

Marine Invertebrate Anthropogenic Noise Research – Trends in Methods and Future Directions

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9 **Abstract**

10 Selecting the correct methods to answer one's chosen question is key to conducting rigorous,
11 evidence-based science. A disciplines' chosen methods are constantly evolving to encompass new
12 insights and developments. Analysing these changes can be a useful tool for identifying knowledge
13 gaps and guiding future studies. Research on the impact of anthropogenic noise on marine
14 invertebrates, a topic with specific methodological challenges, has undergone substantial changes
15 since its beginning in 1982. Using this field as an example, we demonstrate the benefits of such
16 method analysis and resulting framework which has the potential to increase conclusive power and
17 comparability of future studies. We list taxa studied to date, use a range of descriptors to analyse the
18 methods applied, and map changes in experimental design through time. Based upon our analysis,

19 three research strategies are proposed as a best practice framework for investigating effects of noise
20 on marine invertebrates and delivering policy-relevant information.

21

22 **Keywords:** Marine Noise, Anthropogenic Noise, Marine Invertebrates, Methods, Best Practice,
23 Framework

24 **I. Introduction**

25 When seeking to produce rigorous evidence-based science, it is vital to carefully select methods that
26 deliver robust and repeatable results. The chosen methods employed by a particular discipline evolve
27 over time through the incorporation of new techniques and theory. Through this evolution, the
28 shortcomings identified by previous research are addressed, or new parameters of specific interest are
29 included. By studying how chosen methods and experimental designs have changed over time,
30 knowledge gaps can be identified, and a best practice framework created to facilitate the
31 advancement of future studies in said discipline. Here using marine invertebrate anthropogenic noise
32 research as an example, an area of research that possesses both specific methodological challenges
33 and has seen high advancement in recent years, we demonstrate how such an analysis can be
34 conducted.

35 Anthropogenic activity in the oceans has been on the rise since the industrial revolution. Growth in
36 shipping, oil and gas exploration, and more recently the installation of renewable energy devices
37 have led to a sharp rise in the oceanic noise floor on a global scale (Hildebrand, 2009; Ross, 2005).
38 Low-frequency sound pressure (20 - 200 Hz) produced by sonar, shipping, and marine construction,
39 travels through water with little energy loss (Caruthers, 1977), propagating over large distances and
40 remaining in the environment for long periods of time. For particle motion, the noise levels in water
41 drop off far quicker than those of sound pressure, however, vibration can persist through the

42 sediment (> 500 m) and create a layer of increased particle motion in the water layer directly above
43 (Hazelwood and Macey, 2021) which may affect benthic organisms. Over the last century, the
44 increased level of anthropogenic activity has led to a 10 – 100-fold increase in oceanic background
45 noise (Tyack, 2008). With rising pH through climate change, the transparency of the ocean to low-
46 frequency noise is increasing (Brewer and Hester, 2009) potentially doubling this rise in background
47 noise by the end of the twenty-first century (Ilyina et al., 2010).

48 Anthropogenic noise has now been widely recognised as a pollutant in the marine environment.
49 Legislation around the world has been created (e.g., Marine Strategy Framework Directive 2012
50 Descriptor 11, and IMO MEPC.1/Circ.833) to address the observed rise, and to identify the effects
51 that this noise has on marine organisms. Despite this, the growing reliance on maritime transport
52 (Institute of Shipping Economics and Logistics, 2016), and the push for renewable energy (Marine
53 Board, 2010) will continue to increase the noise levels experienced by marine life in the foreseeable
54 future.

55 When concerns over the effects of anthropogenic noise in the oceans first arose, the research focus
56 lay solely on marine mammals (Malme and Thomson, 1973; Myrberg, 1978), organisms known to
57 utilise (and produce) sound in their environment for communication and orientation. As the
58 underwater sound research field developed, its scope broadened to include other taxa, with work
59 encompassing fish (e.g., Schwarz and Greer, 1984), marine reptiles (O'Hara and Wilcox, 1990) and
60 invertebrates (e.g., Lagardère, 1982; Pearson et al., 1994).

61 Interest in the effects of anthropogenic noise on marine invertebrates began at a similar time to that of
62 other taxonomic groups, in the early eighties (Lagardère, 1982). However, it was not until 30 years
63 later that the concern over human generated disturbances significantly sparked research on the effects
64 this noise has on marine invertebrates. Although not considered to be able to hear in the traditional

65 sense, by detecting pressure changes, most marine invertebrates “hear” by the reception of vibratory
66 stimuli where the sound source is not in contact with the animal’s body (Budelmann, 1992). Three
67 types of sensory organs have evolved to allow this detection: internal statocyst systems, chordotonal
68 organs, and superficial body receptor systems (Breithaupt and Tautz, 1988, 1990; Breithaupt, 2002).
69 The recent research advances in this field have shown that man-made noise can alter the biology of
70 marine invertebrates in a number of ways, from behaviour (Wale *et al.*, 2013a; Mooney *et al.*, 2016;
71 Roberts *et al.*, 2016, Wale *et al.*, 2019; Ruiz-Ruiz *et al.*, 2020; Jones *et al.*, 2021), to physiology
72 (Wale *et al.*, 2013b; Langhammer *et al.*, 2016; Solan *et al.*, 2016, Wale *et al.*, 2019; Slater *et al.*,
73 2020), biochemistry (Stefano *et al.*, 2016; Vazzana *et al.*, 2016, 2020a,b; Wale *et al.*, 2019), and
74 genetics (Peng *et al.*, 2016; Zhou *et al.*, 2018; Shi *et al.*, 2019; Hall *et al.*, 2021). The large diversity
75 of invertebrate physiologies, morphologies, and life histories leads to unpredictable responses to
76 anthropogenic noise exposure. For example, noise-induced changes in larval movement speeds and
77 settlement times are often highly variable and species specific (Branscomb and Rittschof, 1984; Pine
78 *et al.*, 2012; Stocks *et al.*, 2012; Wilkens *et al.*, 2012; Jolivet *et al.*, 2016). These variations
79 demonstrate the need to study the responses of a large range of species, including their different life
80 stages, to sound.

81 Despite the current interest in how marine invertebrates react to man-made noise, the full extent of
82 these effects, and the number of species affected, are still poorly understood (Popper *et al.*, 2020;
83 Duarte *et al.*, 2021). To date, invertebrates still only represent a small proportion of the marine noise
84 literature, as highlighted by an ISI Web of Science search generating 275 results for marine
85 mammals, but only 37 for marine invertebrates in the same search (Basic Search, Topic, Search
86 terms: Marine Mammal [replaced with Invertebrate in the second search] Anthropogenic Noise,
87 04/03/2021).

88 Reviews of studies on marine invertebrates and noise have summarised the findings (de Soto, 2016,
89 Carrol *et al.*, 2017), and highlighted current limitations (Hawkins *et al.*, 2014; Hawkins and Popper,
90 2017). Most recently di Franco *et al.* (2020) and Ferrier-Pages *et al.* (2020) have reviewed the effects
91 of noise on Mediterranean and coral-reef invertebrates, respectively. Both reviews focus on study
92 findings to identify the possible consequences of noise on these specific environments, while the
93 methods applied, and potential implications thereof were not considered. Typically (see Hawkins,
94 2014; Hawkins and Popper, 2017; Popper *et al.*, 2020) reviews form their conclusions based on the
95 field of aquatic noise research as a whole, including taxa from different orders, and generalizations
96 have been made that are not always representative of the different subfields and their recent
97 advances, such as the increasing inclusion of particle motion measurements in recent years.

98 Here we present a systematic methodological review focusing on marine invertebrates, identifying
99 and evaluating the approaches taken to date to study the effects of anthropogenic noise on this
100 taxonomic group. Rather than focusing on the results of each study, which have largely been
101 reviewed elsewhere (see, above), here we review the methods used to generate said results. This
102 review aims to (i) identify method trends throughout the history of this field, and based upon this
103 analysis, (ii) develop an actionable best practice framework for the assessment of anthropogenic
104 noise effects in marine invertebrates, considering the identified knowledge gaps. Three research
105 strategies are proposed in a best practice framework that can be followed by those starting in the field
106 of anthropogenic noise research or by established researchers, to help identify the most appropriate
107 methods of study with respect to specific questions. The steps taken in this method analysis for
108 marine invertebrate noise research will also assist researchers from other disciplines to informatively
109 assess their own methods. By generating discipline-specific assessment criteria and best practice
110 frameworks, researchers can help advance their field in a cohesive and comparable direction.

111 **II. Methods**

112 Literature searches were conducted from August 2011 to February 2021 (final search 23 February
113 2021). Searches were performed in the ISI Web of Science database (Basic Search, Topic) covering
114 all available indexes and utilizing an adapted version of the search terms outlined by Williams *et al.*
115 (2015). An additional set of invertebrate specific search terms were used in combination with the
116 above to reduce the number of irrelevant results (Table 1). This led to a total of 5777 hits (including
117 duplicates), with 273 unique results returned when a second search term was included. All results
118 were manually assessed for relevance (whether they were studies on anthropogenic noise and marine
119 invertebrates) leaving 50 papers. The reference lists of all identified relevant papers were searched
120 for additional applicable studies and these were added to the literature found in the Web of Science
121 search. This process was repeated until no new papers were found. Further to this, Google Scholar
122 searches, personal communication, and citation alerts set up in Google Scholar, Mendeley, and
123 ResearchGate since 2011 lead to a final count of 95 studies. Of these, the majority (78) are peer-
124 reviewed literature, the remaining are technical reports produced for government agencies (4),
125 conference proceedings (10), university published research (1), and industry reports (2).

126 Each study was assigned a number of descriptors to characterize the method it used. These
127 descriptors comprise three neutral categories focusing on the type and length of sound exposure used,
128 and the field of biology investigated (see II (1) below). In addition to these, six pairs of opposing
129 descriptors (see II (2), e.g., single vs multiple species) focus on specific components of the applied
130 method or experimental design. A seventh descriptor “pair” looking at dose dependency is also
131 included, with the types of dependency further split into three unique categories (P7 below). The
132 seven descriptor pairs have binary outcomes (exceptions to this can occur when a study has
133 conducted multiple different analyses). One of the identified outcomes indicates a method advantage
134 when studying anthropogenic noise impacts on marine invertebrates, and the other indicates a
135 limitation (see examples given below). These outcomes should not however be considered positive or

136 negative judgements on the quality of the research, as many of the “limitations” have their own
137 advantages and practicalities. For example, in the laboratory/field descriptor pair (P4 below), tank-
138 based studies provide a level of control over exposure conditions that would be unattainable in the
139 field, however, a field component would allow a better representation of the noise field experienced
140 in situ and provide potential validation of any laboratory findings. Therefore, including a field
141 component is seen as the advantage in this descriptor pair.

142 The chosen descriptors are listed below, with descriptions given where necessary. N = Neutral
143 Descriptor, P = Descriptor Pairs.

144 **(1) Neutral Descriptors**

145 N1 - Area of Biology

146 A single study may often contain multiple descriptors.

- 147 – DNA Integrity and Genetics: Studies that measure gene expression through transcriptomics
148 and metabolomics or those that measure changes in DNA integrity.
- 149 – Biochemistry: Studies that measure changes in internal chemical processes to investigate the
150 production of stress-related compounds.
- 151 – Physiology: Studies that measure changing metabolic responses.
- 152 – Morphology and Trauma: Studies that measure changes to morphology, or trauma in tissues
153 and organs.
- 154 – Larval Development: Studies that measure differences in development including inter-stage
155 timing, total development time, mortality, and settlement.
- 156 – Behaviour: Studies relating to animal behaviour.
- 157 – Ecology: Studies relating to species abundance and distribution.

158 – Fisheries: Studies that use catch rates or other fishery production statistics as a metric for
159 noise effects.

160 N2 - Exposure Type

161 Playback of noise recordings e.g., ship noise, through speakers, is a common technique for noise
162 exposure and used both in laboratory and field studies. Exposure to the original noise source is less
163 common in laboratory studies but can occur when the authors are investigating aquarium or
164 aquaculture noise, as well as actively creating sediment vibration in the laboratory (See Roberts *et*
165 *al.*, 2015).

166 – Laboratory: Exposure to noise in aquarium tanks, both large and small (see below).

167 – Field: Exposure to noise in the field, or in a semi-field environment (experiments where sea
168 cages or other holding systems are used in the field).

169 – Playbacks: Exposure to noise either through underwater speakers, in air speakers, shaker
170 tables, or a combination of these, in the laboratory or field.

171 – Source: Exposure to noise directly from the original noise source.

172 At least two of the above-listed descriptors are applied to any of the considered studies. In this
173 analysis, the laboratory and field descriptors are considered together, as are the playbacks and source
174 descriptors. These pairs act independently of each other with one pair being the exposure
175 environment and the other being the noise source.

176 N3 - Exposure Length

177 Hawkins and Popper (2017) describe an acute noise exposure as occurring “for a brief period, usually
178 from a particular source”. In the present review, a maximum length of 6 h was considered as an acute
179 exposure to accommodate studies where a single exposure to an air gun pass were used.

180 When classifying the exposure regime used in each study, the following categories were used (a
181 single study may contain more than one of these exposure types):

- 182 – Acute: A short-term exposure to noise of less than or equal to 6 h.
- 183 – Continuous: A continuous long-term noise exposure of longer than 6 h.
- 184 – Repeated: An exposure where animals are exposed to multiple acute noise events, resulting in
185 an exposure period longer than 6h.
- 186 – Modelled: Responses modelled from recordings of noise levels and previous data on the
187 hearing thresholds and responses of invertebrates, without recording any responses first-hand.
188 For modelled exposures, no other descriptors were assessed.

189 **(2) Descriptor Pairs**

190 In all pairs (P) the first descriptor is considered the limitation and the second the advantage.

191 P1 - Particle Motion

192 This descriptor covers the inclusion of particle motion measurements in a given study. In some
193 instances where the noise stimulus is presented via shaker tables without having measured the exact
194 particle motion the study was ranked as having included particle motion measurements, as the
195 method of exposure can be replicated to produce the same particle motion level. The inclusion of this
196 metric is especially important to calibrate for the unpredictable interference patterns created in
197 laboratory tanks (see descriptor P5).

198 – No Particle Motion Measurements

199 – Particle Motion Measurements

200 P2 - Number of Species

201 Thoroughly investigating the responses of a single species is common in biological studies, as such it
202 should only be considered a limitation when in combination with limitations highlighted in other
203 descriptor pairs (such as a single species combined with a single area of biology).

204 – Single Species

205 – Multiple Species

206 P3 - Number of Areas of Biology

207 These areas refer to those identified in descriptor N3.

208 – Single Area of Biology

209 – Multiple Areas of Biology

210 P4 - Laboratory/Field

211 – Aquarium Only

212 – Field Aspect: This applies to studies that are wholly based in the field, semi-field, or those
213 with a combined laboratory/field approach.

214 P5 - Tank Size

215 The size of exposure tanks applies only to laboratory-based studies and is most relevant to
216 experiments using noise playbacks from speakers. This descriptor focuses specifically on the tank in
217 which the animals are exposed to sound rather than to vials or chambers holding the animals (often
218 important for larval studies) inside an exposure tank. A large tank was defined as a tank in which the
219 animal(s) can be exposed to noise at a distance greater than 1m to the source (Gray *et al.*, 2016), or
220 where the noise field produced would have limited reflection and refraction. Unpredictable

221 interference patterns of the particle motion will occur in all tanks, it is, therefore, important to
222 calibrate for this (see descriptor P1).

223 – Small Tanks: Aquaria where the animal is exposed at a distance closer than 1m to the noise
224 source.

225 – Large Tanks: Aquaria where the animal can be exposed near the centre of the tank at 1m or
226 more from the noise source.

227 P6 - Sample Size

228 Sample size will vary in response to the expected magnitude of the response, the statistical tests
229 chosen to answer the research question, and the type of experiments performed. A smaller sample
230 size, although sometimes necessary, can create large confidence intervals (Ennos, 2000), with
231 variability around the mean decreasing as the sample size increases. Small sample sizes in
232 biochemical and genetic studies are common and should not be considered a limitation. Here, 10
233 replicates were chosen to represent a relatively large sample size, but we acknowledge that the
234 required sample size to detect a given effect is dependent on the levels of variability inherent in the
235 system.

236 – Small Sample Size: Less than 10 replicates per treatment

237 – Large Sample Size: More than or equal to 10 replicates per treatment

238 P7- Dose Dependency

239 Evaluating dose-response relationships is required for identifying the minimum dose of a test
240 stimulus needed to elicit a response, as well as the dose at which said stimulus becomes detrimental
241 or toxic (Yoshimura *et al.*, 1997). Here both the inclusion of dose dependency within a study, as well

242 as the specific aspect of sound measured for establishing dose dependency are considered. A single
243 study can contain multiple sound aspects.

244 – No Dose Dependency

245 – Dose Dependency

246 ○ Frequency

247 ○ Intensity

248 ○ Duration

249

250 A full breakdown of all descriptors assigned to each study is presented in the supplementary material.

251 **III. Results**

252 In this review, we identified 95 studies that have been published on marine invertebrate noise
253 exposure (gathered through search criteria detailed above). These studies cover 80 species from
254 seven phyla (Figure 1), with the majority focusing on commercially important crustaceans, bivalves,
255 and cephalopods. To create a better representation of the effects of noise on marine invertebrates, a
256 more diverse range of species, response parameters, exposure lengths and noise sources need to be
257 researched.

258 **(1) Exposure and Area of Biology (N1, N2, N3)**

259 Research on the impact of anthropogenic noise on marine invertebrates has undergone substantial
260 change since its beginning (Figures 3 – 5), most of which has occurred since 2012. Acute noise
261 exposures have dominated the field throughout its history (Figure 2). However, the studies conducted
262 between 2012 and 2021 have increasingly used continuous noise exposures (17% of the literature)
263 and have started to include modelled noise exposures (2% of the literature) (Figure 3C).

264 One of the most substantial changes is the increase in the use of noise playbacks, which has risen
265 from 38% to 71% of exposures since 2012. Field exposures were abundant prior to 2012 (48% of
266 publications) and, although their frequency has increased of late due to increased research efforts,
267 their relative proportion within the literature has decreased (34%) (Figure 3B).

268 The field has been dominated by behavioural studies from its outset, and this trend has continued
269 until today. Behavioural studies made up 29% of the literature prior to 2012, with this changing to
270 45% between 2012 and 2021 (Figure 3A). Studies focusing on physiology and morphology have
271 fallen from 16% and 23% respectively before 2012 to 10%, and 11%, whereas investigations on
272 larval development have risen from 3% to 6% since 2012. The proportion of experiments looking
273 into biochemical responses has risen from 13% to 16% since 2012, ecological experiments have
274 remained constant (3% prior to 2012, 2% after), and the first experiments on the effects of noise on
275 genetics (Peng *et al.*, 2016) conducted in 2016 (Figure 3A). The study of the effects of noise on
276 invertebrate fisheries has decreased in representation falling from 13% to 4% since 2012 (Figure 3A).

277 **(2) Particle Motion (P1)**

278 Particle motion is the component of sound detected by most fish, and all marine invertebrates, yet it
279 is often neglected in bioacoustic studies (see IV below). To truly characterize the sound field
280 experienced by these animals in their natural environment, and to as accurately as possible reproduce
281 it in tank-based experiments, particle motion must be measured along with the sound pressure.

282 Branscomb and Rittschof (1984) were the first to include particle motion in their analysis. Through
283 the use of a shaker table, the authors were able to effectively characterize the particle motion in their
284 experiment. However, for 28 years particle motion measurements were rarely conducted, accounting
285 for only 10% of studies. Since 2012 however, this knowledge gap has increasingly been addressed as
286 evidenced by 29% of studies in this period having now included particle motion measurements
287 (Figure 4A).

288 **(3) Number of Species (P2)**

289 Responses to anthropogenic noise are often species specific. Therefore, to identify shared responses
290 that can be extrapolated to other taxa, multiple species should ideally be investigated in a single
291 study, with an identical experimental set-up. The number of such studies has been consistent
292 throughout the history of the field, accounting for 25% (27% previously) of assessed publications
293 from 2012 to 2021 (Figure 4B). In contrast, when investigating a single species (75% of studies,
294 Figure 4B), there is an opportunity to comprehensively study multiple aspects of biology at the same
295 time (P3 below, Figure 4C).

296 **(4) Number of Areas of Biology (P3)**

297 To obtain a more complete picture of the way anthropogenic noise affects an organism/taxon,
298 responses must be investigated at multiple levels of biological organization. This allows researchers
299 to uncover the links between more visible behavioural responses and the cryptic responses that may
300 be their underlying drivers. It is becoming increasingly common for authors to explore multiple
301 aspects of an animal's biology, with these studies now accounting for 37% of the total literature, and
302 39% of studies from 2012 to 2021 (Figure 4C).

303 **(5) Laboratory/Field (P4)**

304 When deciding whether to conduct a study in tanks or in the field, a number of factors must be
305 considered. Laboratory-based studies offer a fine degree of control unobtainable in the field, where
306 external factors may influence the exposures, and consequently the final results may be skewed.
307 Conversely, noise exposures presented in a tank will never fully match those experienced in the field
308 and removing animals from their natural environment may artificially influence their responses to
309 stress. Therefore, where viable, the use of field investigations can help validate laboratory results.
310 Although early studies on the responses of marine invertebrates to anthropogenic noise were fully
311 laboratory-based (Branscomb and Rittschof, 1984; Lagardère, 1982; Regnault and Lagardère, 1983),

312 the emphasis quickly switched to studies incorporating a field component (Figure 9). Recently
313 however there has been a resurgence in aquarium only investigations, with a rise from 45% prior to
314 2012 to 66% between 2012 and 2021 (Figure 5A).

315 **(6) Tank Size (P5)**

316 When dealing with noise playbacks, a small tank will often increase the levels of particle motion, as
317 this is greatest close to the noise source, and therefore potentially expose an animal to noise greater
318 than intended. It is therefore important to use large tanks (where the animal can be exposed ≥ 1 m
319 from the noise source or where the noise field produced would have limited reflection, refraction, or
320 interference, Gray *et al.*, 2016), where appropriate, in tank-based experiments that involve noise
321 playbacks (see IV below). For all studies, best practice involves taking particle motion readings at the
322 location where the animal is exposed to noise (Descriptor P1), to give a true representation of the
323 levels they receive. There has been a shift towards large tank studies (> 1 m *sensu* Gray *et al.*, 2016),
324 increasing from 11% of the literature before 2012 to 39% after this point (Figure 5B).

325 **(7) Sample Size (P6)**

326 In general, a larger sample size will allow more robust conclusions regarding the effects
327 anthropogenic noise is having on the organisms/taxa in question and should be strived for wherever
328 possible. However, this is not always feasible, especially when working with complex systems,
329 vulnerable species, limited resources, or specific techniques. The majority of studies have
330 endeavoured to use as large a sample size as was practical. The number of studies that used a small
331 sample size has declined from 33% prior to 2012 to 23% after (Figure 5C).

332 **(8) Dose Dependency (P7)**

333 Prior to 2012, dose dependency measurements were included in 38% of studies (19% frequency, 19%
334 intensity) (Figure 6), whereas only 22% of the studies published between 2012 and 2021 (14%
335 frequency, 14% intensity, 1% duration) incorporated such measurements (Figure 6). Within the latter

336 period, those studies addressing dose dependency often addressed multiple components of the noise
337 exposure (Samson *et al.*, 2014; Roberts *et al.*, 2015;2016a; Mooney *et al.*, 2016; Peng *et al.*, 2016;
338 Charifi *et al.*, 2017).

339 **IV. Discussion**

340 There have been several changes in the methods chosen to investigate the effects of anthropogenic
341 noise on marine invertebrates since the beginning of research in this field, 39 years ago. One of the
342 most substantial changes is the rise in both laboratory-based studies and the use of noise playbacks.
343 Field studies allow animals to be exposed to noise under the most realistic conditions possible, often
344 with the noise coming directly from the source. They also keep the exposure environment accurate to
345 what the animal would experience in a “real world” situation with possible predation, competition,
346 and environmental variables remaining present in the experimental set-up. The rise in laboratory-
347 based studies from 2012 to 2021 is however likely due to the increased level of control garnered from
348 this style of experimentation. As the field progressed there has been a move away from simply
349 focusing on establishing evidence of a response, towards generating a mechanistic understanding of
350 the specific type of organismic reactions exhibited during sound exposure. The use of both noise
351 playbacks and laboratory/aquarium environments gives researchers the opportunity to conduct a
352 range of experiments under controlled conditions, and at relatively low cost compared to field
353 studies. This allows for more in-depth studies and exploration of a wider range of responses.
354 Additionally, laboratory studies are often employed when the alternative field experiment would
355 prove impractical for logistical reasons. Ideally, studies are designed to include both laboratory and
356 field experiments, where the fine-scale control gained in laboratory experiments is coupled with field
357 trials to validate the findings in situ.

358 As the number of laboratory studies has increased so too has the size of the tanks used for these
359 studies. Increasing awareness of the acoustical properties of aquarium tanks, especially concerning

360 the reflection and interference of sound waves and particle motion that subsequently increases the
361 sound intensity, has caused this move away from the use of small tanks. The use of large tanks is
362 especially prudent when dealing with marine invertebrates, where the particle motion component of
363 underwater sound is most important. Large tanks allow animals to be exposed at an adequate distance
364 from both the noise source and any tank walls, such that the received particle motion is not
365 significantly increased. Similarly, the measurements of said particle motion have increasingly been
366 incorporated into studies in recent years. Formerly it was typically neglected, likely due to the high
367 cost of commercially available particle motion sensors which are often covered under export laws
368 due to their original military applications. As these sensors are becoming more readily available, both
369 through the creation of new sensors, and increased collaboration and equipment sharing, particle
370 motion is increasingly becoming a standard measure when characterizing the exposure. Despite the
371 increase in particle motion measurements for noise exposures, there is still a lack of these
372 measurements for the particle motion produced by the original noise source in situ (e.g., that
373 produced by offshore wind turbines). Such measurements need to be included in all future studies
374 (where possible) to help validate the chosen levels of sound exposures and provide policy relevant
375 information on the effects of noise.

376 The selection of the response parameters used in the study of anthropogenic noise has changed in line
377 with the increased use of more technical methods. The first studies to investigate the effects of noise
378 on marine invertebrates focused on behavioural responses. This has remained the dominant topic,
379 being a key focus from 2012 to 2021. The field, however, has also expanded to include biochemical
380 and genetic studies, that can identify the underlying drivers behind, and links between, observed
381 responses. In a similar manner to the inclusion of multiple areas of biology, the number of
382 investigations that use multiple species within an individual study has increased. This has allowed

383 more complex questions to be addressed, such as how noise affects communities, and how different
384 species respond to the same noise exposure, uncovering varying levels of susceptibility to said noise.

385 However, likely because of the higher degree of complexity of the studies, the inclusion of dose
386 dependency measurements has reduced in recent years, with a large number of investigations aimed
387 at identifying the presence of a specific response, rather than the precise level of sound needed to
388 trigger said response. Despite this, dose dependency information is vital for the creation of
389 anthropogenic noise suppression strategies (Pooper *et al.*, 2020), and its inclusion in future work
390 should be encouraged.

391 **(1) Research Strategies**

392 Based upon the above analysis of the methods used in marine invertebrate noise studies, a conceptual
393 framework is presented, suggesting three alternative research strategies for optimizing future research
394 on the effects of noise on marine invertebrates (see Figure 7 and text below).

395 Two of the three strategies give guidelines for either single species (Figure 7 – Research Strategy 1)
396 or multiple species (Figure 7 – Research Strategy 3) experiments with the main focus on behaviour,
397 physiology, larval development, biochemistry, genetics, or morphology and trauma. These studies are
398 likely more laboratory-based or incorporate a laboratory and field design and are ideally fit to the
399 integrative approach advocated below. The third strategy focuses on ecology and fisheries studies
400 (Figure 7 – Research Strategy 2) which are more field based. The three strategies are in line with
401 suggestions of Hebel *et al.* (1997) and Kight and Swaddle (2011) that research should be conducted
402 in a holistic manner, with an integrative approach, to assess the effects of pollutants in the
403 environment. Whilst responses of marine invertebrates to noise in terms of behaviour and physiology
404 are often explored together (Lagardère, 1982; Christian *et al.*, 2003; Payne *et al.*, 2007; Pine *et al.*,
405 2012; McDonald *et al.*, 2014; and Solan *et al.*, 2016), biochemical analysis alongside behavioural

406 observation has only been included in a small number of recent studies (Filiciotto *et al.*, 2014, 2016,
407 2018; Celi *et al.*, 2015; Stefano *et al.*, 2016; and Vazzana *et al.*, 2016). A thorough integrative
408 approach has, to date, only been adopted by a small number (see Day *et al.*, 2016; 2017; Jolivet *et al.*,
409 2016; Peng *et al.*, 2016; Shi *et al.*, 2019, Wale *et al.*, 2019, and Ruiz-Ruiz *et al.*, 2020) that combine
410 response parameters from multiple levels of biological organization. In doing so they have uncovered
411 links between the visually obvious behavioural responses and more cryptic responses to noise
412 exposure.

413 The framework (below) informs the development of future investigations into the effects of noise on
414 marine invertebrates, helping researchers to identify the most appropriate and informative methods
415 with respect to their specific questions. The framework, presented as a research development flow
416 chart (Figure 7) can be worked through to assess the method options of prospective studies. This flow
417 chart is additionally presented in a sequential key format in the supplementary material.

418 Given that all studies involving marine invertebrates should include particle motion measurements at
419 the location the experimental animal receives the stimulus (ideally correlating with source
420 measurements taken in the field) so that the noise field experienced (Popper *et al.*, 2001; Nedelec *et*
421 *al.*, 2016; Hawkins and Popper, 2017) can be accurately characterized and compared across studies,
422 this metric is not specifically mentioned in any of the below strategies.

423 The proposed framework is customisable and can be complemented with study-specific indicators
424 where appropriate to maximise information gained with respect to a specific question. An example of
425 this is larval culture experiments where a multi-generational broodstock is used, and study-specific
426 indicators dealing with this aspect of the method can be added to the framework.

427 **(a) Research Strategy 1**

428 Number of Species – Single

429 Main Field of Biology – Behaviour /Physiology /Larval Development /Biochemistry /Genetics
430 /Morphology & Trauma

431 When studying only one species, in a single experiment, it is beneficial to integrate as many areas of
432 biology as possible (Kight and Swaddle, 2011), for a more comprehensive assessment of how noise
433 affects that species. When the main response parameter investigated is either behavioural or
434 physiological, securing samples for later biochemical and/or genetic analysis will add value.
435 Conversely, when the work focuses on biochemical or genetic responses, then, where possible,
436 changes in behaviour during the noise exposure should be assessed simultaneously or recorded for
437 later analysis.

438 **(b) Research Strategy 2**

439 Main Field of Biology – Ecology/Fisheries

440 Where possible, studies focusing on ecology or fisheries should simultaneously examine the effects
441 of noise on multiple species to gain information at the population or ecosystem level, if the response
442 parameters allow easy comparability between all species studied. If this is not possible and only a
443 single species can be investigated, complementary samples for later biochemical and/or genetic
444 analysis should be taken whenever possible, or behavioural observations or recordings conducted
445 during the exposure.

446 **(c) Research Strategy 3**

447 Number of Species – Multiple

448 Main Field of Biology – Behaviour /Physiology /Larval Development /Biochemistry /Genetics
449 /Morphology & Trauma

450 When investigating the effects of noise on multiple species in an individual study, the parameters
451 tested must be the same or equivalent to allow comparison between species. With multiple species

452 experiments, the identification of species-specific responses in the same experimental/environmental
453 context may only allow a single field of biology to be explored, however, value would be added
454 when including more than one.

455 **(d) Exposure Assessment**

456 Whilst planning any experiments using the research development flow chart (Figure 7) an important
457 question will always relate to whether the study will be performed in the field or the laboratory, and
458 if the latter whether a field component can be included. Both research approaches have their own
459 merits, with a combined approach allowing the fine control of laboratory-based experiments to,
460 where appropriate, generate methods that can be taken into the field where the most realistic
461 environmental and acoustic conditions are present. In laboratory experiments, large tanks should be
462 utilised to reduce an excessive level of particle motion and potential exposure to noise levels greater
463 than intended. All experiments should be conducted with a sample size compatible with the systems,
464 species, resources, and techniques of the study. The sample size should be large enough to allow
465 robust statistical analysis and conclusions about the effects anthropogenic noise is having on the
466 organisms in question. The exposure assessment portion of the research development flowchart
467 covers these questions and should be worked through for all intended research strategies.

468 **V. Conclusions and Future Directions**

469 This review summarized and assessed the methods of studies that have investigated the effects of
470 anthropogenic noise on marine invertebrates from 1982 to 2021. Whilst our assessment revealed a
471 number of “limitations” in the methods or experimental designs applied in said studies, the aim was
472 not to evaluate, *sensu stricto*, the results generated. Instead, by assessing the trends in research
473 methods over time, an accurate picture of marine invertebrate noise research in the past and its
474 evolution to the current state of the art was generated. Our results show that earlier generalizations
475 regarding the current state of the field have underestimated the recent progress made.

476 Most of the changes in the chosen research approach happened between 2012 and 2021, a period
477 characterised by a 3-fold increase in the number of publications (77% of total published studies on
478 the effects of noise on marine invertebrates) compared to 1982 to 2011. Along with the increasing
479 interest and research effort in the field, a number of new trends have developed in the methods
480 chosen. The majority of these trends move the field away from the identified “limitations” towards
481 the identified “advantages” (Figures 4-6). 39% of papers published between 2012 and 2021 have
482 included particle motion measurements, allowing more accurate characterisation of the noise field
483 experienced by the focal animals and providing a higher degree of precision when reproducing noise
484 in tank-based trials. The use of large tanks for playback experiments in combination with particle
485 motion measurements allows conclusive experiments since noise is represented as accurately as
486 possible in the laboratory.

487 Of the studies published since 2012, 34% have also included a field component to help validate
488 results in situ. There has however been a renewed trend towards aquarium-only studies, likely due to
489 their larger potential for fine-scale control and ability to act as a starting point in noise investigations.
490 This is especially useful when studying a species for the first time in this context, given the often
491 difficult logistics and high expense of a field study.

492 Conducting research in a multidisciplinary integrative way, although logistically challenging, allows
493 a more thorough assessment of the effects of anthropogenic noise, and shows not only whether noise
494 affects an organism but potentially how and why these responses occur. There is a developing trend
495 towards studies that focus on a single species in detail, with 39% of papers from 2012 to 2021
496 assessing the effects of noise on multiple levels of biological organization. Such studies generate a
497 more complete understanding of how noise is affecting individual species, both through changes in
498 visible behaviour and more cryptically through physiological and biochemical investigation (see Day
499 *et al.*, 2016, 2017; Filiciotto *et al.*, 2016; Jolivet *et al.*, 2016; Peng *et al.*, 2016; Wale *et al.*, 2019;

500 Ruiz-Ruiz *et al.*, 2020). This way of conducting research forms part of two of the three here
501 suggested strategies for conducting experiments on the effects of noise on marine invertebrates. A
502 third strategy focuses on using multiple species in an individual experiment, a strategy which 25% of
503 studies have followed since 2012. For all three strategies, knowing and considering the sound levels
504 in the environment where an organism originates from is important, as the animals' previous
505 exposure, or naivety, to noise may affect the response elicited in noise exposure experiments (Day *et*
506 *al.*, 2020).

507 The conceptual framework (Figure 7) presented in this review can be used as a guide for future work
508 on marine invertebrates and anthropogenic noise. This formalised way of assessing and identifying
509 the most adequate research methods and experimental design can be adapted not only for other taxa
510 in noise research, but also serve as an outline for methodological analyses in other disciplines where
511 descriptors can be specifically adapted or chosen for that particular field.

512 Looking to the future, there are a number of recommended directions for the field of marine
513 invertebrate noise research. First and foremost is the inclusion of particle motion measurements in all
514 studies. There is also an urgent need for particle motion measurements of noise sources in the field.
515 These measurements will allow future studies to be accurately calibrated, and past studies to be
516 validated against these values, making their findings more policy relevant. For future studies, it
517 would be desirable to investigate an organism on multiple levels of biological organization to enable
518 a more complete understanding of the effects of noise. Where possible, the use of a complementary
519 laboratory and field approach should be taken, where the fine-scale control of tank-based
520 experiments is coupled with field trials to validate the findings in situ. Additionally, if feasible, dose-
521 response relationships should be explored within the study so that the threshold of a particular
522 response can be identified. Regulators often request dose dependency measurements, for
523 incorporation into legislation to help reduce noise levels in the environment and protect marine biota

524 (Popper *et al.*, 2020; Williams *et al.*, 2015b). To improve the translation from research outcomes into
525 policy-making outputs, we advocate the inclusion of this component more frequently in noise-related
526 research.

527 Given the multiple interactions between man and the marine environment, there is an urgent need to
528 work across disciplines and integrate multiple stressors into studies, investigating any stressor
529 interactions that may occur in the “real world”. Long term exposures experiments, looking at both
530 regular and sporadic noise exposure, will help identify any levels of habituation or tolerance that
531 develop, along with identifying effects on growth, reproduction, and multi-generational responses.
532 Similarly, cross-taxa experiments will allow research to be conducted in a holistic manner that
533 assesses noise effects on species interactions, environmental dynamics, and larger ecosystemic
534 effects of anthropogenic noise.

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895

896 **Author Contributions**

897 MW and KD conceived the study. MW undertook the bibliometric analysis, literature evaluation, and
898 designed the evaluation methods. KD and RB contributed to the refinement of these methods. MW
899 led the drafting of the manuscript. KD and RB contributed to the manuscript's development.

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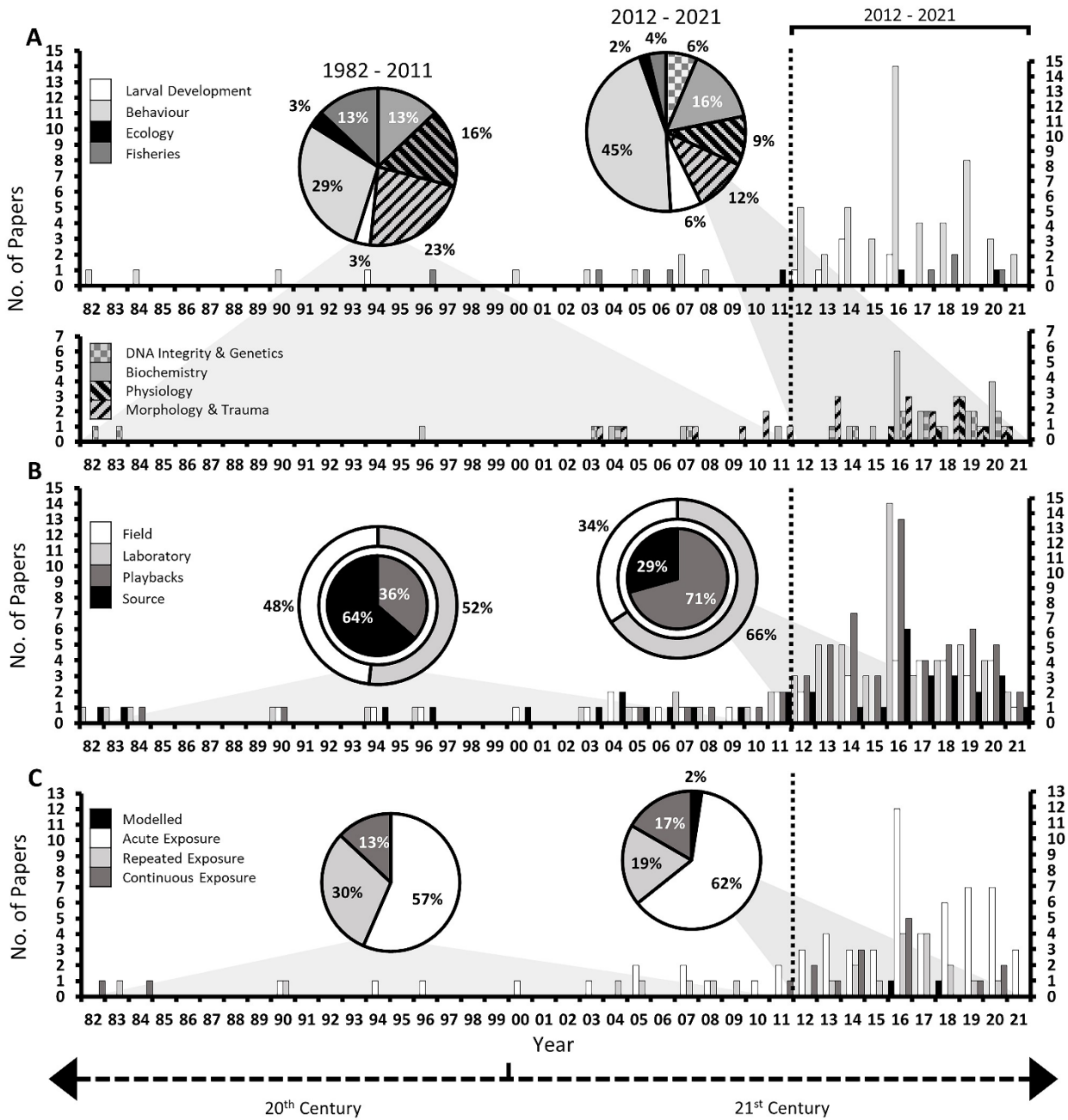
904 **Conflict of Interest**

905 The authors declare that the research was conducted in the absence of any commercial or financial
 906 relationships that could be construed as a potential conflict of interest.

907
 908 Table 1. Terms used in the ISI search. Adapted after Williams *et al.* (2015) with the addition of
 909 invertebrate specific terms. Terms enclosed in quotation marks to omit unrelated publications.

910

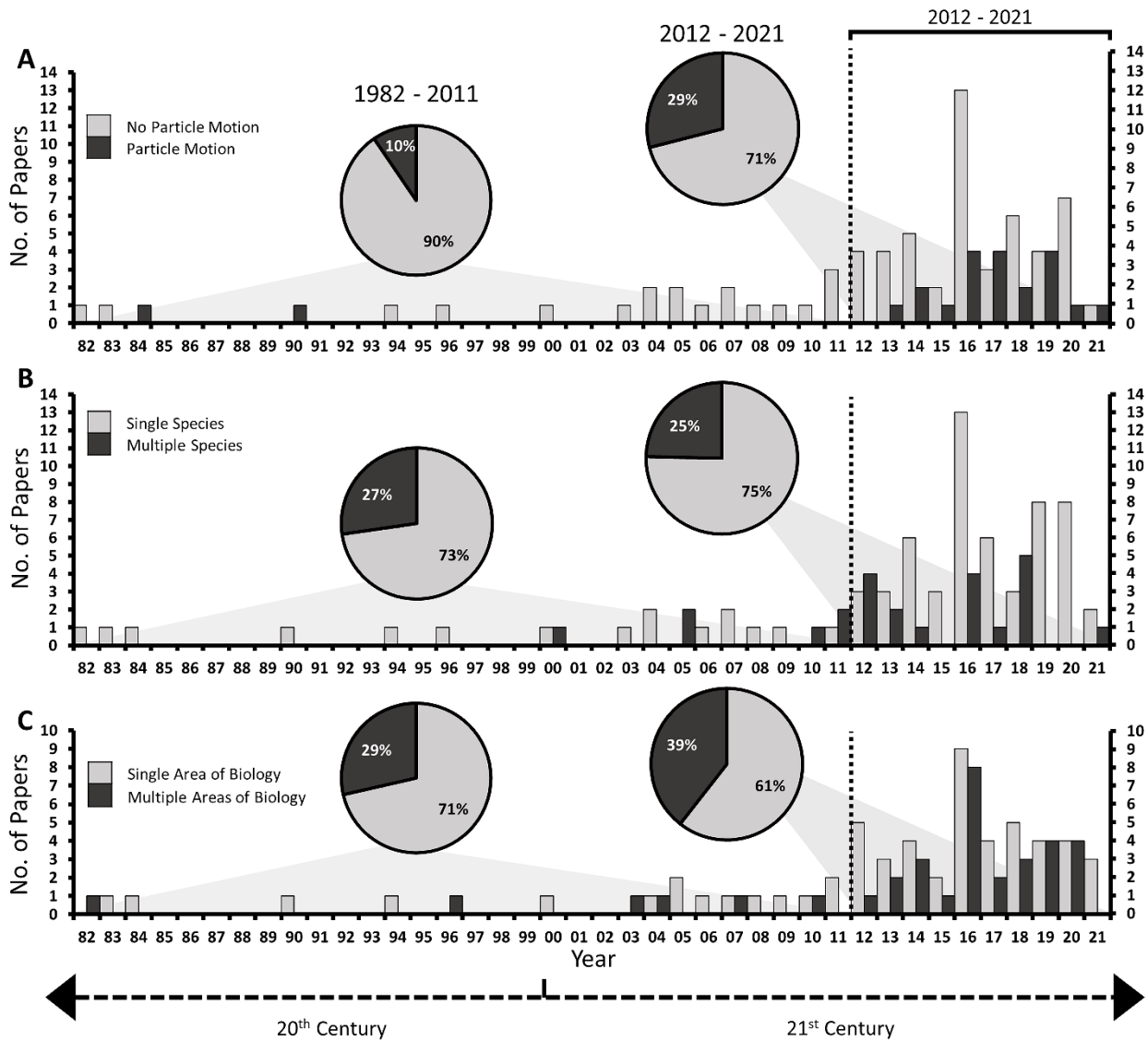
Term 1	Term 2							Without Term 2	
	Crab	Lobster	Clam	Mussel	Scallop	Squid	Invertebrate		
Airgun Noise	1	-	-	-	-	1	4	144	
"Anthropogenic Noise"	24	7	2	5	4	4	167	1506	
Marine Anthropogenic Noise Impact	15	9	2	4	3	5	84	499	
"Marine Noise"	2	1	1	-	-	-	6	49	
"Noise Playbacks"	-	-	-	1	-	-	5	44	
"Ocean Noise"	-	2	-	2	-	2	5	351	
"Pile Driving" Noise	3	4	-	4	-	2	13	396	
"Seismic Survey" Noise	3	6	-	-	1	-	11	619	
"Shipping Noise"	1	1	-	-	-	-	6	208	
Sonar Anthropogenic Noise	-	-	-	-	-	2	5	154	
"Tidal Turbine" Noise	1	-	-	-	-	-	1	35	
"Underwater Noise"	9	14	-	10	3	2	52	1229	
"Wind Farm" Noise	2	6	-	5	-	1	10	543	
							Total (Duplicates not removed)	546	5777
							Total (Duplicates removed)	273	



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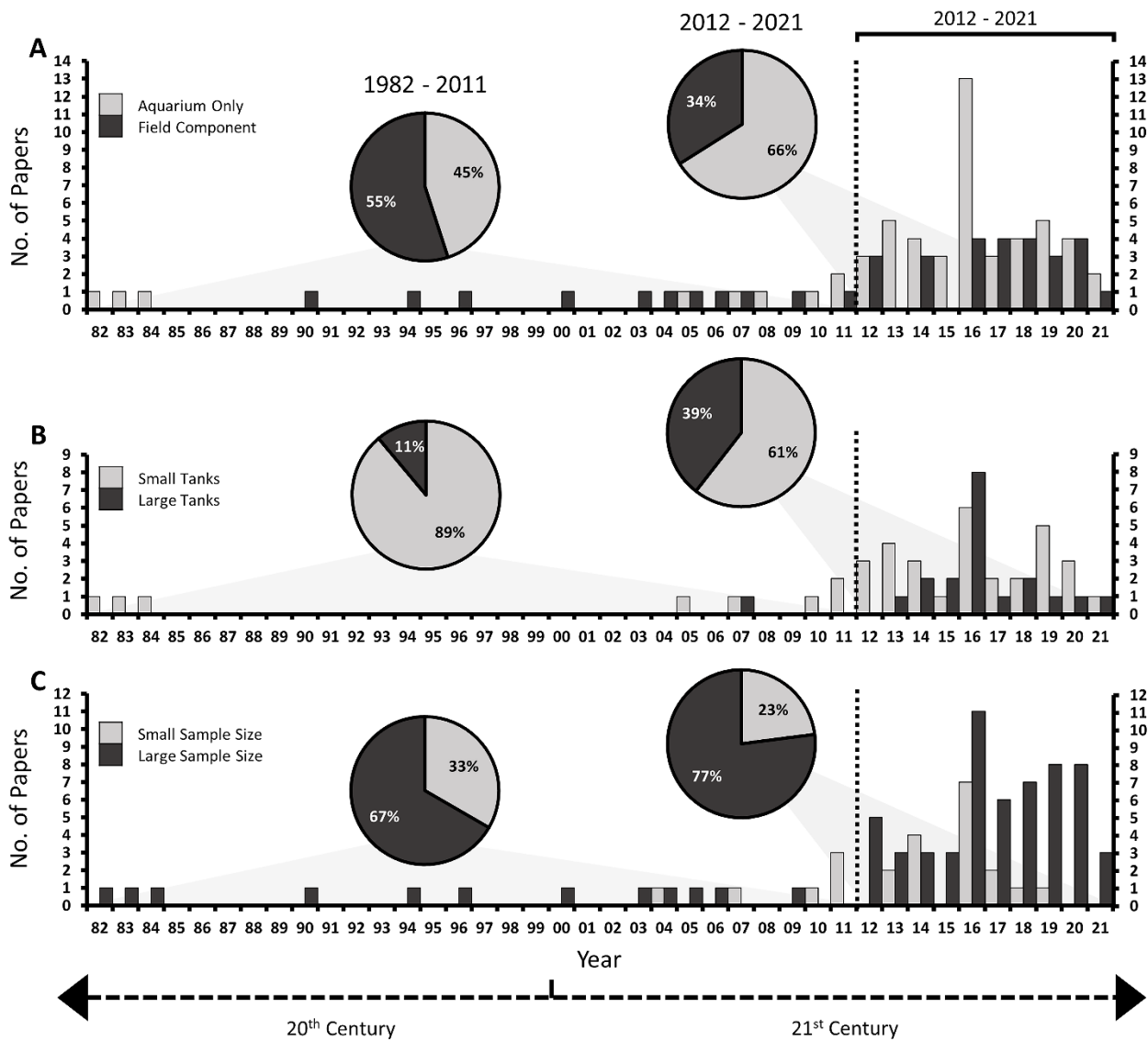
928 Figure 3. Neutral descriptors (N1, N2, N3). (A) Area of biology, (B) exposure type used, and (C)
 929 exposure length, addressed in marine invertebrate noise literature over the 39-year history of the
 930 field. Data presented separately for 1982-2011 (n=22) and 2012-2021 (n=73). Information gained
 931 from 95 total publications.

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935 Figure 4. Descriptor pairs (P1, P2, P3). (A) The inclusion of particle motion measurements, (B)
 936 number of species studied, and (C) number of areas of biology investigated in marine invertebrate
 937 noise literature over the 39-year history of the field. Data presented separately for 1982-2011 (n=22)
 938 and 2012-2021 (n=73). Information gained from 95 total publications.



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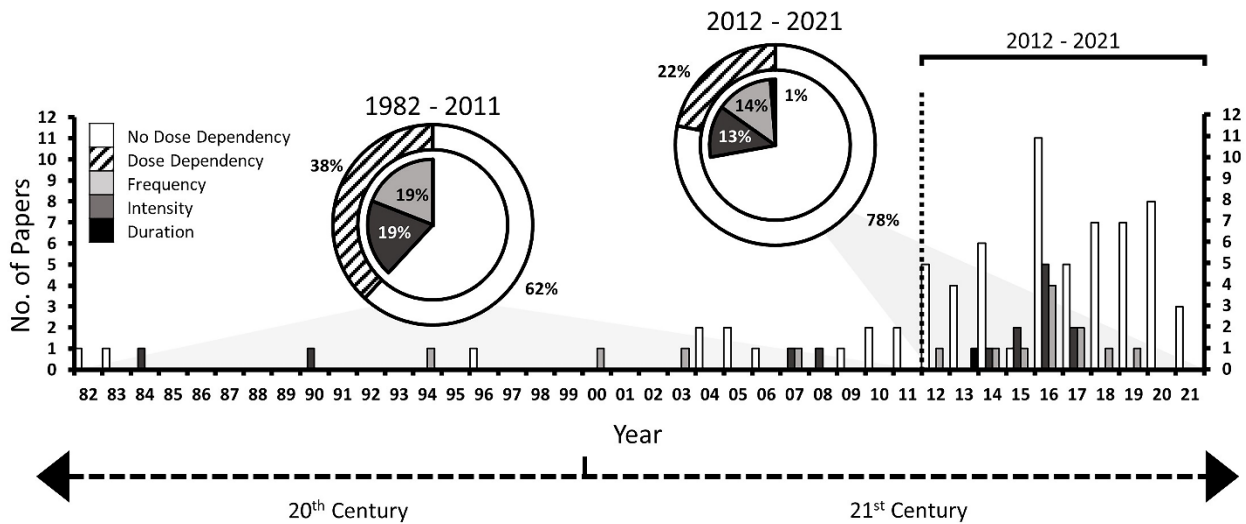
940 Figure 5. Descriptor pairs (P4, P5, P6). (A) Studies with aquarium only experiments and those with a
 941 field component, (B) tank size used in noise exposure, and (C) study sample size in marine
 942 invertebrate noise literature over the 39-year history of the field. Data presented separately for 1982-
 943 2011 (n=22) and 2012-2021 (n=73). Information gained from 95 total publications.

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949 Figure 6. Descriptor pair (P7). The inclusion of dose dependency measurements in marine
 950 invertebrate noise literature over the 39-year history of the field. Dose dependency is further split to
 951 identify the specific aspect of sound measured. Data presented separately for 1982-2011 (n=22) and
 952 2012-2021 (n=73). Information gained from 95 total publications.

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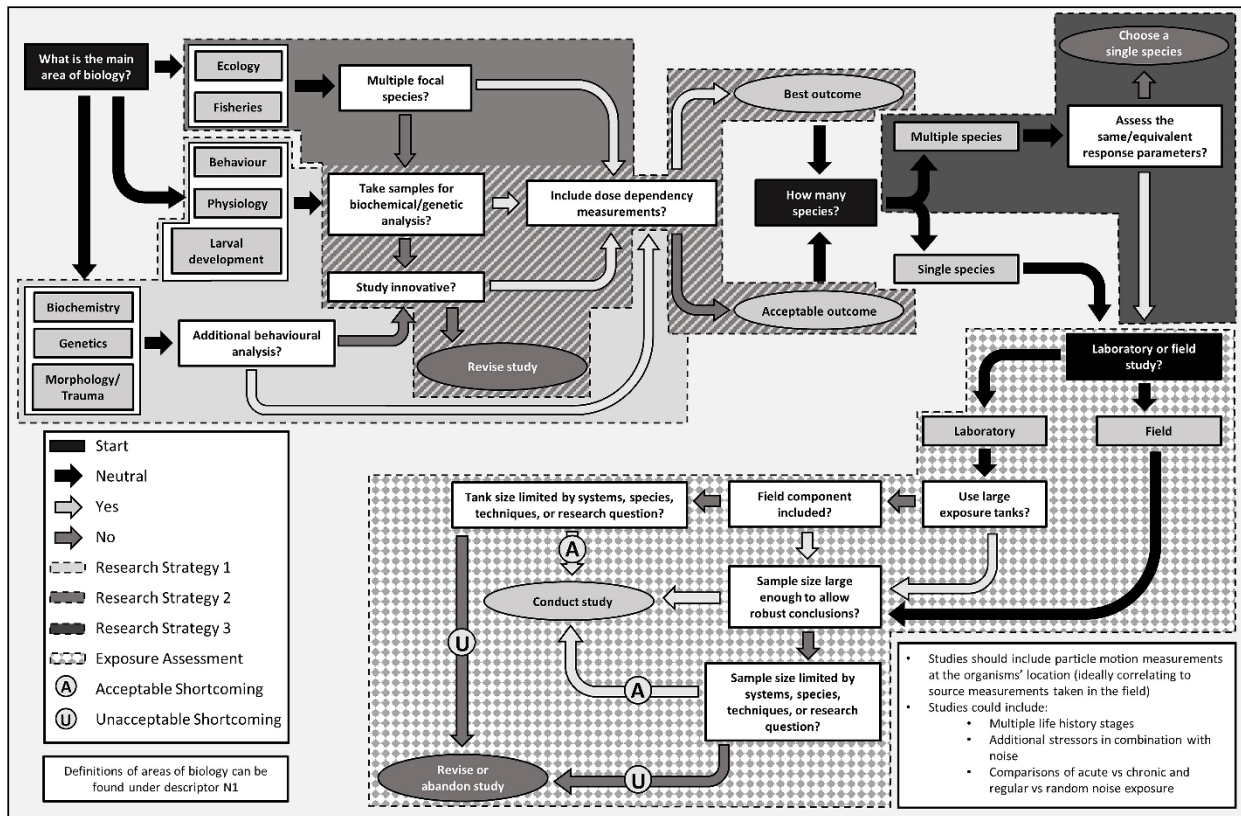
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965 Figure 7. Conceptual research strategy flow chart, to assess methods of prospective studies on the
 966 effects of noise on marine invertebrates.