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The revolution of crossdating in marine paleoecology and paleoclimatology

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1 **Abstract**

2 Over the past century, the dendrochronology technique of crossdating has been widely used to
3 generate a global network of tree-ring chronologies that serves as a leading indicator of
4 environmental variability and change. Only recently, however, has this same approach been
5 applied to growth increments in calcified structures of bivalves, fish, and corals in the world's
6 oceans. As in trees, these crossdated marine chronologies are well replicated, annually
7 resolved and absolutely dated, providing uninterrupted multi-decadal to millennial histories of
8 ocean paleoclimatic and paleoecological processes. Moreover, they span an extensive
9 geographic range, multiple trophic levels, habitats, and functional types, and can be readily
10 integrated with observational physical or biological records. Increment width is the most
11 commonly measured parameter and reflects growth or productivity, though isotopic and
12 elemental composition capture complementary aspects of environmental variability. As such,
13 crossdated marine chronologies constitute powerful observational templates to establish
14 climate-biology relationships, test hypotheses of ecosystem functioning, conduct multi-proxy
15 reconstructions, provide constraints for numerical climate models, and evaluate the precise
16 timing and nature of ocean-atmosphere interactions. These 'present-past-future' perspectives
17 provide new insights into the mechanisms and feedbacks between the atmosphere and marine
18 systems while providing indicators relevant to ecosystem-based approaches of fisheries
19 management.

20

21 **Keywords**

22 Sclerochronology, crossdating, proxy, paleoceanography, dendrochronology, climate change

23

24 **Background**

25 In terrestrial systems, tree-ring data are well replicated from multiple individuals, absolutely
26 dated, and thus constitute the 'gold standard' of high-resolution environmental archives. This

27 level of accuracy is possible through crossdating, a technique that assumes some aspect of the
28 environment influences growth, varies over time, and thereby induces a synchronous growth
29 pattern among samples of a given population and location. Starting at the increment formed
30 during the known year of collection, the synchronous pattern is cross-matched among samples
31 backward through time. If an increment has been missed or falsely identified, the pattern will be
32 offset by a year relative to that in other samples, beginning where the error occurred. Errors are
33 then confirmed and corrected by visually re-examining the sample [1] (Figure 1). The absence
34 of dating errors ensures high-frequency variability is not smeared, attenuated, or blurred, which
35 allows for seamless integration among chronologies, instrumental climate histories, and other
36 observational physical or biological records [2] (Figure 1). Given the wide application of this
37 approach in forests around the globe, over 4,500 tree chronologies are now publicly available
38 through the International Tree-Ring Data Bank (ITRDB; [3]), a rich and diverse resource that
39 has facilitated a number of highly influential, broad-scale reconstructions of climate and
40 disturbance [4-6].

41 Over the past decade an increasing number of studies have demonstrated that the same
42 powerful crossdating approach can be applied to marine organisms (Figure 2). A wide variety of
43 species spanning tropical to polar latitudes are long-lived, form annual growth increments, and
44 are represented in extensive archival collections in fisheries laboratories and museums around
45 the world [7]. Archaeological and sub-fossil specimens are available to further extend records
46 back in time [8-10]. Resulting crossdated sclerochronologies continuously span multiple
47 decades to centuries, are comparable in quality to tree-ring datasets, and capture signals
48 representing a range of depths, habitats, trophic levels, and functional types [8, 11]. These time
49 series are of high value in marine systems where instrumental records > 50 yrs or observational
50 biological records > 20 yrs in length are uncommon [12, 13]. As such, this approach is unlocking
51 a new, vast, global array of data streams in the marine realm to reveal relationships between

52 biological processes and climate, hind-cast past environmental variability, calibrate climate
53 models, and identify key target variables for forecasting into the future.

54

55 **Present**

56 In many marine systems, the fundamental environmental drivers of productivity or functioning
57 remain poorly understood. This is largely due to the scarcity of multidecadal biological time
58 series [12, 13]. However, crossdated marine sclerochronologies serve as growth proxies with
59 the accuracy and temporal extension required to quantify long-term variability and establish
60 robust statistical relationships with observational environmental indices. For example,
61 productivity in the California Current along the west coast of North America has long been
62 assumed to be largely driven by spring and summer conditions when coastal upwelling is
63 strongest and most sustained. However, rockfish (*Sebastes* spp.) chronologies derived from
64 otolith increment widths strongly relate to wintertime upwelling, the amplitude of which varies
65 greatly from year to year [14]. This wintertime volatility is likely imprinted on biology via some
66 preconditioning the system for high productivity during the upcoming warm season or its effects
67 on growing-season length. Moreover, fish increment-width sclerochronologies have been
68 integrated with other observational biological time series such as seabird reproductive success
69 and plankton community composition to demonstrate climate-induced covariance across taxa
70 and trophic levels, which underscores the importance of winter climate in biology [15, 16].
71 Crossdated sclerochronologies and tree-ring chronologies have also been used to document
72 that broad-scale atmospheric phenomena can simultaneously influence factors limiting growth
73 on land, such as precipitation, as well as factors limiting growth at sea, such as coastal
74 upwelling, to induce covariance between marine and terrestrial ecosystem productivity [11, 17].

75 Patterns of synchrony reveal the extent and magnitude to which environmental variability
76 influences biological processes and afford some degree of predictive power, especially when
77 associated climate drivers can be determined. Indeed, crossdating quantifies the extent to which

78 growth anomalies covary within and among populations, and provides exactly dated and well-
79 replicated biological time series with which to identify this synchrony [9, 18, 19] (Figure 2).
80 Human impacts may also be assessed, such as quantifying reduced resilience of corals in
81 heavily populated areas of the Mesoamerican Reef to bleaching events [20]. Such information is
82 highly relevant to coral reef and fisheries management and aiding the desired transition from
83 single stock assessment to ecosystem-based approaches. Crossdated marine chronologies
84 could inform multiple aspects of Integrated Ecosystem Assessment by quantifying multidecadal
85 ranges of variability, long-term changes in biological reference points, climate drivers, and
86 ecosystem indicators [21]. Integrating the growing networks of crossdated sclerochronologies
87 with existing biological observational records has the potential to provide baseline information
88 on biological synchrony and the interactions between climate and human influence.

89

90 **Past**

91 In the marine realm, sediment cores are the most commonly used archives to provide long-term
92 perspectives on environmental variability prior to the instrumental record. These archives often
93 span multiple millennia, have been broadly sampled across the ocean floor, and in some
94 environments may be sub-decadally resolved. Moreover, they capture a diversity of micro-
95 organisms and geochemical proxies to assess long-term environmental variability and biological
96 response [13, 22-24]. Although crossdated marine sclerochronologies very rarely span multiple
97 centuries and are generally limited to the continental shelves (Figure 2), they are annually
98 resolved, absolutely dated, and can be readily calibrated against instrumental records to hind-
99 cast pre-industrial baselines, rates of change, and the frequency of extreme events [8, 25, 26].
100 Relatively long crossdated sclerochronologies allow for the examination of the role that natural
101 external forcing (e.g. total solar irradiance and volcanic aerosols) and internal climate
102 mechanisms and feedbacks (e.g. ocean-atmosphere interactions, ocean circulation and ice
103 related albedo feedbacks) play in driving past marine variability [27]. For example, a millennial-

104 length oxygen stable isotope series from a crossdated bivalve shell growth chronology
105 demonstrated that oceanic changes near Iceland generally preceded those in the atmosphere
106 prior to the industrial period (CE 1000 – 1800); however this relationship reversed after CE 1800
107 likely reflecting anthropogenic influence on the climate [28].

108 For some species and locations, increment width is strongly related to a single climate
109 variable. Along the western North America coastline, seventy percent of the variance in Pacific
110 geoduck (*Panopea generosa*) chronologies can be explained by regional sea surface
111 temperature variability [29, 30]. In other cases, even when there is a high degree of increment-
112 width synchrony among individuals from a given species and site, the environmental drivers of
113 growth rate are complex and less obvious [31-36]. However, other measurement parameters
114 such as isotope signatures, trace and minor elements, or microstructures that are embedded in
115 the precisely dated material [9, 25, 28, 37, 38] may better reflect climate variability, can often be
116 mechanistically linked to aspects of the environment, and used to robustly reconstruct past
117 environments. For example, regionally crossdated bivalve series demonstrate highly
118 synchronous Ba/Ca ratios in shell aragonite potentially related to productivity dynamics [39].
119 Stable carbon (¹³C) isotope values [40] from exactly dated increments provide constraints on
120 carbon cycling and the so-called Suess effect [41, 42] through space and time. Moreover,
121 radiocarbon measurements from exactly dated increments can be used to assess changes in
122 circulation and provide tight constraints for the marine reservoir effect [10, 25, 37]. One of the
123 factors that hinders more accurate ¹⁴C dating in marine sediment cores is the paucity of
124 information about how the marine reservoir age varied back through time. For the late
125 Holocene, crossdated marine sclerochronologies improve this by eliminating dating uncertainty
126 [10, 37].

127 A useful property of sclerochronologies is that they directly target marine environmental
128 variability, including fine-scale processes or those at depth that are not linked to the atmosphere
129 and are thus undetectable by land-based archives [9, 10, 19, 42-44]. Where tree-ring

130 chronologies do capture coupled ocean-atmosphere climate phenomena such as the Pacific
131 Decadal Oscillation, El Niño -Southern Oscillation, or Atlantic Multidecadal Oscillation,
132 crossdated marine archives offer complementary perspectives of habitat and life history that
133 provide a more robust estimate of past climate than any single archive could provide individually
134 [29, 45-47]. Finally, crossdated marine sclerochronologies identify key climate drivers of marine
135 ecosystem functioning, which may be associated with atmospheric processes that influence tree
136 growth. This information provides novel targets for tree-ring based reconstructions. For
137 example, rockfish otolith chronologies in the California Current are influenced by winter
138 upwelling, which is driven by anomalies in atmospheric pressure that also drive drought on land.
139 Thus, moisture-sensitive blue oak (*Quercus douglasii*) tree-ring chronologies can be used to
140 reconstruct a 600-year history of this key indicator of biological functioning and productivity in
141 the California Current marine ecosystem [11].

142

143 **Future**

144 The fundamental knowledge provided by crossdated sclerochronologies on the present and
145 past, as described above, are foundational to accurately predict the future of both the climate
146 system and the marine ecosystems. One such approach is to use these records to compare
147 with, calibrate, test, benchmark, or assimilate into General Circulation Models (GCM) [48].
148 Sclerochronological records can also be used to assess longer-term bias, quantify the amplitude
149 and spatial patterns of uncertainties in GCM runs compared to instrumental data products, and
150 to evaluate climate field reconstruction methods [49]. The quantification and characterization of
151 these uncertainties coupled with the general improvement in our understanding of the forcing
152 mechanisms that drive the coupled ocean-atmosphere climate system will ultimately facilitate
153 the continued improvement of the individual GCMs, enhancing the ability of the numerical
154 models to provide robust simulations of likely future climate change. Numerical models can also
155 be used to identify and guide selection of sites where new chronologies likely have maximum

156 paleoclimatic significance [49, 50]. Finally, crossdated marine chronologies can constrain
157 quasi/multi-decadal climate variability over the past few centuries to millennia [9]. Such
158 information can test and improve the skill of numerical climate models, which poorly capture
159 variability in these spectral domains. Once crossdated sclerochronologies have been
160 constructed [2], novel proxies, such as nitrogen [51] and boron isotopes [52], or emerging
161 geochemical proxies, promise to provide essential constraints on marine ecosystems, ocean
162 acidification, and climate. The recent metagenomic discovery that bivalve shell carbonate
163 contains environmental DNA [53] heralds the possibility of using crossdated shell series to
164 reconstruct marine biodiversity across major anthropogenic transitions, enabling reconstructions
165 of marine ecosystem baselines and rates of biodiversity loss. Ultimately, the long-term histories
166 of climate variability, its coupling with the atmosphere, and impacts on biology will be critical for
167 understanding future climate change and ecosystem impacts.

168

169 **Conclusions**

170 For many long-lived fish and bivalve species, adequate replicates for crossdatable chronologies
171 can be obtained through archival collections, especially if they are commercially important
172 species [7]. For some species such as tropical corals, the expense of sampling can be high, but
173 where replication is available, crossdating can yield annually-resolved, environmentally-
174 sensitive chronologies [20, 25, 54-56]. Crossdating may also be possible with increments (or
175 layers) in coralline algae, deep sea corals, sclerosponges, speleothems, ice cores, varved
176 sediment cores, and perhaps in sub-annual (daily or tidal) increments [57-59]. If increment
177 widths are not visually evident or lack adequate interannual variability, crossdating could be
178 attempted using chemical or morphological properties such as trace and minor element
179 concentrations, isotope signatures, shell microstructures, or even the brightness of the internal
180 banding structure [39, 43, 55]. Crossdating may not be feasible for short-lived species (< 15 yr
181 lifespan) given that time series are insufficiently long to confidently match patterns among

182 individuals, even for sample sets with known collection dates. However, environmentally-
183 sensitive, annually-resolved chronologies appear to be possible [60, 61]. This likely reflects the
184 fact that dating errors are not as impactful in short-lived species as long-lived species for which
185 frameshifts can have effects that extend over decades or centuries. Yet, in the absence of
186 crossdating there will remain some unknown error rate and loss of high-frequency signals, the
187 incidence of which is likely to increase with length of the measurement time series [2].

188 The main thrust of a growing body of literature shows that crossdating is possible and
189 practical for numerous species and environments in the world's oceans. Indeed, crossdating is
190 the technique that truly defines the dendrochronological approach that has been so successful
191 in terrestrial systems. Given that high- and low-frequency signals are retained, these time series
192 can be readily integrated with one another or instrumental records, and further combined with
193 other archives such as sediment cores to evaluate shared patterns in low-frequency time
194 domains [13, 22, 24, 62]. Thus, crossdating and internal replication can be broadly applied to
195 evaluate linkages across ocean basins, ocean-atmosphere connections, and covariance among
196 marine, terrestrial, and freshwater ecosystems. The application and continued development of
197 this technique is now beginning to revolutionize our understanding of biological and climatic
198 processes in marine systems and their interactions with the atmosphere across a range of
199 temporal and spatial scales.

200

201 **Figure Legends**

202 **Figure 1. Crossdating for absolute dating control.** A) Synchronous growth among three
203 Pacific geoduck samples from Dungeness Spit, Washington, USA. Each decade is labeled with
204 a dot; 2000 with three dots; 1950 with two dots B) Measurements of thirty Dungeness Spit
205 samples after age-related growth declines have been removed. Also shown is their mean (the
206 chronology), C) The Dungeness Spit chronology plus two other geoduck chronologies from
207 southern British Columbia, Canada. Superimposed is mean annual sea surface temperature

208 anomaly for the British Columbia coast. Agreement within and among chronologies and
209 instrumental records corroborate absolute dating.

210

211 **Figure 2. Crossdated marine chronologies.** Locations of crossdated tree-ring chronologies
212 available through the International Tree-Ring Databank. Locations of published marine
213 sclerochronologies for which there was replication (generally $n > 5$) and at least some mention of
214 visual cross-matching of patterns among samples. Note: Chronology metadata are provided in
215 Supplementary Table 1.

216

217

218

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416

417 **Author Contributions**

418 BAB led the writing efforts. All authors contributed to writing, literature review, and identifying
419 relevant datasets. BAB and PvdS developed the figures.

420

421 **Data Accessibility**

422 All data used in this study have been published. Citations of these datasets can be found in
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432

433 **Competing Interests**

434 We have no competing interests.

435

436 **Ethical Statement**

437 There was no data collection for this review article; it is based entirely on previously published
438 research.

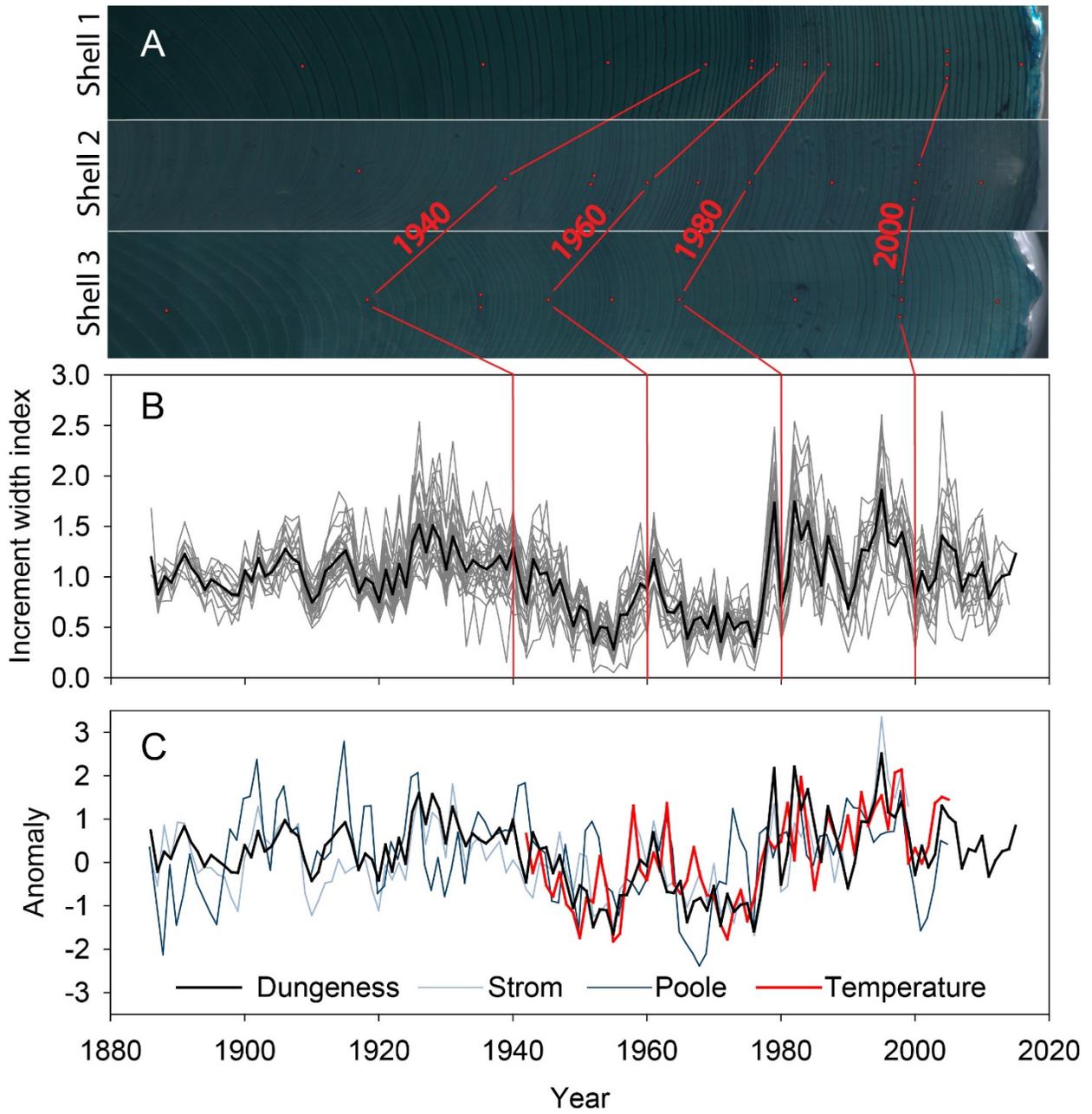


Figure 1

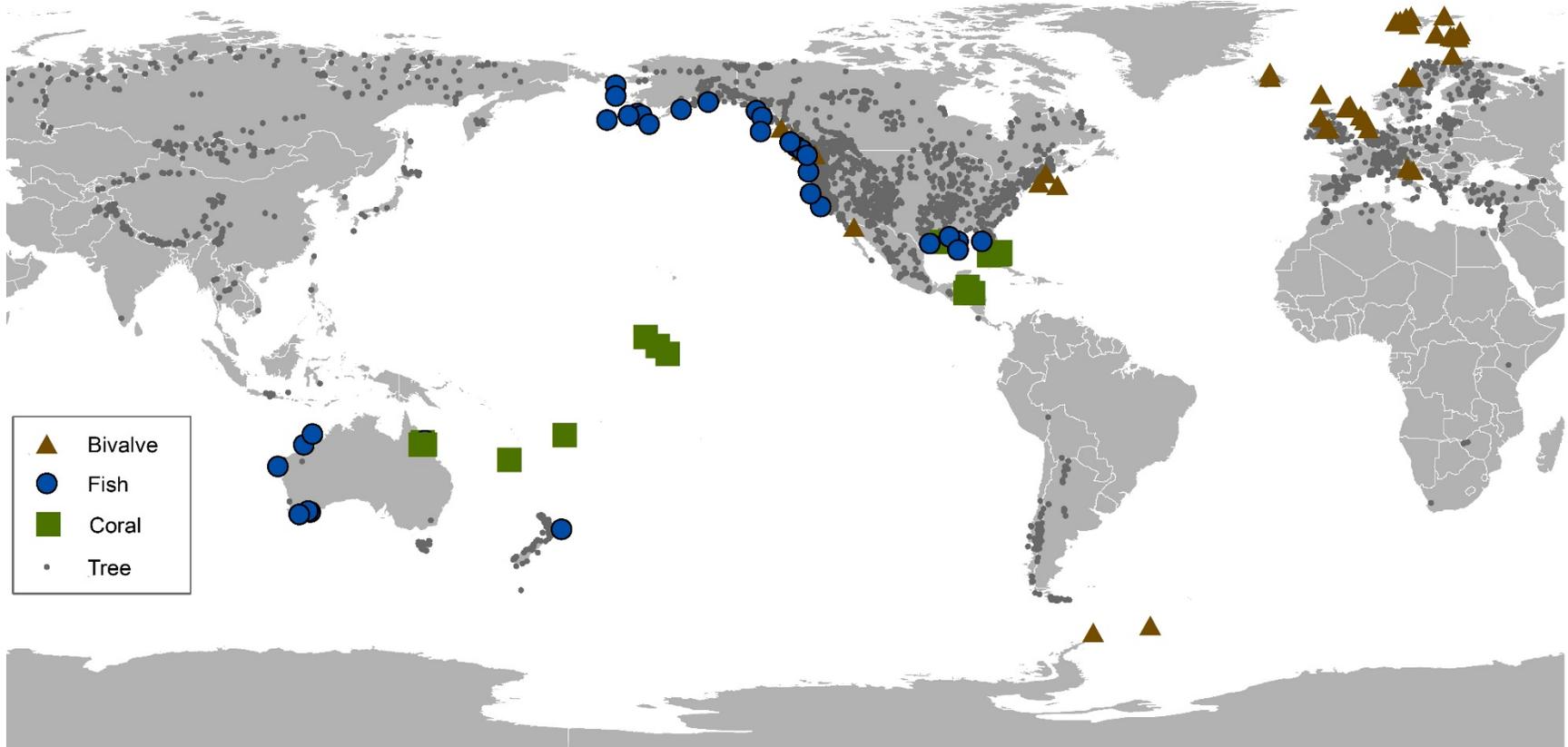


Figure 2