., 2014). RBS is a reversible-jump based substitution model for nucleotide data. This substitution model does not require a fixed substitution model to be assigned to each partition at the beginning of the analysis. Instead, it allows five different substitution models to be explored through the run, to find the substitution model with the best fit to the dataset.

After running in BEAST, log files for both sets of trees were inspected using Tracer v 1.7.1 (Rambaut et al., 2014). The most strongly supported EBSP analysis, based on ESS values, was selected and used for the inference of each species' demographic history. The posterior estimate of the number of population size changes provided a test for a rejection of constant population size. A stable demographic history can be rejected in species that do not include a possibility of zero demographic events in this posterior estimate. Finally, the trees files were uploaded to Rstudio v 0.99.484 (Studio 2012). The Rscript "plotEBSP", provided with the EBSP tutorial (http://www.beast2.org/files/2016/01/ebsp2-tut.zip), was used to generate and visualize the extended Bayesian skyline plots to understand the nature of these demographic events (Heled, 2010).

We treated each species as a single population for the purpose of these analyses. The accuracy of EBSP results require that the sequences were derived from a single population. The small size of the sampling area (Figure 1) and lack of geographic barriers for dispersal, make this a reasonable assumption. This assumption is supported by genome wide, temporal (multi-year) analyses of three species within the deep-pelagic family Myctophidae that reside in the northern Gulf of Mexico (Bernard et al., 2022). Very little instraspecific structure was found, and the authors characterize the GOM lanternfishes as largely panmictic. The samples used in our study were collected alongside those used in the Myctophid research. Given the overlap in habitat, range, and life history traits between lanternfishes and our study species, we believe it is reasonable to assume panmictic populations for our study species within the northern Gulf of Mexico.

2.4 | Population dynamics and vertical migration

We placed species into two categories; those that had undergone an inferred population size change and those that had not. Species placed into the "inferred population size change" group were categorized as such if the inference was uncovered in both the frequency-based and gene tree-based analyses. We further divided species into vertical migrators and non-vertical migrators. The migration type for each species can be found in Table 1. A chi-squared test was used to test for a correlation between inferred population size changes and vertical migrator.

Results of frequency-based statistics analysis.

2

Ш

TAB

3 | RESULTS

3.1 | Summary

The number of sequences generated for each species and marker varied according to sample availability and our ability to achieve amplification. The number of unique sequences obtained for each gene ranged from 10 to 97 (Table 2). The COI dataset included a low of 10 of sequences (*Bathophilus pawneei*) and a high of 97 sequences (*Chauliodus sloani*). The PLAG dataset included a low of 10

-2.209 0.43 ٩N ٩N ₹ ₹ AN ٩N AN ₹ ¥ ч° 115 ¥ 074 ¥ Ă Ă ¥۶ Ā Ă ¥۲ ¥۲ **4**² Tajima's D -1.346-0.477 ₹ Ā ¥ ¥۲ Ą ¥ ¥ ₹ ¥ Note: Tajima's D values that were significant based on the two-tailed test are dark gray. Significant values determined through coalescent simulations are highlighted in light gray. sequences ΗΥΗ # Of AN ₹ ₹ A ¥ AN ΔA AN AN 15 11 -10.151-6.027 -5.836٩Z ٩Z ₹Z ٩Z ₹Z ₹Z ٩Z ٩Z ч° .046 .073 059 ₹Z ¥ ¥ ¥ Ā Ā ¥ ¥ **R**² Tajima's D -1.863-2.162 -2.41 ¥ ₹ ¥ AN ¥ ¥ ¥ ¥ sequences ENC å0 # ٨A ٩Z ٩Z ٩Z ٩N ٩Z ٩Z ٩N 19 12 16 -0.097 -5.778 -2.582 -2.383 -9.189 0.216 -4.89 -0.07 0.2 ₹Z ٩Z L S 068 137 096 .146 .126 086 046 074 121 ¥ ₹ \mathbb{R}^2 Tajima's D -0.395 -0.023 -0.163 -1.346 -1.993 -1.591-2.186-1.165-1.494٩Z ٩N sequences PLAG fo # ₹Z ٩Z 10 12 2 12 10 12 12 11 17 -0.865 -1.008 -0.476 -2.995 -0.476 -0.537 1.761-3.216 -8.668 33.567 -0.68 чĽ 206 133 267 096 227 027 137 182 227 0 \mathbb{R}^2 2 Tajima's D -1.673 -0.026 -0.796 -0.786 -1.149-2.124-1.141-1.141-1.8311.21 -1.83seduences 00 jo # 12 10 97 12 14 12 12 13 11 11 11 Cyclothone pseudopallida Sternoptyx pseudobscura Diplospinus multistriatus Photostomias guernei Scopelogaus mizolepis Bathophilus pawneei Ditropichthys storeri Sigmops elongatus Chauliodus Sloani Cyclothone alba Stomias affinis Species

Ecology and Evolution

WILEY

FV_Ecology and Evolution

sequences (B. pawneei, Cyclothone pseudopallida, and Photostomias guernei) and a high of 17 sequences (Sternoptyx pseudobscura) (see Figure 2 for Photo of P. guernei). The ENC dataset included a low of 12 sequences (Diplospinus multistriatus) and a high of 16 sequences (S. pseudobscura). Finally, the MYH dataset included 11 sequences (S. pseudobscura) and 15 sequences (Stomias affinis). We used two genes for analysis in nine species, three genes in one species, and four genes in one species (Table 2). All sequences have been deposited in Genbank (Accession numbers listed in Table A1).

Frequency-based analyses 3.2

Frequency-based analyses recovered population expansions in 9 of our 11 sampled species (Table 2). In four species (C. sloani, S. pseudobscura, Cyclothone alba, and P. guernei) more than half of the frequency-based tests for all markers inferred population size changes. Weaker support was present in another



FIGURE 2 Photo of Photostomias guernei. Photo by Dante Fenolio.

	3.4 Vertical migration a
	The chi-squared test did not provi
	tween vertical migration and popul
	Table 4). Of the four species with spansions, two (C.sloani and P.gue two (C.alba and S.pseudobscura) do
1 Common Comm	

DISCUSSION

Historic changes in population size are frequently inferred for marine fishes and attributed to major ecological events and past climatic change (Avise, 2000; Grant, 2015). Previous molecular studies however, have largely focused on marine species inhabiting shallower

Study species	Reject constant population	Posterior estimate of population size changes
Bathophilus pawneii	No	[0, 3]
Chauliodus Sloani	Yes	[1, 3]
Cyclothone alba	Yes	[1,3]
Cyclothone pseudopallida	No	[0,3]
Diplospinus multistriatus	No	[0,3]
Ditropichthys storeri	No	[0,3]
Photostomias guernei	No	[1,3]
Scopelogaus mizolepis	No	[0,3]
Sigmops elongatus	No	[0,3]
Sternoptyx pseudobscura	Yes	[1,3]
Stomias affinis	No	[0,3]

Note: These estimates were generated using the gene tree based analyses and provide a test to reject a stable demographic history.

five species (D. multistriatus, Ditropichthys storeri, Scopelogadus mizolepis, Sigmops elongatus, and S. affinis), where less than half of the markers tested produced significant results. No evidence for demographic change was present in B. pawneei or C. pseudopallida.

Gene tree based analysis 3.3

We were able to reject a stable demographic history in four of the 11 species; C. alba, C. sloani, P. guernei, and S. pseudobscura, based on the posterior estimate of the number of population size changes generated in the analyses (Table 3). The estimates suggest a minimum one demographic event and maximum of three demographic events. Population expansions were inferred in every case based on the EBSPs (Figure 3). These four species also shared the strongest evidence for population size changes based on the frequency-based analyses.

nd population dynamics

ide support for a relationship belation size changes (p-value .8190, strong support for population exrnei) are vertical migrators while o not vertically migrate.

TABLE 3 Posterior estimate of population sizes changes.

FIGURE 3 Extended Bayesian skyline plots. The *x*-axis represents time, with the left side of the axis being the most recent time point. The *y*-axis represents relative population size on a log scale. The gray area displays the 95% central posterior density.

Population







TABLE 4 Chi-squared test for significance of vertical migration on the inference of recent population size changes.

	Pop size change inferred	No pop size change inferred		
Vertical migrator	4	3	Chi-squared	0.0524
Non vertical migrator	2	2	p-Value	0.819

Population

environments that are more variable over time in terms of physical conditions such as temperature in comparison to the deep-pelagic. Given the temporal and abiotic stability of the deep-pelagic environment, population sizes of fishes inhabiting this environment might also be predicted to be stable, so that no effective population size changes would be inferred from genetic examination. Nonetheless, we uncovered multiple lines of evidence suggesting population expansions in four of the 11 study species, while demographic events were inferred in an additional five species using frequency-based tests.

4.1 | Interpretation of frequency-based statistics

Departures from neutrality frequently occur due to past demographic events, however other factors such as selective sweeps and reproductive skew may lead to departures from neutrality as well (Birkner et al., 2013; Eldon et al., 2015; Montano, 2016). This has been shown to be true in several marine fishes (Eldon et al., 2015; Niwa et al., 2016). We sought to avoid such issues by employing a multilocus approach, including both mitochondrial and nuclear genes. Selection could be leading to a positive result on a single genes in concert.

Population expansions were indicated using two different types of analyses that were largely in agreement, however the EBSPs suggested fewer instances of demographic change. It is not surprising that these tests would not agree in every case. Simulated datasets demonstrate that the EBSP analyses are prone to false negatives when using fewer than eight loci (Heled & Drummond, 2008). Given the number of loci sequenced, it seems likely that our EBSPs were more conservative in their inference of population expansions than the frequency-based tests.

The generation of sequence data was complicated due to the evolutionary distance separating these species, over 200 million years in some cases (Near et al., 2012). Finding primer sets that successfully amplified genes in multiple study species was the limiting to factor to the number of sequences included in this investigation. In the future, the use of high-throughput sequencing would greatly expand the number of genes available for analyses and provide greater resolution to the demographic histories of the fishes inhabiting the deep-pelagic, likely increasing the number of demographic expansions that are inferred.

4.3 | Genetic evidence furthers recent findings based on the fossil record

While molecular techniques can infer demographic history directly, analyses of the fossil record can uncover trends in local species abundance and community composition over time, which can be indicative of larger demographic trends. Several recent publications have used the fossil record to recreate prehistoric deep-pelagic fish communities. Salvatteci et al. (2022) identified fossilized vertebrae to compare the community structure of fishes inhabiting Humboldt Current at two points in time (the last interglacial and the Holocene) (Salvatteci et al., 2022). The study includes two deep-pelagic species, with one species increasing and the other decreasing in frequency in the Holocene sample. Lin et al. 2023) utilized fossilized otoliths to investigate trends in deep-pelagic fishes in the Warm Pacific Pool over the last 460 thousand years (Lin et al., 2023). They included species from five major deep-pelagic families and found temporal changes in the number of otoliths present in the fossil record as well as the community composition. While some species remained well represented throughout the record others fluctuated greatly. These inferred changes in community composition and abundance could be a record of large-scale fluctuations in range and population sizes in deep-pelagic fishes. Given our widespread inference of population instability, it seems likely that the fossil-based analyses are identifying the same phenomenon.

4.4 | Potential drivers of deep-pelagic fish population dynamics

Our widespread inference of population expansions in deep-pelagic fishes was unexpected. Demographic events are typically attributed to major climate changes that alter the environment, in turn increasing or decreasing the amount of optimal habitat for a given species (Avise, 2000; Grant, 2015). Populations expand or contract in response to these alterations in optimal habitat. Because the deeppelagic domain has been a relatively stable habitat in terms of its size and temperature for millions of years, it would seem likely that the demographic histories of deep-pelagic fishes would be characterized by a lack of expansions/contractions (Clark et al., 2009; Levitus et al., 2012; Robison, 2009). Instead, we uncovered a minimum of four cases of population expansion (identified by both frequencybased statistics and gene tree-based analysis) and possibly nine cases of population expansion (based on frequency-based statistics alone).

We proposed and tested one potential driver of population size change in deep-pelagic fishes, diel vertical migration. We hypothesized that the obligate use of the more volatile epipelagic domain by vertically migrating species may increase their likelihood of undergoing population fluctuations relative to species that do not vertically migrate. Hsieh et al. (2009) provide support for the hypothesis as they reported the larval distribution of fish species with vertically migrating adults changed more rapidly/frequently than non-vertically migrating species (Hsieh et al., 2009). This could be attributed to short-term changes in surface water conditions that impact vertically migrating species but are unfelt by those adults that remain at depth. If vertical migratory habits were the primary driver of population dynamics in deep-pelagic fishes, the demographic histories of vertically migrating species would be characterized by population expansions/contractions, while non-vertically migrating species should be less variable over time. Based on our chi-squared test, we were unable to detect any difference in population dynamics between these two groups. Of the four species with the strongest evidence for population expansions, two are vertical migrators and two are non-vertical migrators. We find vertical migration, to be an unlikely driver of population dynamics in deep-pelagic fishes.

Another feature of deep-pelagic fish biology might explain population dynamics in the fishes inhabiting this environment, a pelagic larval phase, where the larvae of most deep-pelagic fishes reside in the upper 200 m (Bowlin, 2016; Johnson et al., 2009; Moser, 1996). Two lines of evidence support the hypothesis that the physiological tolerances of the larvae residing in the epipelagic domain drive population dynamics in deep-pelagic fishes: longterm monitoring of larval distribution and deep-pelagic patterns of distribution.

Long-term monitoring efforts in transition zones between tropical and subpolar regions have shown that physical conditions, such as sea surface temperature, are key predictors of larval community composition. Furthermore, physical changes in these environments alter the larval composition of the community (Ahlstrom, 1969;

WILEY

Netburn & Koslow, 2018; Sassa et al., 2004; Urias-Leyva et al., 2018). Aceves-Medina et al. (2004) found that the distribution of larvae was congruent with that of the adults. This suggests that as sea surface conditions alter larval distributions, the ranges of adults would change accordingly.

The second piece of evidence for larval control on demography comes from the distribution patterns of deep-pelagic fishes. Most deep-pelagic fishes can broadly be classified as warm-water or cold-water species, and many species have latitudinal biogeographic boundaries (see Table A3 for range description of study species) (Olson, 2001; Pearcy, 1991; Randall, 1981). Within oceanic basins, latitudinal differences in temperature decrease by depth (Vecchione et al., 2015). By 1000m depth the temperature is a near uniform 5°C throughout most of the world's oceans (Helfman et al., 2009; Tyus, 2011). It is therefore noteworthy that even some non-vertically migrating bathypelagic groups such as the whale fishes exhibit strong latitudinal biogeographic boundaries (Paxton, 1989). It seems unlikely that the distribution trends exhibited by deep-pelagic fishes can be explained by physiological constraints on the adults of these species given the relative homogeneity of the environment. Rather, a given species range is constrained to regions with surface waters tolerable to their larvae. If correct periods of warm SST in high latitudes would increase available habitat to deep-pelagic larval fishes and lead to population expansions.

Finally, trophic dynamics could potentially drive changes in population size in deep-pelagic fishes. Vertically migrating fishes in the upper mesopelagic typically forage in surface waters where the food web is supported by recent in situ primary production (Gloeckler et al., 2018; Sutton & Hopkins, 1996). In contrast, some non-migratory fishes that reside in the lower mesopelagic and the bathypelagic largely rely on a suspended, particle-based food web composed of degraded particulate organic matter originating in the epipelagic (Crichton et al., 2023; Eduardo et al., 2023; Gloeckler et al., 2018; Hannides et al., 2020). Thus, the amount of carbon available to non-migratory consumers in the lower mesopelagic and bathypelagic zones is directly linked to the amount of primary production in surface waters and the rate at which it can reach deeper depths.

Changes in ocean temperatures can greatly alter the amount of the particulate organic carbon (POC) that reaches this environment, in turn affecting the amount of food available to support this community (Crichton et al., 2023; John et al., 2013; Olivarez Lyle & Lyle, 2006). Crichton et al. (2023) suggest that bacteria may drive this phenomenon. As oceans warm the metabolic rates of bacteria increase, leading to greater consumption of sinking organic material, and less POC reaching deep waters (Crichton et al., 2023).

The availability of organic carbon at depth may be evident in the fossil record (Boscolo-Galazzo et al., 2021). Deep-pelagic formaninifera diversity and abundance increases as ocean temperatures decrease, a feature attributed to a greater volume of food reaching this habitat (Boscolo-Galazzo et al., 2021; Crichton et al., 2023). This increase in food availability would be expected to positively benefit population sizes for the other members of the deep-pelagic food web, including fish species. If food availability shapes deep-pelagic fish demographics, periods of global warming would lead to population contractions while periods of global cooling would lead to population expansions. This feature would be more pronounced in deeper dwelling species.

5 | CONCLUSIONS

Insights into the nature of deep-pelagic fish population dynamics are currently lacking. Our results demonstrate that despite the longterm stability of the global mesopelagic and bathypelagic domains, the population sizes of the fishes that reside within them are not static in nature. It seems likely that previous changes to the environment, potentially as a result of large-scale changes in climate, have impacted the fish community residing in the deep-pelagic. As we continue to investigate the particular environmental factors that influence demographic changes in these fishes, we will better be able to predict how populations of these fishes will behave in the face of future climate change.

AUTHOR CONTRIBUTIONS

Max D. Weber: Conceptualization (lead); data curation (lead); investigation (equal); writing – original draft (lead). Travis M. Richards: Investigation (equal); writing – review and editing (equal). Tracey T. Sutton: Funding acquisition (lead); investigation (equal); writing – review and editing (equal). Joshua E. Carter: Investigation (equal); writing – review and editing (equal). Ron I. Eytan: Funding acquisition (supporting); investigation (equal); resources (lead); supervision (lead); writing – review and editing (equal).

ACKNOWLEDGEMENTS

This work was supported by a grant from The Gulf of Mexico Research Initiative, and in part by the National Oceanic and Atmospheric Administration's RESTORE Science Program (NA19NOS4510193). Data are publicly available through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at https://data.gulfresearchinitiative.org. We thank M. Hellberg and two anonymous reviewers for their helpful comments on previous versions of the manuscript. We thank D. Fenolio for the high quality photo of one of our study species (Dante@anotheca.com).

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

DNA sequences: available on Genbank. The accession numbers and corresponding sample data are located in Table A1.

ORCID

Max D. Weber D https://orcid.org/0000-0003-2417-7866

REFERENCES

- Abraham, J. P., Baringer, M., Bindoff, N. L., Boyer, T., Cheng, L. J., Church, J. A., Conroy, J. L., Domingues, C. M., Fasullo, J. T., Gilson, J., Goni, G., Good, S. A., Gorman, J. M., Gouretski, V., Ishii, M., Johnson, G. C., Kizu, S., Lyman, J. M., Macdonald, A. M., ... Willis, J. K. (2013). A review of global ocean temperature observations: Implications for ocean heat content estimates and climate change. *Reviews of Geophysics*, *51*, 450–483.
- Aceves-Medina, G., Jiménez-Rosenberg, S. P. A., Hinojosa-Medina, A., Funes-Rodríguez, R., Saldierna-Martínez, R. J., & Smith, P. E. (2004). Fish larvae assemblages in the Gulf of California. *Journal of Fish Biology*, 65, 832–847.
- Agustin, L. Q. (2018). Bathophilus pawneei. http://fishbase.org/summary/ Bathophilus-pawneei
- Ahlstrom, E. H. (1969). Mesopelagic and bathypelagic fishes in the California current region. *California Cooperative Oceanic Fisheries Investigations Reports*, 13, 39–44.
- Alheit, J., & Hagen, E. (1997). Long-term climate forcing of European herring and sardine populations. *Fisheries Oceanography*, 6, 130–139.
- Almada, V. C., Almada, F., Francisco, S. M., Castilho, R., & Robalo, J. I. (2012). Unexpected high genetic diversity at the extreme northern geographic limit of *Taurulus bubalis* (Euphrasen, 1786). *PLoS One*, 7, e44404.
- Avise, J. C. (2000). Phylogeography: The history and formation of species. Harvard University Press.
- Barham, E. G. (1966). Deep scattering layer migration and composition: Observations from a diving saucer. *Science*, *151*, 1399–1403.
- Bernard, A. M., Finnegan, K. A., Sutton, T. T., Eytan, R. I., Weber, M. D., & Shivji, M. S. (2022). Population genomic dynamics of mesopelagic lanternfishes *Diaphus dumerilii*, *Lepidophanes guentheri*, and *Ceratoscopelus warmingii* (Family: Myctophidae) in the Gulf of Mexico. *Deep Sea Research Part I: Oceanographic Research Papers*, 185, 103786.
- Birkner, M., Blath, J., & Eldon, B. (2013). Statistical properties of the sitefrequency spectrum associated with A-coalescents. Genetics, 195, 1037–1053.
- Boscolo-Galazzo, F., Crichton, K. A., Ridgwell, A., Mawbey, E. M., Wade, B. S., & Pearson, P. N. (2021). Temperature controls carbon cycling and biological evolution in the ocean twilight zone. *Science*, 371, 1148–1152.
- Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C. H., Xie, D., Suchard, M. A., Rambaut, A., & Drummond, A. J. (2014). BEAST 2: A software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, 10, e1003537.
- Bowlin, N. M. (2016). Ontogenetic changes in the distribution and abundance of early life history stages of mesopelagic fishes off California. University of California.
- Carnaval, A. C., Hickerson, M. J., Haddad, C. F., Rodrigues, M. T., & Moritz, C. (2009). Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. *Science*, *323*, 785–789.
- Clarke, T. A. (1983). Sex ratios and sexual differences in size among mesopelagic fishes from the central Pacific Ocean. *Marine Biology*, 73, 203–209.
- Clark, P. U., Archer, D., Pollard, D., Blum, J. D., Rial, J. A., Brovkin, V., Mix, A. C., Pisias, N. G., & Roy, M. (2006). The middle Pleistocene transition: Characteristics, mechanisms, and implications for long-term changes in atmospheric pCO₂. *Quaternary Science Reviews*, 25, 3150–3184.
- Clark, P. U., Dyke, A. S., Shakun, J. D., Carlson, A. E., Clark, J., Wohlfarth, B., Mitrovica, J. X., Hostetler, S. W., & McCabe, A. (2009). The last glacial maximum. *Science*, 325, 710–714.
- Clarke, T. A., & Wagner, P. J. (1976). Vertical distribution and other aspects of the ecology of certain mesopelagic fishes taken near Hawaii. *Fishery Bulletin*, 74(3), 635–645.
- Cook, A. B., Sutton, T. T., Galbraith, J. K., & Vecchione, M. (2013). Deeppelagic (0–3000m) fish assemblage structure over the mid-Atlantic

WEBER ET AL.

ridge in the area of the Charlie-Gibbs fracture zone. *Deep Sea Research Part II: Topical Studies in Oceanography, 98, 279–291.*

- Crichton, K. A., Wilson, J. D., Ridgwell, A., Boscolo-Galazzo, F., John, E. H., Wade, B. S., & Pearson, P. N. (2023). What the geological past can tell us about the future of the ocean's twilight zone. *Nature Communications*, 14, 2376.
- Eduardo, L. N., Lucena-Frédou, F., Lanco Bertrand, S., Lira, A. S., Mincarone, M. M., Nunes, G. T., Frédou, T., Soares, A., le Loc'h, F., Pelage, L., Schwamborn, R., Travassos, P., Martins, K., Lira, S. M. A., Figueiredo, G. A. A., Júnior, T. V., Ménard, F., & Bertrand, A. (2023). From the light blue sky to the dark deep sea: Trophic and resource partitioning between epipelagic and mesopelagic layers in a tropical oceanic ecosystem. *Science of the Total Environment*, 878, 163098.
- Eldon, B., Birkner, M., Blath, J., & Freund, F. (2015). Can the site-frequency spectrum distinguish exponential population growth from multiplemerger coalescents? *Genetics*, 199, 841–856.
- Etter, R., Rex, M. A., Chase, M. R., & Quattro, J. M. (2005). Population differentiation decreases with depth in deep-sea bivalves. *Evolution*, 59, 1479–1491.
- Eytan, R. I., & Hellberg, M. E. (2010). Nuclear and mitochondrial sequence data reveal and conceal different demographic histories and population genetic processes in Caribbean reef fishes. *Evolution: International Journal of Organic Evolution*, 64, 3380–3397.
- Fu, Y.-X. (1997). Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics*, 147, 915–925.
- Glenn, T. (2019). PEG precipitation of PCR products. http://labs.mcdb.lsa. umich.edu/labs/olsen/files/PCR.pdf
- Gloeckler, K., Choy, C. A., Hannides, C. C. S., Close, H. G., Goetze, E., Popp, B. N., & Drazen, J. C. (2018). Stable isotope analysis of micronekton around Hawaii reveals suspended particles are an important nutritional source in the lower mesopelagic and upper bathypelagic zones. *Limnology and Oceanography*, 63, 1168–1180.
- Grant, W. S. (2015). Problems and cautions with sequence mismatch analysis and Bayesian skyline plots to infer historical demography. *Journal of Heredity*, 106, 333–346.
- Gugger, P. F., Ikegami, M., & Sork, V. L. (2013). Influence of late Quaternary climate change on present patterns of genetic variation in valley oak, Quercus lobata Née. Molecular Ecology, 22, 3598–3612.
- Hannides, C. C., Popp, B. N., Close, H. G., Benitez-Nelson, C. R., Cassie,
 A., Gloeckler, K., Wallsgrove, N., Umhau, B., Palmer, E., & Drazen, J.
 C. (2020). Seasonal dynamics of midwater zooplankton and relation
 to particle cycling in the North Pacific Subtropical Gyre. *Progress in* Oceanography, 182, 102266.
- Heled, J. (2010). Extended Bayesian skyline plot tutorial. tutorial.east.bio. ed.ac.uk/Tutorials
- Heled, J., & Drummond, A. J. (2008). Bayesian inference of population size history from multiple loci. *BMC Evolutionary Biology*, *8*, 289.
- Helfman, G., Collette, B. B., Facey, D. E., & Bowen, B. W. (2009). The diversity of fishes: Biology, evolution, and ecology. John Wiley & Sons.
- Ho, S. Y., & Shapiro, B. (2011). Skyline-plot methods for estimating demographic history from nucleotide sequences. *Molecular Ecology Resources*, 11, 423–434.
- Hsieh, C. H., Kim, H. J., Watson, W., Di Lorenzo, E., & Sugihara, G. (2009). Climate-driven changes in abundance and distribution of larvae of oceanic fishes in the southern California region. *Global Change Biology*, 15, 2137–2152.
- John, E. H., Pearson, P. N., Coxall, H. K., Birch, H., Wade, B. S., & Foster, G. L. (2013). Warm ocean processes and carbon cycling in the Eocene. *Philosophical Transactions of the Royal Society A: Mathematical*, *Physical and Engineering Sciences*, 371, 20130099.
- Johnson, G. D., Paxton, J. R., Sutton, T. T., Satoh, T. P., Sado, T., Nishida, M., & Miya, M. (2009). Deep-sea mystery solved: Astonishing larval transformations and extreme sexual dimorphism unite three fish families. *Biology Letters*, 5, 235–239. https://doi.org/10.1098/rsbl. 2008.0722

- Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P., & Drummond, A. (2012). Geneious basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, 28, 1647–1649.
- Kenaley, C. P. (2009). Revision of Indo-Pacific species of the loosejaw dragonfish genus Photostomias (Teleostei: Stomiidae: Malacosteinae). Copeia, 2009, 175–189.
- Lancraft, T. M., Hopkins, T. L., & Torres, J. J. (1988). Aspects of the ecology of the mesopelagic fish Gonostoma elongatum (Gonostomatidae, Stomiiformes) in the eastern Gulf of Mexico. Marine Ecology Progress Series. Oldendorf, 49(1), 27-40.
- Lanfear, R., Calcott, B., Ho, S. Y., & Guindon, S. (2012). PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29, 1695–1701.
- Levitus, S., Antonov, J. I., Boyer, T. P., Baranova, O. K., Garcia, H. E., Locarnini, R. A., Mishonov, A. V., Reagan, J. R., Seidov, D., Yarosh, E. S., & Zweng, M. M. (2012). World ocean heat content and thermosteric sea level change (0–2000m), 1955–2010. *Geophysical Research Letters*, 39.
- Lin, C. H., Wei, C. L., Ho, S. L., & Lo, L. (2023). Ocean temperature drove changes in the mesopelagic fish community at the edge of the Pacific Warm Pool over the past 460,000 years. *Science Advances*, 9(27), eadf0656.
- McEachran, J., & Fechhelm, J. D. (1998). Fishes of the Gulf of Mexico. University of Texas Press.
- Miya, M., & Nemoto, T. (1986). Life history and vertical distribution of the mesopelagic fish Cyclothone alba (family Gonostomatidae) in Sagami Bay, Central Japan. Deep Sea Research Part A. Oceanographic Research Papers, 33(8), 1053–1068.
- Montano, V. (2016). Coalescent inferences in conservation genetics: Should the exception become the rule? *Biology Letters*, 12, 20160211.
- Mora, C., Wei, C. L., Rollo, A., Amaro, T., Baco, A. R., Billett, D., Bopp, L., Chen, Q., Collier, M., Danovaro, R., Gooday, A. J., Grupe, B. M., Halloran, P. R., Ingels, J., Jones, D. O. B., Levin, L. A., Nakano, H., Norling, K., Ramirez-Llodra, E., ... Yasuhara, M. (2013). Biotic and human vulnerability to projected changes in ocean biogeochemistry over the 21st century. *PLoS Biology*, 11, e1001682.
- Moser, H. G. (1996). The early life stages of fishes in the California current region. *California Cooperative Oceanic Fisheries Investigations Atlas*, 33, 1505.
- Mundy, B. C. (2005). Checklist of the fishes of the Hawaiian Archipelago. Bishop Museum Bulletins in Zoology, 6, 1–704.
- Near, T. J., Eytan, R. I., Dornburg, A., Kuhn, K. L., Moore, J. A., Davis, M. P., Wainwright, P. C., Friedman, M., & Smith, W. L. (2012). Resolution of ray-finned fish phylogeny and timing of diversification. Proceedings of the National Academy of Sciences of the United States of America, 109, 13698–13703.
- Netburn, A. N., & Koslow, J. A. (2018). Mesopelagic fish assemblages across oceanic fronts: A comparison of three frontal systems in the southern California current ecosystem. *Deep Sea Research Part I: Oceanographic Research Papers*, 134, 80–91.
- Niwa, H.-S., Nashida, K., Yanagimoto, T., & Grant, H. e. W. S. (2016). Reproductive skew in Japanese sardine inferred from DNA sequences. *ICES Journal of Marine Science*, 73, 2181–2189.
- Nye, J. A., Link, J. S., Hare, J. A., & Overholtz, W. J. (2009). Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Marine Ecology Progress Series*, 393, 111–129.
- Olivarez Lyle, A., & Lyle, M. W. (2006). Missing organic carbon in Eocene marine sediments: Is metabolism the biological feedback that maintains end-member climates? *Paleoceanography*, 21.
- Olson, D. B. (2001). Biophysical dynamics of western transition zones: A preliminary synthesis. *Fisheries Oceanography*, 10, 133–150.

- Paxton, J. R. (1989). Synopsis of the whalefishes (family Cetomimidae) with descriptions of four new genera. *Records of the Australian Museum*, 41, 135-206.
- Pearcy, W. G. (1991). Biology of the transition region. NOAA Technical Report NMFS, 105, 39–55.
- Priede, I. G. (2017). *Deep-sea fishes: Biology, diversity, ecology and fisheries*. Cambridge University Press.
- Rambaut, A., Drummond, A., & Suchard, M. (2014). *Tracer* v1. 6. http:// beast.bio.ed.ac.uk.Tracer
- Ramos-Onsins, S. E., & Rozas, J. (2002). Statistical properties of new neutrality tests against population growth. *Molecular Biology and Evolution*, *19*, 2092–2100.
- Randall, J. E. (1981). Examples of antitropical and antiequatorial distribution of Indo-West-Pacific fishes. *Pacific Science*, *35*, 197–209.
- Robalo, J. I., Castilho, R., Francisco, S. M., Almada, F., Knutsen, H., Jorde, P. E., Pereira, A. M., & Almada, V. C. (2012). Northern refugia and recent expansion in the North Sea: The case of the wrasse Symphodus melops (Linnaeus, 1758). Ecology and Evolution, 2, 153–164.
- Robison, B. H. (2009). Conservation of deep pelagic biodiversity conservation de la biodiversidad pelágica profunda. Conservation Biology, 23, 847–858. https://doi.org/10.1111/j.1523-1739.2009.01219.x
- Rozas, J., Ferrer-Mata, A., Sánchez-DelBarrio, J. C., Guirao-Rico, S., Librado, P., Ramos-Onsins, S. E., & Sánchez-Gracia, A. (2017). DnaSP 6: DNA sequence polymorphism analysis of large data sets. *Molecular Biology and Evolution*, 34, 3299–3302.
- Sakuma, K., Ueda, Y., Hamatsu, T., & Kojima, S. (2014). Contrasting population histories of the deep-sea demersal fish, *Lycodes matsubarai*, in the Sea of Japan and the Sea of Okhotsk. *Zoological Science*, 31, 375–382.
- Salvatteci, R., Schneider, R. R., Galbraith, E., Field, D., Blanz, T., Bauersachs, T., Crosta, X., Martinez, P., Echevin, V., Scholz, F., & Bertrand, A. (2022). Smaller fish species in a warm and oxygenpoor Humboldt current system. *Science*, 375, 101–104.
- Sassa, C., Kawaguchi, K., Oozeki, Y., Kubota, H., & Sugisaki, H. (2004). Distribution patterns of larval myctophid fishes in the transition region of the western North Pacific. *Marine Biology*, 144, 417–428.
- Stephens, M., & Scheet, P. (2001). Estimating population haplotype frequencies from pooled DNA samples using PHASE algorithm. *American Journal of Human Genetics*, 68, 978–989.
- Stephens, M., & Scheet, P. (2005). Accounting for decay of linkage disequilibrium in haplotype inference and missing-data imputation. *The American Journal of Human Genetics*, 76, 449–462.
- Sutton, T. (2013). Vertical ecology of the pelagic ocean: Classical patterns and new perspectives. *Journal of Fish Biology*, 83, 1508–1527.
- Sutton, T. T., Clark, M. R., Dunn, D. C., Halpin, P. N., Rogers, A. D., Guinotte, J., Bograd, S. J., Angel, M. V., Perez, J. A. A., Wishner, K., Haedrich, R. L., Lindsay, D. J., Drazen, J. C., Vereshchaka, A., Piatkowski, U., Morato, T., Błachowiak-Samołyk, K., Robison, B. H., Gjerde, K. M., ... Heino, M. (2017). A global biogeographic classification of the mesopelagic zone. *Deep Sea Research Part I: Oceanographic Research Papers*, 126, 85–102.
- Sutton, T. T., & Hopkins, T. (1996). Trophic ecology of the stomiid (Pisces: Stomiidae) fish assemblage of the eastern Gulf of Mexico: Strategies, selectivity and impact of a top mesopelagic predator group. *Marine Biology*, 127, 179–192.
- Tajima, F. (1989). Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics*, *123*, 585–595.
- Thurber, A. R., Sweetman, A. K., Narayanaswamy, B. E., Jones, D. O. B., Ingels, J., & Hansman, R. L. (2014). Ecosystem function and services provided by the deep sea. *Biogeosciences*, 11, 3941–3963.
- Torres, A. G. (2018). Sigmops elongatus.
- Tyus, H. M. (2011). Ecology and conservation of fishes. CRC Press.
- Urias-Leyva, H., Aceves-Medina, G., Avendaño-Ibarra, R., Saldierna-Martínez, R. J., Gómez-Gutiérrez, J., & Robinson, C. J. (2018). Regionalization in the distribution of larval fish assemblages during winter and autumn in the Gulf of California. *Latin American Journal* of Aquatic Research, 46, 20–36.

WILEY_Ecology and Evolution _

- Varela, A. I., Ritchie, P. A., & Smith, P. J. (2012). Low levels of global genetic differentiation and population expansion in the deep-sea teleost Hoplostethus atlanticus revealed by mitochondrial DNA sequences. *Marine Biology*, 159, 1049–1060.
- Vecchione, M., Falkenhaug, T., Sutton, T., Cook, A., Gislason, A., Hansen, H. Ø., Heino, M., Miller, P. I., Piatkowski, U., Porteiro, F., Søiland, H., & Bergstad, O. A. (2015). The effect of the North Atlantic Subpolar Front as a boundary in pelagic biogeography decreases with increasing depth and organism size. *Progress in Oceanography*, 138, 105–115.
- Watling, L., Guinotte, J., Clark, M. R., & Smith, C. R. (2013). A proposed biogeography of the deep ocean floor. *Progress in Oceanography*, 111, 91–112.

Zamarro, J., & Lloris, D. (1999). New northern limit for the distribution of Sternoptyx pseudobscura Baird, 1971 (Pisces: Sternoptychidae) in the Atlantic.

How to cite this article: Weber, M. D., Richards, T. M., Sutton, T. T., Carter, J. E., & Eytan, R. I. (2024). Deep-pelagic fishes: Demographic instability in a stable environment. *Ecology and Evolution*, 14, e11267. <u>https://doi.org/10.1002/</u> ece3.11267

APPENDIX

WILEY

TABLE A1 (Continued)

TABLE A1 List of GenBank accession numbers					Accession		
ADLE AT LISUO GENDANK ACCESSION HUMDERS.			Species	Gene	number	Specimen ID	
- ·		Accession		Chauliodus sloani	COI	OP132453	DPND_3938
Species	Gene	number	Specimen ID	Chauliodus sloani	COI	OP132454	DPND_4109
Bathophilus pawneei	COI	OP131918	DPND_1336	Chauliodus sloani	COI	OP132455	DPND_4119
Bathophilus pawneei	COI	OP131919	DPND_1900	Chauliodus sloani	COI	OP132456	DPND_4120
Bathophilus pawneei	COI	OP131920	DPND_1914	Chauliodus sloani	COI	OP132457	DPND_4121
Bathophilus pawneei	COI	OP131921	DPND_1985	Chauliodus sloani	COI	OP132458	DPND_4138
Bathophilus pawneei	COI	OP131922	DPND_2001	Chauliodus sloani	COI	OP132459	DPND_4139
Bathophilus pawneei	COI	OP131923	DPND_2002	Chauliodus sloani	COI	OP132460	DPND_4212
Bathophilus pawneei	COI	OP131924	DPND_2267	Chauliodus sloani	COI	OP132461	DPND_4278
Bathophilus pawneei	COI	OP131925	RIE_0008	Chauliodus sloani	COI	OP132462	DPND_4465
Bathophilus pawneei	COI	OP131926	RIE_0313	Chauliodus sloani	COI	OP132463	DPND_4528
Bathophilus pawneei	COI	OP131927	RIE_0516	Chauliodus sloani	COI	OP132464	DPND_4529
Chauliodus sloani	COI	OP132420	DPND_1241	Chauliodus sloani	COI	OP132465	DPND_4546
Chauliodus sloani	COI	OP132421	DPND_1556	Chauliodus sloani	COI	OP132466	DPND_4551
Chauliodus sloani	COI	OP132422	DPND_1557	Chauliodus sloani	COI	OP132467	DPND_4649
Chauliodus sloani	COI	OP132423	DPND_1605	Chauliodus sloani	COI	OP132468	DPND_4693
Chauliodus sloani	COI	OP132424	DPND_1669	Chauliodus sloani	COI	OP132469	DPND_4694
Chauliodus sloani	COI	OP132425	DPND_1695	Chauliodus sloani	COI	OP132470	DPND_4695
Chauliodus sloani	COI	OP132426	DPND_1877	Chauliodus sloani	COI	OP132471	DPND_4736
Chauliodus sloani	COI	OP132427	DPND_1895	Chauliodus sloani	COI	OP132472	DPND_4920
Chauliodus sloani	COI	OP132428	DPND_1896	Chauliodus sloani	COI	OP132473	DPND_4946
Chauliodus sloani	COI	OP132429	DPND_1937	Chauliodus sloani	COI	OP132474	DPND_5014
Chauliodus sloani	COI	OP132430	DPND_1997	Chauliodus sloani	COI	OP132475	DPND_5015
Chauliodus sloani	COI	OP132431	DPND_2027	Chauliodus sloani	COI	OP132476	DPND_5050
Chauliodus sloani	COI	OP132432	DPND_2037	Chauliodus sloani	COI	OP132477	DPND_5126
Chauliodus sloani	COI	OP132433	DPND_2097	Chauliodus sloani	COI	OP132478	DPND_5302
Chauliodus sloani	COI	OP132434	DPND_2181	Chauliodus sloani	COI	OP132479	DPND_5334
Chauliodus sloani	COI	OP132435	DPND_2208	Chauliodus sloani	COI	OP132480	DPND_5335
Chauliodus sloani	COI	OP132436	DPND_2260	Chauliodus sloani	COI	OP132481	DPND_5398
Chauliodus sloani	COI	OP132437	DPND_2387	Chauliodus sloani	COI	OP132482	DPND_5426
Chauliodus sloani	COI	OP132438	DPND_2418	Chauliodus sloani	COI	OP132483	DPND_5427
Chauliodus sloani	COI	OP132439	DPND_2490	Chauliodus sloani	COI	OP132484	DPND_5467
Chauliodus sloani	COI	OP132440	DPND_2528	Chauliodus sloani	COI	OP132485	DPND_5468
Chauliodus sloani	COI	OP132441	DPND_2699	Chauliodus sloani	COI	OP132486	DPND_5500
Chauliodus sloani	COI	OP132442	DPND_2731	Chauliodus sloani	COI	OP132487	DPND_5573
Chauliodus sloani	COI	OP132443	DPND_2756	Chauliodus sloani	COI	OP132488	DPND_5574
Chauliodus sloani	COI	OP132444	DPND_2757	Chauliodus sloani	COI	OP132489	DPND_5593
Chauliodus sloani	COI	OP132445	DPND_2813	Chauliodus sloani	COI	OP132490	DPND_5610
Chauliodus sloani	COI	OP132446	DPND_2958	Chauliodus sloani	COI	OP132491	DPND_5634
Chauliodus sloani	COI	OP132447	DPND_3621	Chauliodus sloani	COI	OP132492	DPND_5665
Chauliodus sloani	COI	OP132448	DPND_3682	Chauliodus sloani	COI	OP132493	DPND_5675
Chauliodus sloani	COI	OP132449	DPND_3774	Chauliodus sloani	COI	OP132494	DPND_5680
Chauliodus sloani	COI	OP132450	DPND_3789	Chauliodus sloani	COI	OP132495	DPND_5682
Chauliodus sloani	COI	OP132451	DPND_3790	Chauliodus sloani	COI	OP132496	DPND_5723
Chauliodus sloani	COI	OP132452	DPND_3937	Chauliodus sloani	COI	OP132497	DPND_5741
							_

Gene

COI

COI COI

COI

COI

COI

COI

COI

COI COI

COI

COI

COI

COI

COI

TABLE A1 (Continued)

Species

Chauliodus sloani

Cyclothone alba

Cyclothone pseudopallida

Cyclothone pseudopallida Cyclothone pseudopallida

Cyclothone pseudopallida

Cyclothone pseudopallida

Cyclothone pseudopallida

Cyclothone pseudopallida

Cyclothone pseudopallida

Cyclothone pseudopallida Cyclothone pseudopallida

Cyclothone pseudopallida

Cyclothone pseudopallida

Cyclothone pseudopallida

Cyclothone pseudopallida

ition Open A	ccess	
		TABLE A1 (Continue
ssion		
ber	Specimen ID	Species
32498	RIE_18	Diplospinus multistriatus
32499	RIE_236	Diplospinus multistriatus
32500	RIE_510	Diplospinus multistriatus
32501	RIE_576	Diplospinus multistriatus
32502	RIE_642	Diplospinus multistriatus
32503	RIE_690	Diplospinus multistriatus
32504	RIE_698	Diplospinus multistriatus
32505	RIE_912	Diplospinus multistriatus
32506	RIE_913	Diplospinus multistriatus
32507	RIE_914	Diplospinus multistriatus
32508	RIE_948	Diplospinus multistriatus
32509	RIE_0994	Diplospinus multistriatus
32510	DPND_5114	Ditropichthys storeri
32511	DPND_4579	Ditropichthys storeri
32512	DPND_2788	Ditropichthys storeri
32513	DPND_3505	Ditropichthys storeri
32514	DPND_4717	Ditropichthys storeri
32515	DPND_4008	Ditropichthys storeri
32516	DPND_3987	Ditropichthys storeri
81971	RIE_0349	Ditropichthys storeri
31972	RIE_0350	Ditropichthys storeri
31973	RIE_0351	Ditropichthys storeri
31974	RIE_0031	Ditropichthys storeri

ed)

	Accession number	Specimen ID
	OP132498	RIE_18
OF	P132499	RIE_236
С	P132500	RIE_510
•	OP132501	RIE_576
	OP132502	RIE_642
	OP132503	RIE_690
	OP132504	RIE_698
	OP132505	RIE_912
	OP132506	RIE_913
	OP132507	RIE_914
•	OP132508	RIE_948
	OP132509	RIE_0994
	OP132510	DPND_5114
(OP132511	DPND_4579
	OP132512	DPND_2788
0	OP132513	DPND_3505
	OP132514	DPND_4717
1	OP132515	DPND_4008
	OP132516	- DPND 3987
	OP131971	RIE 0349
	OP131972	RIF_0350
(OP131973	RIF_0351
	OP131974	RIE 0031
	OP131975	RIF 0252
	OP131976	RIE 0253
(OP131977	RIF 0254
	OP131978	RIF 0255
	OP131979	RIF 0344
	OP131980	RIF 0345
1	OP131981	RIE_0347
	OP131982	RIE_0347
` `	DF 101702	DIE 0250
	OP131704	DIE 0257
	08131985	RIE_033/
	OP131986	KIE_0077
	OP131987	KIE_0354
	OP131988	RIE_0239
	OP131989	RIE_0360
	OP131990	RIE_0477
	OP131991	RIE_0493
	OP131992	RIE_0544
	OP131993	DPND_4547
	OP131994	DPND_4483
	OP131995	RIE_0238
	OP131996	RIE_0358
	OP131997	RIE_0492

Ecology and Evolution

15 of 21

WILEY

TABLE A1 (Continued)

Species	Gene	Accession number	Specimen ID
Scopelogadus mizolepis	COI	OP132164	RIE_0954
Sigmops elongatus	COI	OP132179	RIE_0278
Sigmops elongatus	COI	OP132180	RIE_0279
Sigmops elongatus	COI	OP132181	RIE_0280
Sigmops elongatus	COI	OP132182	RIE_0002
Sigmops elongatus	COI	OP132183	RIE_0017
Sigmops elongatus	COI	OP132184	RIE_0097
Sigmops elongatus	COI	OP132185	RIE_0182
Sigmops elongatus	COI	OP132186	RIE_0204
Sigmops elongatus	COI	OP132187	RIE_0205
Sigmops elongatus	COI	OP132188	RIE_0206
Sigmops elongatus	COI	OP132189	RIE_0244
Sigmops elongatus	COI	OP132190	RIE_0277
Sternoptyx pseudobscura	COI	OP132242	RIE_0415
Sternoptyx pseudobscura	COI	OP132243	RIE_0417
Sternoptyx pseudobscura	COI	OP132244	RIE_0078
Sternoptyx pseudobscura	COI	OP132245	RIE_0195
Sternoptyx pseudobscura	COI	OP132246	RIE_0196
Sternoptyx pseudobscura	COI	OP132247	RIE_0197
Sternoptyx pseudobscura	COI	OP132248	RIE_0200
Sternoptyx pseudobscura	COI	OP132249	RIE_0201
Sternoptyx pseudobscura	COI	OP132250	RIE_0223
Sternoptyx pseudobscura	COI	OP132251	RIE_0224
Sternoptyx pseudobscura	COI	OP132252	RIE_0226
Sternoptyx pseudobscura	COI	OP132253	DPND_3772
Sternoptyx pseudobscura	COI	OP132254	DPND_4225
Stomias affinis	COI	OP132165	RIE_0237
Stomias affinis	COI	OP132166	RIE_0517
Stomias affinis	COI	OP132167	DPND_3645
Stomias affinis	COI	OP132168	DPND_1314
Stomias affinis	COI	OP132169	DPND_1543
Stomias affinis	COI	OP132170	DPND_1639
Stomias affinis	COI	OP132171	RIE_0917
Stomias affinis	COI	OP132172	RIE_0466
Stomias affinis	COI	OP132173	RIE_0577
Stomias affinis	COI	OP132174	DPND_1201
Stomias affinis	COI	OP132175	DPND_1315
Bathophilus pawneei	PLAG1	OP149759	DPND_1336
Bathophilus pawneei	PLAG1	OP149760	DPND_1336
Bathophilus pawneei	PLAG1	OP149761	DPND_1900
Bathophilus pawneei	PLAG1	OP149762	DPND_1900
Bathophilus pawneei	PLAG1	OP149763	DPND_1914
Bathophilus pawneei	PLAG1	OP149764	DPND_1914
Bathophilus pawneei	PLAG1	OP149765	DPND_1985
Bathophilus pawneei	PLAG1	OP149766	DPND_1985

		Accession	
Species	Gene	number	Specimen ID
Bathophilus pawneei	PLAG1	OP149767	DPND_2001
Bathophilus pawneei	PLAG1	OP149768	DPND_2001
Bathophilus pawneei	PLAG1	OP149769	DPND_2002
Bathophilus pawneei	PLAG1	OP149770	DPND_2002
Bathophilus pawneei	PLAG1	OP149771	DPND_2267
Bathophilus pawneei	PLAG1	OP149772	DPND_2267
Bathophilus pawneei	PLAG1	OP149773	RIE_313
Bathophilus pawneei	PLAG1	OP149774	RIE_313
Bathophilus pawneei	PLAG1	OP149775	RIE_516
Bathophilus pawneei	PLAG1	OP149776	RIE_516
Bathophilus pawneei	PLAG1	OP149777	RIE_8
Bathophilus pawneei	PLAG1	OP149778	RIE_8
Cyclothone alba	PLAG1	OP149779	RIE_252
Cyclothone alba	PLAG1	OP149780	RIE_252
Cyclothone alba	PLAG1	OP149781	RIE_253
Cyclothone alba	PLAG1	OP149782	RIE_253
Cyclothone alba	PLAG1	OP149783	RIE_254
Cyclothone alba	PLAG1	OP149784	RIE_254
Cyclothone alba	PLAG1	OP149785	RIE_255
Cyclothone alba	PLAG1	OP149786	RIE_255
Cyclothone alba	PLAG1	OP149787	RIE_31
Cyclothone alba	PLAG1	OP149788	RIE_31
Cyclothone alba	PLAG1	OP149789	RIE_344
Cyclothone alba	PLAG1	OP149790	RIE_344
Cyclothone alba	PLAG1	OP149791	RIE_345
Cyclothone alba	PLAG1	OP149792	RIE_345
Cyclothone alba	PLAG1	OP149793	RIE_347
Cyclothone alba	PLAG1	OP149794	RIE_347
Cyclothone alba	PLAG1	OP149795	RIE_348
Cyclothone alba	PLAG1	OP149796	RIE_348
Cyclothone alba	PLAG1	OP149797	RIE_349
Cyclothone alba	PLAG1	OP149798	RIE_349
Cyclothone alba	PLAG1	OP149799	RIE_350
Cyclothone alba	PLAG1	OP149800	RIE_350
Cyclothone alba	PLAG1	OP149801	RIE_351
Cyclothone alba	PLAG1	OP149802	RIE_351
Cyclothone pseudopallida	PLAG1	OP149803	RIE_238
Cyclothone pseudopallida	PLAG1	OP149804	RIE_238
Cyclothone pseudopallida	PLAG1	OP149805	RIE_239
Cyclothone pseudopallida	PLAG1	OP149806	RIE_239
Cyclothone pseudopallida	PLAG1	OP149807	RIE_357
Cyclothone pseudopallida	PLAG1	OP149808	RIE_357
Cyclothone pseudopallida	PLAG1	OP149809	RIE_358
Cyclothone pseudopallida	PLAG1	OP149810	RIE_358
Cyclothone pseudopallida	PLAG1	OP149811	RIE 359

(Continues)

TABLE A1 (Continued)

Creation	Cana	Accession	Cu a siman ID	Creation	Cana	Accession	Curacius en ID
Species	Gene	number	Specimen ID	Species	Gene	numper	Specimen ID
Cyclothone pseudopallida	PLAG1	OP149812	RIE_359	Ditropichthys storeri	PLAG1	OP149857	DPND_4130
Cyclothone pseudopallida	PLAG1	OP149813	RIE_360	Ditropichthys storeri	PLAG1	OP149858	DPND_4130
Cyclothone pseudopallida	PLAG1	OP149814	RIE_360	Ditropichthys storeri	PLAG1	OP149859	DPND_4210
Cyclothone pseudopallida	PLAG1	OP149815	RIE_477	Ditropichthys storeri	PLAG1	OP149860	DPND_4210
Cyclothone pseudopallida	PLAG1	OP149816	RIE_477	Ditropichthys storeri	PLAG1	OP149861	RIE_243
Cyclothone pseudopallida	PLAG1	OP149817	RIE_492	Ditropichthys storeri	PLAG1	OP149862	RIE_243
Cyclothone pseudopallida	PLAG1	OP149818	RIE_492	Ditropichthys storeri	PLAG1	OP149863	RIE_438
Cyclothone pseudopallida	PLAG1	OP149819	RIE_493	Ditropichthys storeri	PLAG1	OP149864	RIE_438
Cyclothone pseudopallida	PLAG1	OP149820	RIE_493	Ditropichthys storeri	PLAG1	OP149865	RIE_522
Cyclothone pseudopallida	PLAG1	OP149821	RIE_544	Ditropichthys storeri	PLAG1	OP149866	RIE_522
Cyclothone pseudopallida	PLAG1	OP149822	RIE_544	Photostomias guernei	PLAG1	OP149867	RIE_107
Diplospinus multistriatus	PLAG1	OP149823	DPND_2718	Photostomias guernei	PLAG1	OP149868	RIE_107
Diplospinus multistriatus	PLAG1	OP149824	DPND_2718	Photostomias guernei	PLAG1	OP149869	RIE_176
Diplospinus multistriatus	PLAG1	OP149825	RIE_171	Photostomias guernei	PLAG1	OP149870	RIE_176
Diplospinus multistriatus	PLAG1	OP149826	RIE_171	Photostomias guernei	PLAG1	OP149871	RIE_337
Diplospinus multistriatus	PLAG1	OP149827	RIE_240	Photostomias guernei	PLAG1	OP149872	RIE_337
Diplospinus multistriatus	PLAG1	OP149828	RIE_240	Photostomias guernei	PLAG1	OP149873	RIE_400
Diplospinus multistriatus	PLAG1	OP149829	RIE_413	Photostomias guernei	PLAG1	OP149874	RIE_400
Diplospinus multistriatus	PLAG1	OP149830	RIE_413	Photostomias guernei	PLAG1	OP149875	RIE_401
Diplospinus multistriatus	PLAG1	OP149831	RIE_495	Photostomias guernei	PLAG1	OP149876	RIE_401
Diplospinus multistriatus	PLAG1	OP149832	RIE_495	Photostomias guernei	PLAG1	OP149877	RIE_459
Diplospinus multistriatus	PLAG1	OP149833	RIE_713	Photostomias guernei	PLAG1	OP149878	RIE_459
Diplospinus multistriatus	PLAG1	OP149834	RIE_713	Photostomias guernei	PLAG1	OP149879	RIE_461
Diplospinus multistriatus	PLAG1	OP149835	RIE_882	Photostomias guernei	PLAG1	OP149880	RIE_461
Diplospinus multistriatus	PLAG1	OP149836	RIE_882	Photostomias guernei	PLAG1	OP149881	RIE_506
Diplospinus multistriatus	PLAG1	OP149837	RIE_883	Photostomias guernei	PLAG1	OP149882	RIE_506
Diplospinus multistriatus	PLAG1	OP149838	RIE_883	Photostomias guernei	PLAG1	OP149883	RIE_514
Diplospinus multistriatus	PLAG1	OP149839	RIE_884	Photostomias guernei	PLAG1	OP149884	RIE_514
Diplospinus multistriatus	PLAG1	OP149840	RIE_884	Photostomias guernei	PLAG1	OP149885	RIE_551
Diplospinus multistriatus	PLAG1	OP149841	RIE_885	Photostomias guernei	PLAG1	OP149886	RIE_551
Diplospinus multistriatus	PLAG1	OP149842	RIE_885	Photostomias guernei	PLAG1	OP149887	RIE_552
Diplospinus multistriatus	PLAG1	OP149843	RIE_886	Photostomias guernei	PLAG1	OP149888	RIE_552
Diplospinus multistriatus	PLAG1	OP149844	RIE_886	Photostomias guernei	PLAG1	OP149889	RIE_81
Diplospinus multistriatus	PLAG1	OP149845	RIE_887	Photostomias guernei	PLAG1	OP149890	RIE_81
Diplospinus multistriatus	PLAG1	OP149846	RIE_887	Scopelogadus mizolepis	PLAG1	OP149891	DPND_1298
Ditropichthys storeri	PLAG1	OP149847	DPND_1466	Scopelogadus mizolepis	PLAG1	OP149892	DPND_1298
Ditropichthys storeri	PLAG1	OP149848	DPND_1466	Scopelogadus mizolepis	PLAG1	OP149893	DPND_1299
Ditropichthys storeri	PLAG1	OP149849	DPND_2251	Scopelogadus mizolepis	PLAG1	OP149894	DPND_1299
Ditropichthys storeri	PLAG1	OP149850	DPND_2251	Scopelogadus mizolepis	PLAG1	OP149895	DPND_1379
Ditropichthys storeri	PLAG1	OP149851	DPND_2989	Scopelogadus mizolepis	PLAG1	OP149896	DPND_1379
Ditropichthys storeri	PLAG1	OP149852	DPND_2989	Scopelogadus mizolepis	PLAG1	OP149897	DPND_1380
Ditropichthys storeri	PLAG1	OP149853	DPND_3302	Scopelogadus mizolepis	PLAG1	OP149898	DPND_1380
Ditropichthys storeri	PLAG1	OP149854	DPND_3302	Scopelogadus mizolepis	PLAG1	OP149899	DPND_2220
Ditropichthys storeri	PLAG1	OP149855	DPND_3911	Scopelogadus mizolepis	PLAG1	OP149900	DPND_2220
Ditropichthys storeri	PLAG1	OP149856	DPND_3911	Scopelogadus mizolepis	PLAG1	OP149901	DPND_2511

Ecology and Evolution

17 of 21

WILEY

TABLE A1 (Continued)

Species	Gene	Accession number	Specimen ID	Species	Gene	Accession number	Specimen ID
Scopelogadus mizolepis	PLAG1	OP149902	DPND_2511	Sternoptyx pseudobscura	PLAG1	OP149947	RIE_201
Scopelogadus mizolepis	PLAG1	OP149903	DPND_2512	Sternoptyx pseudobscura	PLAG1	OP149948	RIE_201
Scopelogadus mizolepis	PLAG1	OP149904	DPND_2512	Sternoptyx pseudobscura	PLAG1	OP149949	RIE_223
Scopelogadus mizolepis	PLAG1	OP149905	DPND_4271	Sternoptyx pseudobscura	PLAG1	OP149950	RIE_223
Scopelogadus mizolepis	PLAG1	OP149906	DPND_4271	Sternoptyx pseudobscura	PLAG1	OP149951	RIE_224
Scopelogadus mizolepis	PLAG1	OP149907	RIE_41	Sternoptyx pseudobscura	PLAG1	OP149952	RIE_224
Scopelogadus mizolepis	PLAG1	OP149908	RIE_41	Sternoptyx pseudobscura	PLAG1	OP149953	RIE_225
Scopelogadus mizolepis	PLAG1	OP149909	RIE_518	Sternoptyx pseudobscura	PLAG1	OP149954	RIE_225
Scopelogadus mizolepis	PLAG1	OP149910	RIE_518	Sternoptyx pseudobscura	PLAG1	OP149955	RIE_226
Scopelogadus mizolepis	PLAG1	OP149911	RIE_954	Sternoptyx pseudobscura	PLAG1	OP149956	RIE_226
Scopelogadus mizolepis	PLAG1	OP149912	RIE_954	Sternoptyx pseudobscura	PLAG1	OP149957	RIE_415
Sigmops elongatus	PLAG1	OP149913	RIE_17	Sternoptyx pseudobscura	PLAG1	OP149958	RIE_415
Sigmops elongatus	PLAG1	OP149914	RIE_17	Sternoptyx pseudobscura	PLAG1	OP149959	RIE_417
Sigmops elongatus	PLAG1	OP149915	RIE_182	Sternoptyx pseudobscura	PLAG1	OP149960	RIE_417
Sigmops elongatus	PLAG1	OP149916	RIE_182	Sternoptyx pseudobscura	PLAG1	OP149961	RIE_537
Sigmops elongatus	PLAG1	OP149917	RIE_204	Sternoptyx pseudobscura	PLAG1	OP149962	RIE_537
Sigmops elongatus	PLAG1	OP149918	RIE_204	Sternoptyx pseudobscura	PLAG1	OP149963	RIE_538
Sigmops elongatus	PLAG1	OP149919	RIE_205	Sternoptyx pseudobscura	PLAG1	OP149964	RIE_538
Sigmops elongatus	PLAG1	OP149920	RIE_205	Sternoptyx pseudobscura	PLAG1	OP149965	RIE_539
Sigmops elongatus	PLAG1	OP149921	RIE_206	Sternoptyx pseudobscura	PLAG1	OP149966	RIE_539
Sigmops elongatus	PLAG1	OP149922	RIE_206	Sternoptyx pseudobscura	PLAG1	OP149967	RIE_78
Sigmops elongatus	PLAG1	OP149923	RIE_244	Sternoptyx pseudobscura	PLAG1	OP149968	RIE_78
Sigmops elongatus	PLAG1	OP149924	RIE_244	Sternoptyx pseudobscura	PLAG1	OP149969	RIE_915
Sigmops elongatus	PLAG1	OP149925	RIE_277	Sternoptyx pseudobscura	PLAG1	OP149970	RIE_915
Sigmops elongatus	PLAG1	OP149926	RIE_277	Chauliodus sloani	ENC1	OP149971	DPND_1556
Sigmops elongatus	PLAG1	OP149927	RIE_278	Chauliodus sloani	ENC1	OP149972	DPND_1556
Sigmops elongatus	PLAG1	OP149928	RIE_278	Chauliodus sloani	ENC1	OP149973	DPND_1669
Sigmops elongatus	PLAG1	OP149929	RIE_279	Chauliodus sloani	ENC1	OP149974	DPND_1669
Sigmops elongatus	PLAG1	OP149930	RIE_279	Chauliodus sloani	ENC1	OP149975	DPND_1695
Sigmops elongatus	PLAG1	OP149931	RIE_280	Chauliodus sloani	ENC1	OP149976	DPND_1695
Sigmops elongatus	PLAG1	OP149932	RIE_280	Chauliodus sloani	ENC1	OP149977	DPND_1877
Sigmops elongatus	PLAG1	OP149933	RIE_2	Chauliodus sloani	ENC1	OP149978	DPND_1877
Sigmops elongatus	PLAG1	OP149934	RIE_2	Chauliodus sloani	ENC1	OP149979	DPND_1895
Sigmops elongatus	PLAG1	OP149935	RIE_97	Chauliodus sloani	ENC1	OP149980	DPND_1895
Sigmops elongatus	PLAG1	OP149936	RIE_97	Chauliodus sloani	ENC1	OP149981	DPND_1896
Sternoptyx pseudobscura	PLAG1	OP149937	DPND_3772	Chauliodus sloani	ENC1	OP149982	DPND_1896
Sternoptyx pseudobscura	PLAG1	OP149938	DPND_3772	Chauliodus sloani	ENC1	OP149983	DPND_1937
Sternoptyx pseudobscura	PLAG1	OP149939	RIE_195	Chauliodus sloani	ENC1	OP149984	DPND_1937
Sternoptyx pseudobscura	PLAG1	OP149940	RIE_195	Chauliodus sloani	ENC1	OP149985	DPND_2027
Sternoptyx pseudobscura	PLAG1	OP149941	RIE_196	Chauliodus sloani	ENC1	OP149986	DPND_2027
Sternoptyx pseudobscura	PLAG1	OP149942	RIE_196	Chauliodus sloani	ENC1	OP149987	DPND_2037
Sternoptyx pseudobscura	PLAG1	OP149943	RIE_197	Chauliodus sloani	ENC1	OP149988	DPND_2037
Sternoptyx pseudobscura	PLAG1	OP149944	RIE_197	Chauliodus sloani	ENC1	OP149989	DPND_2097
Sternoptyx pseudobscura	PLAG1	OP149945	RIE_200	Chauliodus sloani	ENC1	OP149990	DPND_2097
Sternoptyx pseudobscura	PLAG1	OP149946	RIE_200	Chauliodus sloani	ENC1	OP149991	DPND_2208

(Continues)

TABLE A1 (Continued)

		Accession				Accession	
Species	Gene	number	Specimen ID	Species	Gene	number	Specimen ID
Chauliodus sloani	ENC1	OP149992	DPND_2208	Sternoptyx pseudobscura	ENC1	OP150037	RIE_196
Chauliodus sloani	ENC1	OP149993	DPND_2260	Sternoptyx pseudobscura	ENC1	OP150038	RIE_196
Chauliodus sloani	ENC1	OP149994	DPND_2260	Sternoptyx pseudobscura	ENC1	OP150039	RIE_197
Chauliodus sloani	ENC1	OP149995	DPND_2387	Sternoptyx pseudobscura	ENC1	OP150040	RIE_197
Chauliodus sloani	ENC1	OP149996	DPND_2387	Sternoptyx pseudobscura	ENC1	OP150041	RIE_200
Chauliodus sloani	ENC1	OP149997	DPND_2418	Sternoptyx pseudobscura	ENC1	OP150042	RIE_200
Chauliodus sloani	ENC1	OP149998	DPND_2418	Sternoptyx pseudobscura	ENC1	OP150043	RIE_201
Chauliodus sloani	ENC1	OP149999	DPND_2490	Sternoptyx pseudobscura	ENC1	OP150044	RIE_201
Chauliodus sloani	ENC1	OP150000	DPND_2490	Sternoptyx pseudobscura	ENC1	OP150045	RIE_224
Chauliodus sloani	ENC1	OP150001	DPND_2528	Sternoptyx pseudobscura	ENC1	OP150046	RIE_224
Chauliodus sloani	ENC1	OP150002	DPND_2528	Sternoptyx pseudobscura	ENC1	OP150047	RIE_225
Chauliodus sloani	ENC1	OP150003	DPND_2669	Sternoptyx pseudobscura	ENC1	OP150048	RIE_225
Chauliodus sloani	ENC1	OP150004	DPND_2669	Sternoptyx pseudobscura	ENC1	OP150049	RIE_226
Chauliodus sloani	ENC1	OP150005	DPND_2756	Sternoptyx pseudobscura	ENC1	OP150050	RIE_226
Chauliodus sloani	ENC1	OP150006	DPND_2756	Sternoptyx pseudobscura	ENC1	OP150051	RIE_415
Chauliodus sloani	ENC1	OP150007	DPND_2757	Sternoptyx pseudobscura	ENC1	OP150052	RIE_415
Chauliodus sloani	ENC1	OP150008	DPND_2757	Sternoptyx pseudobscura	ENC1	OP150053	RIE_417
Diplospinus multistriatus	ENC1	OP150009	DPND_2718	Sternoptyx pseudobscura	ENC1	OP150054	RIE_417
Diplospinus multistriatus	ENC1	OP150010	DPND_2718	Sternoptyx pseudobscura	ENC1	OP150055	RIE_537
Diplospinus multistriatus	ENC1	OP150011	RIE_171	Sternoptyx pseudobscura	ENC1	OP150056	RIE_537
Diplospinus multistriatus	ENC1	OP150012	RIE_171	Sternoptyx pseudobscura	ENC1	OP150057	RIE_538
Diplospinus multistriatus	ENC1	OP150013	RIE_240	Sternoptyx pseudobscura	ENC1	OP150058	RIE_538
Diplospinus multistriatus	ENC1	OP150014	RIE_240	Sternoptyx pseudobscura	ENC1	OP150059	RIE_539
Diplospinus multistriatus	ENC1	OP150015	RIE_413	Sternoptyx pseudobscura	ENC1	OP150060	RIE_539
Diplospinus multistriatus	ENC1	OP150016	RIE_413	Sternoptyx pseudobscura	ENC1	OP150061	RIE_78
Diplospinus multistriatus	ENC1	OP150017	RIE_495	Sternoptyx pseudobscura	ENC1	OP150062	RIE_78
Diplospinus multistriatus	ENC1	OP150018	RIE_495	Sternoptyx pseudobscura	ENC1	OP150063	RIE_915
Diplospinus multistriatus	ENC1	OP150019	RIE_713	Sternoptyx pseudobscura	ENC1	OP150064	RIE_915
Diplospinus multistriatus	ENC1	OP150020	RIE_713	Sternoptyx pseudobscura	MYH6	OP150065	DPND_4225
Diplospinus multistriatus	ENC1	OP150021	RIE_882	Sternoptyx pseudobscura	MYH6	OP150066	DPND_4225
Diplospinus multistriatus	ENC1	OP150022	RIE_882	Sternoptyx pseudobscura	MYH6	OP150067	RIE_195
Diplospinus multistriatus	ENC1	OP150023	RIE_883	Sternoptyx pseudobscura	MYH6	OP150068	RIE_195
Diplospinus multistriatus	ENC1	OP150024	RIE_883	Sternoptyx pseudobscura	MYH6	OP150069	RIE_196
Diplospinus multistriatus	ENC1	OP150025	RIE_884	Sternoptyx pseudobscura	MYH6	OP150070	RIE_196
Diplospinus multistriatus	ENC1	OP150026	RIE_884	Sternoptyx pseudobscura	MYH6	OP150071	RIE_197
Diplospinus multistriatus	ENC1	OP150027	RIE_885	Sternoptyx pseudobscura	MYH6	OP150072	RIE_197
Diplospinus multistriatus	ENC1	OP150028	RIE_885	Sternoptyx pseudobscura	MYH6	OP150073	RIE_200
Diplospinus multistriatus	ENC1	OP150029	RIE_886	Sternoptyx pseudobscura	MYH6	OP150074	RIE_200
Diplospinus multistriatus	ENC1	OP150030	RIE_886	Sternoptyx pseudobscura	MYH6	OP150075	RIE_201
Diplospinus multistriatus	ENC1	OP150031	RIE_887	Sternoptyx pseudobscura	MYH6	OP150076	RIE_201
Diplospinus multistriatus	ENC1	OP150032	RIE_887	Sternoptyx pseudobscura	MYH6	OP150077	RIE_223
Sternoptyx pseudobscura	ENC1	OP150033	DPND_3772	Sternoptyx pseudobscura	MYH6	OP150078	RIE_223
Sternoptyx pseudobscura	ENC1	OP150034	DPND_3772	Sternoptyx pseudobscura	MYH6	OP150079	RIE_224
Sternoptyx pseudobscura	ENC1	OP150035	RIE_195	Sternoptyx pseudobscura	MYH6	OP150080	RIE_224
Sternoptyx pseudobscura	ENC1	OP150036	RIE_195	Sternoptyx pseudobscura	MYH6	OP150081	RIE_226

TABLE A1 (Continued)

		Accession	
Species	Gene	number	Specimen ID
Sternoptyx pseudobscura	MYH6	OP150082	RIE_226
Sternoptyx pseudobscura	MYH6	OP150083	RIE_415
Sternoptyx pseudobscura	MYH6	OP150084	RIE_415
Sternoptyx pseudobscura	MYH6	OP150085	RIE_417
Sternoptyx pseudobscura	MYH6	OP150086	RIE_417
Sternoptyx pseudobscura	MYH6	OP150087	RIE_537
Sternoptyx pseudobscura	MYH6	OP150088	RIE_537
Sternoptyx pseudobscura	MYH6	OP150089	RIE_538
Sternoptyx pseudobscura	MYH6	OP150090	RIE_538
Sternoptyx pseudobscura	MYH6	OP150091	RIE_539
Sternoptyx pseudobscura	MYH6	OP150092	RIE_539
Sternoptyx pseudobscura	MYH6	OP150093	RIE_78
Sternoptyx pseudobscura	MYH6	OP150094	RIE_78
Stomias affinis	MYH6	OP150095	DPND_1201
Stomias affinis	MYH6	OP150096	DPND_1201
Stomias affinis	MYH6	OP150097	DPND_1302
Stomias affinis	MYH6	OP150098	DPND_1302
Stomias affinis	MYH6	OP150099	DPND_1314
Stomias affinis	MYH6	OP150100	DPND_1314
Stomias affinis	MYH6	OP150101	DPND_1315
Stomias affinis	MYH6	OP150102	DPND_1315
Stomias affinis	MYH6	OP150103	DPND_1408
Stomias affinis	MYH6	OP150104	DPND_1408
Stomias affinis	MYH6	OP150105	DPND_1543
Stomias affinis	MYH6	OP150106	DPND_1543
Stomias affinis	MYH6	OP150107	DPND_1639
Stomias affinis	MYH6	OP150108	DPND_1639
Stomias affinis	MYH6	OP150109	DPND_3645
Stomias affinis	MYH6	OP150110	DPND_3645
Stomias affinis	MYH6	OP150111	RIE_466
Stomias affinis	MYH6	OP150112	RIE_466
Stomias affinis	MYH6	OP150113	RIE_577
Stomias affinis	MYH6	OP150114	RIE_577
Stomias affinis	MYH6	OP150115	RIE_917
Stomias affinis	MYH6	OP150116	RIE_917

19 of 21

-WILEY-

Gene	Primer name	Primer sequence
COI	FISH1F	TCAACCAACCACAAAGACATTGGCAC
COI	FISH1R	TAGACTTCTGGGTGGCCAAAGAATCA
COI	FISH2F	TCGACTAATCATAAAGATATCGGCAC
COI	FISH2R	ACTTCAGGGTGACCGAAGAATCAGAA
COI	BOLD_COI_Forward	TTCTCCACCAACCACAARGAYATYGG
COI	BOLD_COI_Reverse	CACCTCAGGGTGTCCGAARAAYCARAA
COI	FISHCOI_F	TCAACYAATCAYAAAGATATYGGCAC
COI	FISHCOI_R	ACTTCYGGGTGRCCRAARAATCA
ENC	Perc_ENC_F	TTCCTRGAGAGAAACCTTCACC
ENC	Perc_ENC_R	GAYGGAGARGCNGGGAGGCAGCC
PLAG	Perc_PLAG_F	CATGAYCCYAACAARGARGCCTT
PLAG	Perc_PLAG_R	TGRCARCCCATGCCCATAGCTG
MYH	Perc_MYH_F	ACYAARAGRGTYATYCAGTACT
МҮН	Perc_MYH_R	CCRAKGGMRTAGTAGACYTGRTC

TABLE A2 List of primers used.

WEBER ET AL.

•	specie
-	of study
:	escription
-	Kange d
(Ρ
L C	ВСЕ
	∢

TABLE A3 Range descri	otion of study species.				
Species	Range description	Oceans inhabited	Latitudes inhabited	Citations	Notes
Bathophilus pawneei	Circumglobal; Tropical	Atlantic, Indian, Pacific	36° N-34° S	Agustin (2018)	
Chauliodus sloani	Circumglobal; Tropical and Polar	Atlantic, Indian, Pacific	50° N-50° S	Mundy (2005)	Less common but records exist from individuals as far as 70° N–56° S (Priede, 2017)
Cyclothone alba	Circumglobal; Tropical	Atlantic, Indian, Pacific	40° N-40° S	Miya and Nemoto (1986)	
Cyclothone pseudopallida	Circumglobal; Tropical and Polar	Atlantic, Indian, Pacific	65° N-30° S	Mundy (2005)	
Diplospinus multistriatus	Circumglobal; Tropical	Atlantic, Indian, Pacific	40° N-40° S	Mundy (2005)	
Ditropichthys storeri	Circumglobal; Tropical	Atlantic, Indian, Pacific	48° N-43° S	Paxton (1989)	
Photostomias guernei	Non circumglobal; Tropical	Atlantic	40° N-3° N	Kenaley (2009)	
Scopelogadus mizolepis	Circumglobal; Tropical	Atlantic, Indian, Pacific	40° N-22° S	Mundy (2005)	
Sigmops elongatus	Circumglobal; Tropical and Polar	Atlantic, Indian, Pacific	65° N-35° S	Torres (2018)	
Sternoptyx pseudobscura	Circumglobal; Tropical	Atlantic, Indian, Pacific	40° N-40° S	Mundy (2005) and Zamarro and Lloris (1999)	One record from 42° N and 47° N
Stomias affinis	Circumglobal; Tropical	Atlantic, Indian, Pacific	35° N-39° S	Priede (2017)	