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### Marine Ecology: progress series

DOI:

[10.3354/meps11659](https://doi.org/10.3354/meps11659)

Published: 01/04/2016

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

*Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):*

Jenkins, S., & Yrayzoz, M. U. (2016). Temporal scale of field experiments in benthic ecology. *Marine Ecology: progress series*, 547, 273-286. <https://doi.org/10.3354/meps11659>

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**Temporal scale of field experiments in benthic ecology**

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Running head: Duration of experiments in benthic ecology

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10 **Abstract**

11 The issue of scale in ecology is all-pervasive, with recognition that most ecological questions  
12 are scale dependent. Scaling up has become part of the lexicon of experimental ecology, and  
13 in marine benthic systems has resulted in numerous advances. While it is clear that  
14 manipulative experiments in benthic systems have been conducted over increasing spatial  
15 scales, it is less clear whether the notion of scaling up has been applied to temporal scale.  
16 Here, we examine the temporal scale at which experiments have been undertaken before  
17 reviewing longer term studies to examine the insights gained from extending the duration of  
18 observation following perturbation. Field experiments which examined  
19 population/community responses to perturbations, and studies which monitored the  
20 consequences of natural disturbances, were identified over the period 1980-2013. The median  
21 length of study was 10 months and only 12% of studies were carried out over more than 3  
22 years. Neither the median study length, nor the proportion of studies longer than 2 or 3 years,  
23 showed a trend over the 33 years. Review of experiments with a duration of 3 years or more  
24 revealed numerous benefits of a long-term approach. Some of these were unexpected, but  
25 others were predictable based on life history traits of dominant organisms, slow successional  
26 patterns, or response variables related to longer term community level responses, such as  
27 stability. The review suggests modest investment in resources to extend the duration of  
28 experiments can bring substantial benefits and hence consideration of experimental duration  
29 should be one of the primary decisions in planning field experiments.

30

31 Keywords: field experiments; long term; perturbation; scaling up; temporal scale

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## 37 **Introduction**

38 Our understanding of ecological processes in the marine benthic environment has been built  
39 on a foundation of manipulative experiments over the past half century or so, in a range of  
40 intertidal and shallow sub-tidal systems. Both soft and hard substrata habitats have been  
41 utilised by experimental ecologists, intent on understanding the processes structuring marine  
42 assemblages, and hence explaining patterns in abundance, distribution and diversity of species  
43 (see Raffaelli & Hawkins 1996 for review). Marine ecological experiments have also  
44 contributed to important advances in ecological theory (e.g. Connell 1961, Paine 1966,  
45 Dayton 1975, Menge & Sutherland 1976, Bertness & Callaway 1994). The intertidal zone is  
46 favoured by experimental ecologists owing to the logistical ease of working on marine  
47 communities when the tide is out, combined with a sharp marine/terrestrial environmental  
48 gradient which is conducive to investigations of the interaction of physical and biological  
49 processes. Additionally, the intertidal is inhabited by organisms which are generally small  
50 and sessile/slow moving and hence amenable to experimental manipulation (Connell 1972,  
51 Paine 1977, Underwood 2000) and in the case of hard substrate, the environment is two-  
52 dimensional in nature. Sub-tidal work is more challenging, but there is still a vast body of  
53 experimental research undertaken in this environment, either through the use of SCUBA or  
54 suspending experiments from floating or fixed structures. Focal habitats for experimental  
55 research in the coastal zone include coral reefs, seagrass beds, subtidal rocky reefs, intertidal  
56 rocky shores, mud-flats and beaches and sub-tidal soft sediment systems.

57 The development of experimental ecology in marine systems and the advances made over the  
58 past 50 years or so are well documented (see Paine 1994, Underwood 2000, Castilla 2000 for  
59 reviews). One area which has received increasing attention, in marine as well as terrestrial  
60 and freshwater habitats, is the issue of scale (Wiens 1989, Levin 1992, Schneider 2001, Ellis  
61 & Schneider 2008). Schneider (2001) neatly summarised three components to the problem of  
62 scale: problems in ecology often exist at decadal time scales over large ecosystems; most  
63 variables can only be measured in small areas over short time scales; patterns and processes  
64 observed at small scales do not necessarily hold at large scales. It is increasingly recognised  
65 that environmental drivers and ecological processes operate over a range of different spatial  
66 and temporal scales and over the past two decades, scale, in a quantitative sense, has been  
67 increasingly incorporated into experimental work (Ellis & Schneider 2008).

68 Ecologists in coastal marine systems have been key in developing a framework in which  
69 understanding from manipulative experiments may be scaled up through the comparative  
70 experimental approach (Menge et al. 2002). Identical replicated experiments are conducted at  
71 multiple sites often over some environmental gradient (e.g. Menge et al. 1997, Jenkins et al.  
72 2001, Coleman et al. 2006), thus allowing determination of the extent to which large scale  
73 physical conditions, which are not amenable to manipulation, can modify ecological  
74 processes. This 'scaling up' approach has led to a number of important developments in  
75 understanding of coastal systems, particularly in recognising the importance of latitudinal  
76 variation in temperature (e.g. Leonard 1999, Sanford 1999, Jenkins et al. 2001), regional  
77 variation in productivity (Menge et al. 1997, Broitman et al. 2001) and large scale variation in  
78 recruitment regime (Connolly & Roughgarden 1998). Studies of systems in contrasting  
79 oceanographic regimes have made progress in integrating small, medium and large scale  
80 processes and in particular have shown that benthic assemblages in shallow water or intertidal  
81 areas do not operate in isolation from the planktonic, pelagic realm (Menge et al. 2003).

82 In considering scale, attention has not solely focused on variation in space, with increasingly  
83 sophisticated ecological experiments examining processes at a range of different temporal  
84 scales. For example the importance of seasonality in determining the magnitude and direction  
85 of ecological processes is now recognised in experiments through manipulations being  
86 performed at different times of the year, and it is not uncommon for multiple starting dates to  
87 be nested within season in order to provide unconfounded tests of seasonal effects (e.g.  
88 Jenkins et al. 2005). Another aspect of temporal scale is the variability of events through  
89 time. Benedetti-Cecchi (2003) highlighted that temporal variability in the occurrence of  
90 perturbations is generally expressed in terms of the frequency of events, but argues that a  
91 more appropriate approach which avoids confounding the variance with the mean effect size  
92 (i.e. a more frequent disturbance is also more intense) is to design experiments in which levels  
93 of intensity, and those of variability, are chosen independently. His work has led to  
94 numerous studies explicitly assessing the importance of temporal variance in perturbations  
95 (e.g. Incera et al. 2010, Maggi et al. 2012, Oliveira et al. 2014).

96 Consideration of temporal scale also clearly needs to take account of the duration of any  
97 particular manipulative experiment. Underwood (2000), based on the assertion of Connell &  
98 Sousa (1983) that studies should encompass a period as long as the turnover of individuals in  
99 resident species, suggests that on Australian rocky shores a period of between 5 and 7 years  
100 might be appropriate, but also considers studies may need to be much longer to allow analyses

101 of equilibria. Yodzis (1988) considered that for the impact of a press perturbation to be  
102 known, a long term approach is required. He recommended adopting a rule of thumb such  
103 that the time scale of observation should approximate to two times the sum of the generation  
104 times of a pressed species (i.e. one whose density has been modified) and the potentially  
105 impacted species of interest. It is debateable whether all experiments require such duration,  
106 and clearly there are specific questions which can be addressed by much shorter studies. For  
107 example Menge (1997) tested the assertion that indirect effects may take longer to become  
108 apparent, following a manipulation, than direct effects, by determining the relationship  
109 between duration of experiment and the importance of indirect effects using 23 rocky  
110 intertidal interaction webs. He concluded that in the case studies examined, which ranged in  
111 length from 0.5 to 156 months, *'interpretations of community dynamics are not likely to be*  
112 *distorted because experiments were too brief'* (p.812). Thus, based on addressing a very  
113 specific goal, that of quantifying indirect effects in community dynamics, Menge (1997)  
114 considered the experiments he reviewed as being sufficiently long.

115 In most fields of marine benthic ecology there has been a lack of explicit consideration of  
116 experimental duration. A field of burgeoning research that has recently recognised the serious  
117 implications of a short term approach is in Biodiversity and Ecosystem Functioning (BEF)  
118 work (Hooper et al. 2005, O'Connor & Crowe 2005, Raffaelli 2006, Crowe et al. 2012, Duffy  
119 et al. 2012). Crowe et al. (2012) used existing meta-analyses (Cardinale et al. 2007,  
120 Stachowicz et al. 2007) to review the temporal scale of biodiversity-ecosystem functioning  
121 (BEF) studies conducted in both laboratory and field settings (in marine, terrestrial and  
122 freshwater environments). The authors argue that limiting the temporal extent of experiments  
123 has a marked effect on the conclusions regarding the importance of biodiversity in ecosystems  
124 and the mechanism by which biodiversity may exert an effect; short term experiments will  
125 over-emphasise the importance of dominant species (a species identity effect) relative to  
126 complementarity among species. Stachowicz et al. (2008a) examined the effect of seaweed  
127 diversity on cover over a period of three years. They showed that seaweed cover in diverse  
128 treatments only exceeded that in the best performing monoculture after a period of 18 months,  
129 a period much longer than many biodiversity studies (Crowe et al. 2012). These observations  
130 might reasonably be seen as strong arguments for lengthening the duration of BEF  
131 experiments (although doing so in any multi-trophic manner incorporating large, mobile long  
132 lived consumers will be enormously challenging (Raffaelli 2006)).

133

134 Although many aspects of temporal scale have been addressed through ecological  
135 experiments in recent decades, it is debateable whether the scaling up approach, so prevalent  
136 in considerations of spatial scale, has been applied to temporal scale. Thus it is unclear  
137 whether the overall length of experimental study (i.e. scaling up in time) has increased,  
138 despite numerous publications tentatively expressing concern at the paucity of longer term  
139 experimentation (e.g. Connell & Sousa 1983, Underwood 2000, Raffaelli 2006). Such calls  
140 have no doubt been influenced by the perceived benefits of long term experimentation  
141 (Underwood 2000; Crowe et al 2012). Here, we examine the temporal scale at which  
142 ecological experiments (which apply some form of perturbation) are undertaken in intertidal  
143 and shallow sub-littoral environments before reviewing the literature to highlight the range of  
144 insights gained from long term experiments. We finish by considering the challenges  
145 associated with increasing the temporal extent of marine benthic experiments and the way in  
146 which these may be addressed.

#### 147 **Review of experimental duration**

148 As outlined above there have been a number of calls for longer term experimentation, but a  
149 factor which may act counter to such a move is the increasing pressure on scientists to publish  
150 their work. While publication of research in a vibrant international literature is the life-blood  
151 of science, the pressure to publish could be argued to lead to a short term approach, with  
152 researchers rushing to publish each new piece of research. It is very easy to see how this  
153 short term approach can influence our approach to experimental ecology. Why spend 5 years  
154 undertaking an experiment when a paper can be published on the basis of results collected  
155 over a period of 18 months? By reviewing the literature (including both marine focused and  
156 general ecological journals) we hope to determine what range of temporal scales experimental  
157 marine ecologists are working at and whether the approach to experimental duration has  
158 changed over a 33 year period. This review is limited to assessment of the effects of  
159 perturbation on marine systems; thus long term monitoring *per se* is not considered although  
160 it is acknowledged that this approach may often address similar questions.

#### 161 Methods

162 We examined literature published over a 33 year period in two of the leading marine  
163 ecological journals, Marine Ecology Progress Series (MEPS) and Journal of Experimental  
164 Marine Biology and Ecology (JEMBE), and three general ecological journals, Ecology, Oikos  
165 and Oecologia in order to examine the temporal scale and sampling frequency of field

166 perturbation experiments in shallow sub-tidal and intertidal benthic environments. In  
167 selecting publications, all types of pulse and press perturbations were included, from  
168 manipulations which simulate some form of natural or anthropogenic disturbance event, to  
169 those in which the density or presence of one or more particular species is altered. In addition  
170 to manipulation of biota we included perturbations to the physical environment, for example  
171 modification of the nutrient or light regime. One very common type of study was one in  
172 which new substrata (often simple PVC panels) were introduced into the environment. Such  
173 perturbations may be considered analogous to clearance of biota in natural communities, since  
174 both provide bare space, free from competitors.

175 In considering which studies to include, the main criterion beyond inclusion of an appropriate  
176 perturbation was the response variable measured. In general, studies were included which  
177 measured the community or population response of macro-organisms to a perturbation (i.e.  
178 meiofauna and microbial communities were rejected). Studies where the research aim was  
179 solely to examine some process rate, such as growth or mortality, or the effect of disturbance  
180 on an organisms' body condition, were excluded. In addition, studies which examined only a  
181 behavioural response were not included. One difficult judgement to be made was in studies  
182 designed to examine spatial or temporal patterns in the arrival of animals or algae i.e.  
183 settlement/recruitment. Where the aims of such work were only short term in nature, i.e.  
184 examination of settlement, such studies were not included since settlement can be clearly  
185 defined as a short term process (Jenkins et al. 2009). However, use of the term recruitment is  
186 more problematic. Because of its variable use in benthic ecology with no defined time period  
187 over which it applies (Keough & Downes 1982, Jenkins et al. 2009) studies examining  
188 recruitment were included unless the aim of the study was clearly related to understanding  
189 processes determining the arrival of propagules and subsequent settlement (e.g. Reinhardt et  
190 al. 2013) rather than the development of a benthic population or community.

191 In addition to manipulative experiments implemented by the experimenter, numerous studies  
192 examine the consequences of events or implementation of management structures not under  
193 the control of the experimenter. These include investigations of natural disturbances such as  
194 extreme weather events (e.g. Tegner et al. 1997) or human-induced perturbations such as  
195 pollution (e.g. Jacobs 1980), the exclusion of humans from Marine Protected Areas (Castilla  
196 & Bustamante 1989) and managed realignment of coastal limits through intentional flooding  
197 (Hughes et al. 2009). These `natural experiments` were included in our review of literature



198 whenever data were available prior to the perturbation taking place, such that a true temporal  
199 control existed.

200 Using the criteria outlined above, all publications in MEPS, JEMBE, Ecology, Oikos and  
201 Oecologia at four yearly intervals from 1981 to 2013 were initially reviewed by examination  
202 of the title and abstract. Following identification of potential papers the full text was read and  
203 then either rejected or the appropriate information extracted. This approach was taken rather  
204 than performing a search based on keywords because of the difficulty in creating suitable  
205 search terms which would highlight appropriate papers without bias. Our search through  
206 12,557 titles (6940 in general ecological journals; 5617 in marine ecological journals)  
207 identified a total of 263 publications containing 322 independent experiments over the nine  
208 publication years. These represented an average of 3.5% and 1.3% of the studies published in  
209 marine and general ecological journals respectively (or 15.9% of the marine related papers  
210 published in general journals). Although there was no obvious directional change over the 33  
211 years of review in the proportion of appropriate studies selected in each year in either journal  
212 type, there was a general increase in the number of studies from which data were extracted  
213 owing to the huge increase in number of publications in all journals over time (from 299/564  
214 in 1981 to 823/831 in 2013 for marine/general ecological journals respectively). In order to  
215 allow good representation of experimental work in earlier years, additional publications were  
216 sought for the earliest five dates by examining studies published up to two years before (and  
217 in the case of 1981, two years after). This approach was taken in the same way as described  
218 above, until a minimum of 10 independent experiments in both marine ecological and general  
219 ecological journals were identified for each of the four-yearly periods. This resulted in 293  
220 publications containing 352 studies being reviewed.

221 The temporal scale of experiments in all 352 studies was determined as the length of time  
222 from initial sampling, immediately prior to the perturbation, to the final sampling event.  
223 Where multiple experiments within a single publication were conducted with the aim to  
224 examine a single goal or hypothesis, the maximum length of experimentation was  
225 documented. In determining the sampling interval (i.e. length of time between each sampling  
226 event) an average value over the period of the study was calculated. For example, in a ten  
227 month study examining the influence of bivalve shell material introduced to a mudflat on  
228 colonisation by burrowing thalassinidean shrimp, Feldman et al. (1997) made observations 1  
229 month after the perturbation and after ten months. Here, the average sampling interval was  
230 recorded as 5 months. The habitats in which experiments were undertaken were classified as

231 inter-tidal or sub-tidal. In micro-tidal regimes such as the Mediterranean (e.g. Maggi et al.  
232 2009) and Baltic (e.g. Lindegarth et al. 2001) studies undertaken in areas frequently exposed  
233 to air through variations in pressure and wind were classified as intertidal. The Caribbean  
234 fringing reef studied by Kilar & MacLachlan (1989) is exposed to air only during particular  
235 conditions, at certain times of the year, and was therefore considered sub-tidal. The  
236 classification of habitat type (rock, soft sediment, sea-grass, coral, mangrove, salt-marsh,  
237 artificial substrate) was generally clear cut. Cobble and boulder habitat were considered  
238 simply as rock rather than creating a novel category.

239 Classification of experiments as pulse or press was clear-cut in most cases. Pulse experiments  
240 were defined as those receiving a one-off, perturbation which was generally short in temporal  
241 extent compared to the temporal scale of the study. The introduction of artificial substrata  
242 such as PVC panels (e.g. Valdivia et al. 2005) or newly quarried boulders (e.g. Chapman  
243 2013) was considered a pulse disturbance, analogous in many ways to the creation of bare  
244 space by a single disturbance event. In cases where both pulse and press perturbations were  
245 implemented, the experiments were invariably classified as press. For example in numerous  
246 studies, novel substrata were introduced in order to examine the consequences of a particular  
247 press manipulation, such as light and sediment (Connell 2005) or herbivores (Kaehler &  
248 Williams 1997). Other studies (e.g. Russell & Connell 2005) combined pulse manipulations  
249 such as the one-off removal of a particular species with continued press perturbations such as  
250 addition of nutrients. Rather than class these as a combination of both pulse and press, they  
251 were classed as press. In some studies, multiple perturbations were applied through time  
252 (Jewett et al. 2005, Incera et al. 2009, Minchinton & Fels 2013) and again here it was  
253 considered that the principle of an ongoing perturbation (although not continuous) justified  
254 categorisation as press.

## 255 Results and Discussion

256 64 % of the 352 studies over the 33 years were from marine journals (MEPS and JEMBE)  
257 whereas 36 % were published in general ecological journals (OIKOS, Ecology, Oecologia).  
258 The studies were split almost exactly equally between the intertidal (49.7%) and the sub-tidal  
259 (50.3%) zones. Of the eleven different habitats identified the most common was inter-tidal  
260 rocky shore (31% of studies) followed by sub-tidal rocky reef (14%) and then sub-tidal  
261 artificial substrate and sub-tidal coral reef (9% each). 62 % of the studies were categorised as  
262 press (217 studies) whilst the rest were considered as pulse (135).

263 Examination of the frequency distribution of study length across 33 years showed a clear  
264 skew to a shorter time frame (Figure1). The highest proportion (24% and 33% for marine and  
265 general ecological journals respectively) were very short (between 0 and 3 months), with  
266 obvious peaks at 9-12 and 21-24 months for marine journals (presumably due to the logical  
267 attraction of terminating experiments at one and two years respectively) (Figure 1). Most  
268 studies (85% for marine and 82% for general ecological journals) lasted two years or less and  
269 only 39 of the 352 studies were conducted over a period of 3 years or more. Of these, 17  
270 studies were of a period of 5 years or more. The median length of study over the period  
271 reviewed was 11 months in marine journals, 9 months in general ecological journals and 10  
272 months overall (Figure 2). Although the median study length varied among years for marine  
273 journals (Kruskal Wallis test, Chi-Square = 19.427; df =8; P=0.013) there was no apparent  
274 trend in study length with time.

275 Study length showed differences between habitat (intertidal versus subtidal) and between  
276 perturbation type (pulse versus press) (Figure 3). The median length of inter-tidal studies (12  
277 months) was significantly longer than sub-tidal studies (8 months ) (Mann Whitney U test:  
278  $Z=-2.407$ ;  $p=0.016$  (Figure 3A). In the intertidal zone, 30% of studies were conducted over 2  
279 years or more, approximately double that in the sub-tidal. The median study duration of pulse  
280 experiments (14 months) was significantly longer than press experiments (6 months) (Mann  
281 Whitney U test:  $Z=-4.762$ ;  $p<0.001$ ) (Figure 3A) and a far greater proportion lasted two years  
282 or longer (35% of pulse compared to only 16% for press).

283 There was a significant positive relationship between experimental duration and sampling  
284 interval ( $F_{1,347} = 108.5$ ;  $P < 0.001$ ). Thus, as experiments got longer the time between  
285 sampling events increased. However, the relationship was weak ( $r^2 = 0.236$ ), driven partially  
286 by the fact that a sampling interval (the dependent variable) cannot be greater than the  
287 experimental duration (the predictor variable) and indeed many studies well beyond the  
288 median duration had short sampling intervals of between 0.5 and 3 months.

289 In discussing the need for a longer term approach Underwood (2000, p.68) states that '*the*  
290 *majority of ecological studies are quite short, usually three to five years*'. In fact, our  
291 analysis of 352 studies over 33 years shows that for experiments (i.e. where some form of  
292 manipulation or perturbation has taken place, as opposed to purely observational work) the  
293 median length of study was only 10 months and only 12% of published work was over a  
294 period greater than 3 years. Patterns were similar irrespective of the type of journal (marine

295 specific versus general ecological) in which papers were published. These results were quite  
296 clear in indicating that calls for an increase in the temporal scale of studies have not led to any  
297 general increase in experimental duration over the past 3 decades. This is true whether  
298 considering the median duration of studies or the proportion which are longer than 24 or 36  
299 months.

300 Different approaches can be taken to make an argument for the benefits of longer term  
301 experimental duration. One is in demonstrating that longer term experiments reveal, for  
302 example, differences in effect sizes compared to short term experiments. Such an approach is  
303 fraught with problems in designing a non-biased analysis, since often the benefits of long  
304 term experimentation are revealed not in a single bigger outcome but in multi-faceted results  
305 which provide greater insight into ecological complexities. Below we address such  
306 complexity by reviewing a range of longer term studies (generally greater than three years)  
307 which have revealed greater insight than could be achieved by equivalent short term work.

## 308 **Insights from long term experiments**

### 309 Controlled manipulations

310 There are a diversity of reasons for conducting long term experiments including: study of long  
311 lived species (e.g. Clarke & Allaway 1993; Jenkins et al. 2004) and slow successional change  
312 (Yakovis et al 2005); work in polar regions where development rates are much slower (Konar  
313 2007, Beuchel & Gulliksen 2008); the search for long lived ecological phenomena such as  
314 alternate stable states (Petraitis & Dudgeon 2005); determination of the nature and extent of  
315 temporal community fluctuations in disturbed systems (Dye 1998). Defining how long to run  
316 field experiments is a difficult task but the number of studies in marine coastal systems which  
317 show differences between control and treatment plots more than 5 years (Clarke & Allaway  
318 1993, Cervin et al. 2005, Viejo 2009, Schiel & Lilley 2011) and in some cases more than 10  
319 years (Dye 1998, Jenkins et al. 2004, Beuchel & Gulliksen 2008) after a perturbation suggest  
320 that to address many community level questions experiments should run for years rather than  
321 months. Differences among treatments are not simply limited to community structure but also  
322 to overall community productivity (Tait & Schiel 2011) and to community stability (Dye  
323 1998). For example, Tait & Schiel (2011) showed that 90 months after removal of the fucoid  
324 canopy alga *Hormosira banksii*, community primary productivity was only between 40% to  
325 60% that of control areas. The reasons for slow recovery may be because successional  
326 development is inhibited (sensu Connell & Slatyer 1977) by early colonisers (e.g. Sutherland

327 & Karlson 1977), communities are dominated by slow growing species (e.g. Jenkins et al.  
328 2004) or the environment is conducive to slow development, for example in polar regions  
329 (e.g. Beuchel & Gulliksen 2008).

330 In polar regions disturbance can have a profound effect on community structure owing to very  
331 slow, and in many cases, an almost complete lack of recovery (Dayton & Oliver 1977, Barnes  
332 1996, Konar 2007). For example, Konar (2007) found that 4 years after clearance of sub-tidal  
333 boulders on the Alaskan north coast, cover of biota had only reached 2%, despite the fact that  
334 bare surface in the community in general was scarce (< 10%). A similar lack of colonisation  
335 (a total of 2 serpulid polychaetes present after 3 years, and reports of bare surfaces after 5  
336 years) on a settlement panel array was observed in McMurdo Sound, Antarctica (Dayton  
337 1989). This was followed at some point by bryozoan, hydroid, soft coral, and sponge  
338 colonisation leading to 'heavily covered' surfaces (Dayton 1989, p.1486). Low recruitment  
339 and slow growth may characterise polar regions, with physically driven episodic events  
340 driving a punctuated succession (Dayton 1989). Such an environment clearly requires long  
341 term experimental work.

342 One argument for conducting long term experiments is that they can reveal quite unexpected  
343 results. Jenkins et al. (1999a,b, 2004) report the results of factorial manipulations of the long  
344 lived canopy species *Ascophyllum nodosum* and the keystone grazer *Patella vulgata* on  
345 sheltered canopy dominated shores of the Isle of Man. Short term results over a period of one  
346 to two years included the die back of understory turfing algae, opening up of bare space and  
347 replacement of the *Ascophyllum* canopy with alternative more opportunistic shorter lived  
348 fucoid species, *Fucus vesiculosus* and *F.serratus*. However it was the longer term  
349 observations over 6 years (Jenkins et al. 1999a) and then twelve years (Jenkins et al. 2004)  
350 which revealed the importance of *Ascophyllum* in limiting patellid limpet populations; loss of  
351 the facilitatory function of the canopy on understory turfing algae, and hence the opening up  
352 of bare space, resulted in enhancement of limpet recruitment, leading to populations up to six  
353 times greater in abundance over a decade after canopy loss. Here, experimental work  
354 demonstrated the stabilising function of turfing algae in the undisturbed community. Other  
355 work has recognised how the dense low lying nature of turfing algae, combined with sediment  
356 trapping ability (Connell et al. 2014) contributes to stability or slow succession (e.g. Cervin et  
357 al. 2005, Schiel & Lilley 2011).

358 It is frequently stated that coastal marine systems are ideal environments in which to conduct  
359 manipulative experiments because dominant organisms have relatively short generation times  
360 and hence experiments may be conducted over short time scales. However it is debatable  
361 whether generation times in primary producers, key consumers and dominant space occupiers  
362 (which are often a number of years) are short enough to justify this view (Beuchel &  
363 Gulliksen 2008). Species life history traits are important determinants for the recovery of  
364 communities following disturbance in a range of different ecosystems including saltmarshes  
365 (e.g. Bertness 1991), mangroves (e.g. Clarke & Allaway 1993) and rocky shores (e.g.  
366 Methratta & Petraitis 2008), and species longevity, as well as mode and rate of colonisation,  
367 have clear implications for experimental duration. Methratta & Petraitis (2008) examined  
368 recovery from disturbance on rocky shores focusing on species with contrasting longevity,  
369 barnacles and furoid algae. They showed that differences in life history traits of dominant  
370 species modified successional trajectories at different spatial scales over a 5 year period.  
371 Understanding of the population dynamics and community structuring role of long lived  
372 species will invariably require longer term studies than investigation into species with short  
373 generation times, clearly demonstrated by the nine year study on mangrove regeneration of  
374 Clarke & Allaway (1993) and the three year study of Bertness (1991) on *Spartina* competitive  
375 interactions. On rocky shores *Ascophyllum nodosum*, a dioecious, long-lived species  
376 (Aberg 1992), with low rates of recruitment rate and slow growth rate (Aberg & Pavia 1997,  
377 Cervin et al. 2005) has been the focus of a number of long term studies in the NE and NW  
378 Atlantic (e.g. Jenkins et al. 1999a,b, 2004, Cervin et al. 2005, Ingolffson & Hawkins 2008,  
379 Araújo et al. 2012). Araújo et al. (2012) showed that the impacts of human trampling can  
380 have long term (5 years) effects on understory community structure in stands of *Ascophyllum*  
381 *nodosum*. Even small scale (25 × 25cm) disturbance events can have long lasting effects on  
382 *Ascophyllum* understory communities (Cervin et al. 2005); small scale loss of *Ascophyllum*  
383 canopy led to a change in community structure still apparent after 7 years. Such effects can  
384 occur despite recovery of the long lived biomass dominants. Schiel & Lilley (2011) showed  
385 differences between disturbed and control understory communities 8 years after removal of  
386 the *Hormosira* canopy even though this dominant furoid returned to a nearly closed canopy.

387 Communities composed of long lived individuals are often described as stable, but in reality  
388 may only be stable as a consequence of the long lived nature of their components (Connell &  
389 Sousa 1983). Long term observations following perturbations, especially where dominant  
390 biota are long lived, are essential to judge the stability of communities and consequent

391 properties of ecosystems (Farrell 1988, Hooper et al. 2005). Hooper et al. (2005) points out  
392 that theoretical work on stability has outpaced the ability of empirical work to test predictions,  
393 essentially because of the time and resource requirements of long term experimental work  
394 required to determine the fate of all adults over at least one complete turnover (Connell &  
395 Sousa 1983). The problem of time scale is one which has dogged the sometimes vigorous  
396 debate surrounding the existence, or otherwise, of alternate stable states (see Petraitis &  
397 Dudgeon 2004 for review). The question of whether systems can occupy more than one  
398 equilibrium point and hence support different stable communities in the same habitat  
399 (Lewontin 1969, Connell & Sousa 1983, Peterson 1984, Petraitis & Latham 1999, Petraitis et  
400 al. 2009) has been addressed in a number of different marine coastal assemblages including  
401 coral reefs (Scheffer et al. 2001), rocky shores (Paine et al. 1985, Petraitis & Latham 1999),  
402 sub-tidal rocky reefs (Simenstad et al. 1978) and soft sediments (van de Koppel et al. 2001).  
403 Part of the problem in answering what at first sight seems a relatively simple question is that  
404 spatial and temporal scale are an intractable part of defining stability. Connell & Sousa  
405 (1983) argued that experimental tests of stability require long term experiments where '*the*  
406 *fate of all adults of the population or community must either be followed for a minimal period*  
407 *of at least one complete turnover, or their replacement probabilities estimated*' (p.808).  
408 Others disagree (Peterson 1984, Sutherland 1990) and over the last decade or so Petraitis and  
409 co-workers (e.g. Petraitis & Latham 1999, Petraitis & Dudgeon 2005, Petraitis et al. 2009)  
410 have implemented manipulations which although long term by the standards of this review do  
411 not reach the temporal standards defined by Connell & Sousa (1983). The possibility that  
412 mussel beds and stands of *Ascophyllum nodosum* represent alternative states in sheltered bays  
413 of the Gulf of Maine was tested through initiating pulse disturbances (clearance of the  
414 *Ascophyllum* canopy) of different sizes and monitoring successional pathways over a nine  
415 year period (Petraitis et al. 2009). The shift from *Ascophyllum* assemblage to mussel bed in  
416 37% of large clearances, nine years after disturbance, is argued by Petraitis et al. (2009) to  
417 show that these communities represent multiple stable states on the intertidal shore of the Gulf  
418 of Maine. They go on to present a conceptual framework which combines this view with the  
419 prevailing paradigm of environmentally driven consumer control (Lubchenco & Menge 1978,  
420 Bertness et al. 2002). Irrespective of tests of ecological theory, investigation of how the scale  
421 of disturbance affects successional trajectory clearly requires a long term approach in this  
422 environment at least, as evidenced by the diversity of successional responses among clearing  
423 sizes and sites over a six year period (Petraitis & Dudgeon 2005).

424

425 Natural perturbations and Marine Protected Areas

426 The majority of ecological experimentation involves small scale, controlled manipulation,  
427 which, if of sufficient duration, may give insight into the time scale of recovery of marine  
428 communities following perturbation. However, Schiel and Lilley (2011) point out the  
429 limitation of such approaches in understanding recovery at coast-wide scales, where  
430 propagule supply may be limiting. Underwood (1998, p.292) makes a cogent argument to  
431 ‘grab opportunities afforded by dramatic events, such as unusually severe weather and large-  
432 scale changes brought about by natural agents’ to enable a longer term and larger scale  
433 approach to ecology. Observations, over temporal and spatial scales well beyond standard  
434 controlled experiments following mass die-offs (Levitan 1988, Linares et al. 2005), large  
435 disturbance events such as ice scour (McCook & Chapman 1997), storms (Hughes 1989,  
436 Underwood 1998), earthquakes (Castilla 1988), human management intervention (Hughes et  
437 al. 2009) and pollution (Southward & Southward 1978) have created insight into ecological  
438 processes. McCook and Chapman (1997) assessed the impacts of large scale ice scouring on  
439 exposed rocky shores in Nova Scotia over a 5 year period, and showed that many  
440 experimental effects noted over shorter time scales (McCook & Chapman 1991,1992) were  
441 not apparent after longer periods, suggesting that much of the variation within the exposed  
442 shore habitat is temporary. They also argue that the temporal dominance of *Fucus* observed  
443 over mussels over a 5 year period, and no evidence of competitive superiority by mussels,  
444 should lead to caution in assuming any general applicability of previously stated general  
445 models of community structure based on the work of Menge and Sutherland (1976, 1987).  
446 Such conclusions, based on long term observations following large scale perturbations,  
447 present a cautionary note to basing environmental management advice on a theoretical  
448 framework based predominantly on the short term and small scale. Underwood (1998) makes  
449 the point that observations following disturbance can give rise to hypotheses regarding  
450 mechanisms which can then be tested through small scale, shorter term experiments. He  
451 observed variable rates of recovery in the canopy alga *Hormosira banksii* over a seven year  
452 period following an extremely large storm and then used short term experimental  
453 manipulations to test two alternative models: 1) that the rate of recovery was a function of the  
454 severity of disturbance; 2) recovery was determined by the activities of grazers. A similar  
455 combined approach was taken by Carroll and Highsmith (1996). A severe freeze in Alaska  
456 coincided with a spring low tide series leading to high levels of mussel mortality, but little



457 effect on the mussels' principal predator *Nucella lima* which winters in the sub-tidal. A  
458 combination of observations over 3 years and experimental manipulations demonstrated that  
459 the extreme event 'set the framework for a shift in balance of the interaction' between  
460 predator and prey (Carroll & Highsmith 1996, p.130). In the presence of high numbers of *N.*  
461 *lima*, mussels were unable to recover over a 3 year period despite annual recruitment events.

462 One type of 'experiment' in coastal marine environments which by its nature tends to be long  
463 term is the implementation of Marine Protected Areas (MPA's). By totally or partially  
464 excluding the extractive activities of humans (Sciberras et al. 2015) MPA's establish a  
465 (usually) large scale experiment (Castilla 1999, Diaz et al. 2003) which can be used for  
466 understanding long-term dynamics (Castilla 2000) and has led to enormous ecological insight  
467 in coastal marine systems, particularly into the prevalence, time scale and magnitude of  
468 trophic cascades (reviewed by Castilla 1999). For example in Chile, Duran and Castilla  
469 (1989) report the results of a five year study of the consequences of exclusion of human food  
470 gatherers from the rocky intertidal and shallow sub-tidal at Las Cruces in central Chile. The  
471 cessation of human exploitation of the carnivorous muricid gastropod *Concholepas*  
472 *concholepas* or 'loco' led to significant enhancement of its density and consequent strong  
473 predatory control of previously dominating mussels. These cascading effects resulted in an  
474 elevation of intertidal diversity and subsequent domination by barnacles.

475 The majority of marine reserves or protected areas are established to protect fisheries-targeted  
476 species, including benthic organisms such as lobsters, scallops, abalone and the Chilean  
477 'loco'. Such organisms are generally long lived relative to the majority of benthic organisms  
478 studied in perturbation experiments. Because the focus of MPA studies has often been to  
479 establish effects on these relatively long lived target species (e.g. Duran & Castilla 1989,  
480 Hoskin et al. 2011), and because the temporal scale of the press manipulation (reduction or  
481 elimination of human disturbance) is not limited by the normal drivers of ecological  
482 experimentation (e.g. researchers funds), it is not surprising that published studies of MPAs  
483 are often long term. Harvested species may show a significant lag in response (e.g. Beukers-  
484 Stewart et al. 2005), but benthic prey may also show many years to respond to enhanced  
485 predation. For example sea urchins can take many years to respond to changes in predator  
486 numbers, (e.g. 13 years in New Zealand, 7 years, in Tasmania, 15 years in Kenya; see  
487 Babcock et al. 2010 and references therein). Thus indirect effects on organisms that occur  
488 through cascading trophic interactions can take substantially longer to develop than direct  
489 effects (Babcock et al. 2010). This observation may explain why species assemblages in

490 older reserves often differ from recently created reserves (Micheli et al. 2004) and could lead  
491 to failure to identify trophic cascades owing to a lack of sufficient temporal scale (Shears &  
492 Babcock 2003).

493 The large scale, uncontrolled nature of MPA experiments can lead to considerable insight into  
494 the nature of the relationship between environmental and biotic drivers of community state  
495 when observations are conducted over sufficient time scale (Babcock et al. 2010, Fraschetti et  
496 al. 2013). Fraschetti et al. (2013, p.11) consider a long term approach is essential because  
497 *'ecological components may respond differently and over varying temporal scales'*. They  
498 used a nine year series of observations inside and outside an MPA in SE Italy to examine the  
499 role of protection in determining temporal and spatial variability. They showed that protected  
500 assemblages, with relatively long lived invertebrates and macroalgae, displayed spatial and  
501 temporal homogeneity in marked contrast to a mosaic of changing disturbed patches outside  
502 the MPA. Thus, at a local scale, protection enhanced community stability. However, there  
503 were also a number of idiosyncratic results, where the effects of protection did not match  
504 expectations. Here, it is likely that multiple processes, some derived from variation in  
505 environmental context, were acting simultaneously. Similarly Shears and Babcock (2003)  
506 demonstrated long term effects (25 years) of protection in a trophic cascade in the Leigh  
507 marine reserve in New Zealand mediated through the decline of urchins. However, urchin  
508 decline was also observed over the short term (possibly as a consequence of disease) at some  
509 unprotected sites.

510 Studies of the effect of protection from human disturbance are often made at a single point in  
511 time through comparison of protected and unprotected sites, often many years after  
512 establishment of the protection regime. Although suffering from difficulties in firmly  
513 ascribing observed spatial differences to protection effects (Underwood 1991), these studies  
514 are logistically relatively easy to implement and can (limitations accepted) give important  
515 long term insight. For example Mumby et al. (2006) sampled fish and benthic assemblages of  
516 Caribbean reef systems 18 years after implementation of a fishing ban. A net doubling of  
517 grazing pressure from parrot fishes in protected areas led to a four-fold reduction in  
518 macroalgal cover (Mumby et al. 2006) and consequently a two fold increase in coral  
519 recruitment (Mumby et al. 2007). Clearly such observations tell us nothing of the rate of  
520 change in fish or benthic assemblages, nor the temporal dynamic between interacting species,  
521 but does demonstrate the strong top down control exerted by key fish consumers in supporting  
522 the health of Caribbean coral reefs. As a note of caution to accepting conclusions based on

523 such an approach, a review of six time series studies showed that increases in target species  
524 following protection were not always as high as expected on the basis of studies with no  
525 temporal replication (Babcock et al. 2010). Thus, understanding how communities change  
526 through time following protection is likely to lead to a far greater mechanistic understanding  
527 of protection effects.

528

## 529 **Conclusions**

530 It is clear from our review of experimental duration over 33 years, that the majority of  
531 manipulative experiments in benthic systems, examining community or population responses  
532 of macro-organisms, are reasonably short (two years or less). It is also clear, from reviewing  
533 a range of experiments operating over a longer time scale, that a long term approach can yield  
534 considerable insight, and in many cases alter conclusions based on the same experiments  
535 conducted over shorter time scales. Thus we argue that although many short studies will be  
536 perfectly valid, in general, increasing the period over which observations are made following  
537 experimental manipulations will yield important benefits.

538 Limitations on the temporal extent of marine benthic experiments are numerous, and range  
539 from the logistical to considerations of motive and reward. Raffaelli and Moller (2000)  
540 showed through interviews of experimentalists that decisions regarding duration of field  
541 experiments were predominantly pragmatic. Temporal scale was often based on the time  
542 available in a studentship, or grant, or the difficulties of maintaining the experiment in a  
543 hostile environment. However, there are a number of simple, practical approaches that can be  
544 implemented to lengthen experimental duration. First and foremost when planning  
545 manipulative field experiments Diaz et al. (2003) stress the need for foresight and the  
546 acquisition of long-term funding where possible. However, extending sampling regimes may  
547 not necessarily be costly. A common approach where the temporal scale has been extended is  
548 to sample at regular intervals over the first year or so of an experiment and then sample at  
549 much lower frequencies over a number of years (e.g. Jenkins et al. 2004, Viejo 2009).  
550 Extending an experiment over multiple years generally requires some foresight in  
551 experimental establishment (e.g. use of secure, non corrosive, preferably stainless steel,  
552 markers and a mapping system of spatial replicates which can be utilised by persons other  
553 than the original experimenter), plus the motivation to revisit experimental sites over multiple

554 years. This can be achieved long after the original experimenter (e.g. student, post-doctoral  
555 scientist) has moved on to new pastures.

556

557 In promoting a longer term approach to experimentation it is reasonable to consider the role  
558 of reviewers and editors. Working over an appropriate temporal scale to address the question  
559 posed is an integral part of experimental design and hence should be considered as an issue  
560 ranking in importance alongside appropriate replication and independence of sampling units.  
561 Whether it currently is, or not, is debatable. That may be because the question is much less  
562 tangible. It is always likely that extending an experiment will give additional insight but the  
563 cost-benefit relationship of extended monitoring for potentially marginal gains is probably  
564 complex and difficult to pin down. However, it is clear from the review of long term studies  
565 above, that an increased mechanistic understanding of marine ecological processes can be  
566 gained from a longer term approach and understanding the longer-term consequences of  
567 impacts on benthic systems is a crucial part of determining management options in the face of  
568 global change.

569

## 570 **Acknowledgements**

571 This work was supported by a Brazilian FAPESP Visiting Researcher grant to the first author.  
572 Facilities were kindly supplied by the Departamento de Ciências do Mar, Universidade  
573 Federal de São Paulo - Campus Baixada Santista, Brazil. The manuscript was much  
574 improved by the comments of five anonymous reviewers.

575

576

## 577 **References**

- 578 Åberg P (1992) Size based demography of the seaweed *Ascophyllum nodosum* in stochastic  
579 environments. *Ecology* 73:1488-1501
- 580 Åberg P, Pavia H (1997) Temporal and multiple scale variation in juvenile and adult  
581 abundance of the brown alga *Ascophyllum nodosum*. *Mar Ecol Prog Ser* 158:111-119
- 582 Araújo RM, Sousa-Pinto I, Serrão EA, Åberg P (2012) Recovery after trampling disturbance  
583 in a canopy-forming seaweed population. *Mar Biol* 159:697–707

- 584 Babcock RC, Shears NT, Alcala AC, Barrett NS, Edgar GJ, Lafferty KD, McClanahan TR,  
585 Russ GR (2010) Decadal trends in marine reserves reveal differential rates of change  
586 in direct and indirect effects. *Proc Natl Acad Sci USA* 107:18256-18261
- 587 Barnes DKA (1996) Low levels of colonisation in Antarctica: the role of bryozoans in early  
588 community development. In: Gordon D, Smith A, Grant-Mackie A (eds) *Bryozoans in*  
589 *space and time*. National Institute of Water & Atmospheric Research Ltd. Wellington,  
590 p 19–28
- 591 Benedetti-Cecchi L (2003) The importance of the variance around the mean effect size of  
592 ecological processes. *Ecology* 84:2335-2346
- 593 Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends Ecol Evol*  
594 9:191-193
- 595 Bertness MD, Trussell GC, Ewanchuk PJ, Silliman BR (2002) Do alternate stable community  
596 states exist in the Gulf of Maine rocky intertidal zone? *Ecology* 83:3434-3448
- 597 Beuchel F, Gulliksen B (2008) Temporal patterns of benthic community development in an  
598 Arctic fjord (Kongsfjorden, Svalbard): results of a 24-year manipulation study. *Polar*  
599 *Biology* 31:913-924
- 600 Beukers-Stewart BD, Vause BJ, Mosley MWJ, Rossetti HL, Brand AR (2005) Benefits of  
601 closed area protection for a population of scallops. *Mar Ecol Prog Ser* 298:189–204,
- 602 Broitman BR, Navarrete SA, Smith F, Gaines SD (2001) Geographic variation of  
603 southeastern Pacific intertidal communities. *Mar Ecol Prog Ser* 224:21-34
- 604 Carroll ML, Highsmith RC (1996) Role of catastrophic disturbance in mediating *Nucella-*  
605 *Mytilus* interactions in the Alaskan rocky intertidal. *Mar Ecol Prog Ser* 138:125-133
- 606 Castilla JC (1988) Earthquake-caused coastal uplift and its effects on rocky intertidal kelp  
607 communities. *Science* 242:440–443
- 608 Castilla JC (1999) Coastal marine communities: trends and perspectives from human-  
609 exclusion experiments. *Trends Ecol Evol* 14:280-283
- 610 Castilla JC (2000) Roles of experimental marine ecology in coastal management and  
611 conservation. *J Exp Mar Biol Ecol* 250:3-21
- 612 Castilla JC, Bustamante R (1989) Human exclusion from rocky intertidal of Las-Cruces,  
613 central Chile - effects on *Durvillaea-antarctica* (Phaeophyta, durvilleales). *Mar Ecol*  
614 *Prog Ser* 50:203-214
- 615 Cervin G, Aberg P, Jenkins SR (2005) Small-scale disturbance in a stable canopy dominated  
616 community: implications for macroalgal recruitment and growth. *Mar Ecol Prog Ser*  
617 305:31-40
- 618 Chapman MG (2013) Constructing replacement habitat for specialist and generalist molluscs-  
619 the effect of patch size. *Mar Ecol Prog Ser* 473:201-214
- 620 Coleman RA, Underwood AJ, Benedetti-Cecchi L, Aberg P, Arenas F, Arrontes J, Castro J,  
621 Hartnoll RG, Jenkins SR, Paula J, Della Santina P, Hawkins SJ (2006) A continental  
622 scale evaluation of the role of limpet grazing on rocky shores. *Oecologia* 147:556-564
- 623 Connell JH (1961) The influence of interspecific competition and other factors on the  
624 distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710-723
- 625 Connell JH (1972). Community interactions on marine rocky intertidal shores. *Annu Rev Ecol*  
626 *Syst* 3: 169-192
- 627 Connell JH, Slayter RO (1977) Mechanisms of succession in natural communities and their  
628 role in community stability and organization. *Am Nat* 111:1119-1144

- 629 Connell JH, Sousa WP (1983) On the evidence needed to judge ecological stability or  
630 persistence *Am Nat* 121:789-824
- 631 Connell SD (2005) Assembly and maintenance of subtidal habitat heterogeneity: synergistic  
632 effects of light penetration and sedimentation. *Mar Ecol Prog Ser* 289:53-61
- 633 Connell SD, Foster MS, Airoidi L (2014) What are algal turfs? Toward a better  
634 understanding of turfs. *Mar Ecol Prog Ser* 495:299-307
- 635 Connolly SR, Roughgarden J (1998) A latitudinal gradient in northeast Pacific intertidal  
636 community structure: Evidence for an oceanographically based synthesis of marine  
637 community theory. *Am Nat* 151:311-326
- 638 Crowe TP, Bracken MES, O'Connor NE (2012) Reality check: issues of scale and abstraction  
639 in biodiversity research and potential solutions. In: Solan M, Aspden R, Paterson D  
640 (eds) *Marine biodiversity and ecosystem functioning: frameworks, methodologies and  
641 integration*. Oxford University Press Oxford
- 642 Davis AR, Ward DW (2009) Establishment and persistence of species-rich patches in a  
643 species-poor landscape: role of a structure-forming sub-tidal barnacle. *Mar Ecol Prog  
644 Ser* 380:187-198
- 645 Dayton PK (1975) Experimental evaluation of ecological dominance in a rocky intertidal  
646 algal community. *Ecol Monogr* 45:137-159
- 647 Dayton PK (1989) Inter-decadal variation in an Antarctic sponge and its predators from  
648 oceanographic climate shifts. *Science* 245:1484–1486
- 649 Dayton PK, Oliver JS (1977) Antarctic soft-bottom benthos in oligotrophic and eutrophic  
650 environments. *Science* 197:55–58
- 651 Diaz S, Symstad AJ, Chapin FS, Wardle DA, Huenneke LF (2003) Functional diversity  
652 revealed by removal experiments. *Trends Ecol Evol* 18:140-146
- 653 Duffy JE, Stachowicz JJ, Bruno JF (2012) Multi-trophic biodiversity and the responses of  
654 marine ecosystems to global change In: Solan M, Aspden R, Paterson D (eds) *Marine  
655 biodiversity and ecosystem functioning: frameworks, methodologies and integration*.  
656 Oxford University Press, Oxford
- 657 Duran LR, Castilla JC (1989) Variation and persistence of the middle rocky intertidal  
658 community of central Chile, with and without human harvesting. *Mar Biol* 103:555-  
659 562
- 660 Dye AH (1998) Community-level analyses of long-term changes in rocky littoral fauna from  
661 South Africa. *Mar Ecol Prog Ser* 164:47-57
- 662 Ellis J, Schneider DC (2008) Spatial and temporal scaling in benthic ecology. *J Exp Mar Biol  
663 Ecol* 366:92-98
- 664 Farrell TM (1988) Community stability: effects of limpet removal and reintroduction in a  
665 rocky intertidal community. *Oecologia* 75:190-197
- 666 Feldman KL, Armstrong DA, Eggleston DB, Dumbauld BR (1997) Effects of substrate  
667 selection and post-settlement survival on recruitment success of the thalassinidean  
668 shrimp *Neotrypaea californiensis* to inter-tidal shell and mud habitats. *Mar Ecol Prog  
669 Ser* 150:121-136
- 670 Fraschetti S, Guarnieri G, Bevilacqua S, Terlizzi A, Boero F (2013) Protection enhances  
671 community and habitat stability: evidence from a Mediterranean marine protected  
672 area. *Plos ONE* 8(12): e81838. doi:10.1371/journal.pone.0081838
- 673 Goodsell PJ, Connell SD (2005) Historical configuration of habitat influences the effects of  
674 disturbance on mobile invertebrates. *Mar Ecol Prog Ser* 299:79-87

- 675 Grant DL, Clarke PJ, Allaway WG (1993) The response of grey mangrove (*Avicennia marina*  
676 (Forsk.) Vierh.) seedlings to spills of crude oil. *J Exp Mar Biol Ecol* 171: 273-295.
- 677 Green DS, Crowe TP (2013) Physical and biological effects of introduced oysters on  
678 biodiversity in an intertidal boulder field. *Mar Ecol Prog Ser* 482:119-132
- 679 Holmes NJ, Harriott VJ, Banks SA (1997) Latitudinal variation in patterns of colonisation of  
680 cryptic calcareous marine organisms. *Mar Ecol Prog Ser* 155:103-113
- 681 Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM,  
682 Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA  
683 (2005) Effects of biodiversity on ecosystem functioning: A consensus of current  
684 knowledge. *Ecol Monogr* 75:3-35
- 685 Hoskin MG, Coleman RA, von Carlshausen E, Davis CM (2011) Variable population  
686 responses by large decapod crustaceans to the establishment of a temperate marine no-  
687 take zone. *Can J Fish Aquat Sci* 68:185-200
- 688 Hughes TP Community structure and diversity of coral reefs: the role of history. *Ecology* 70:  
689 275-279
- 690 Hughes RG, Fletcher PW, Hardy MJ (2009) Successional development of saltmarsh in two  
691 managed realignment areas in SE England, and prospects for saltmarsh restoration.  
692 *Mar Ecol Prog Ser* 384:13-22
- 693 Incera M, Bertocci I, Benedetti-Cecchi L (2010) Effects of mean intensity and temporal  
694 variability of disturbance on the invasion of *Caulerpa racemosa* var. *cylindracea*  
695 (*Caulerpales*) in rock pools. *Biol Inv* 12:501-514
- 696 Incera M, Olabarria C, Troncoso JS, Lopez J (2009) Response of the invader *Sargassum*  
697 *muticum* to variability in nutrient supply. *Mar Ecol Prog Ser* 377:91-101
- 698 Ingolfsson A, Hawkins SJ (2008) Slow recovery from disturbance: a 20 year study of  
699 *Ascophyllum* canopy clearances. *J Mar Biol Assoc UK* 88:689-691
- 700 Jacobs R (1980) Effects of the Amoco-Cadiz oil-spill on the seagrass community at Roscoff  
701 with special reference to the benthic infauna. *Mar Ecol Prog Ser* 2:207-212
- 702 Jenkins SR (2009) Settlement and recruitment In: M W (ed) *Marine Hard Bottom*  
703 *Communities: Patterns, Dynamics, Diversity and Change*. Springer, Verlag
- 704 Jenkins SR, Arenas F, Arrontes J, Bussell J, Castro J, Coleman RA, Hawkins SJ, Kay S,  
705 Martinez B, Oliveros J, Roberts MF, Sousa S, Thompson RC, Hartnoll RG (2001)  
706 European-scale analysis of seasonal variability in limpet grazing activity and  
707 microalgal abundance. *Mar Ecol Prog Ser* 211:193-203
- 708 Jenkins SR, Coleman RA, Della Santina P, Hawkins SJ, Burrows MT, Hartnoll RG (2005)  
709 Regional scale differences in the determinism of grazing effects in the rocky intertidal.  
710 *Mar Ecol Prog Ser* 287:77-86
- 711 Jenkins SR, Hawkins SJ, Norton TA (1999a) Direct and indirect effects of a macroalgal  
712 canopy and limpet grazing in structuring a sheltered inter-tidal community. *Mar Ecol*  
713 *Prog Ser* 188:81-92
- 714 Jenkins SR, Norton TA, Hawkins SJ (1999b) Interactions between canopy forming algae in  
715 the eulittoral zone of sheltered rocky shores on the Isle of Man. *J Mar Biol Assoc UK*  
716 79:341-349
- 717 Jenkins SR, Norton TA, Hawkins SJ (2004) Long term effects of *Ascophyllum nodosum*  
718 canopy removal on mid shore community structure. *J Mar Biol Assoc UK* 84:327-329
- 719 Jewett EB, Hines AH, Ruiz GM (2005) Epifaunal disturbance by periodic low levels of  
720 dissolved oxygen: native vs. invasive species response. *Mar Ecol Prog Ser* 304:31-44

- 721 Kaehler S, Williams GA (1997) Do factors influencing recruitment ultimately determine the  
722 distribution and abundance of encrusting algae on seasonal tropical shores? *Mar Ecol*  
723 *Prog Ser* 156:87-96
- 724 Keough MJ, Downes BJ (1982) Recruitment of marine-invertebrates - the role of active larval  
725 choices and early mortality. *Oecologia* 54:348-352
- 726 Kilar JA, McLachlan J (1989) Effects of wave exposure on the community structure of a  
727 plant-dominated, fringing-reef platform - intermediate disturbance and disturbance-  
728 mediated competition. *Mar Ecol Prog Ser* 54:265-276
- 729 Konar B (2007) Recolonization of a high latitude hard-bottom nearshore community. *Polar*  
730 *Biology* 30:663-667
- 731 Leonard GH (1999) Positive and negative effects of intertidal algal canopies on recruitment  
732 and survival of barnacles. *Mar Ecol Prog Ser* 178:241-249
- 733 Levin S (1992) The problem of pattern and scale in ecology. *Ecology* 72:1943-1967
- 734 Levitan DR (1988) Algal-urchin biomass responses following mass mortality of *Diadema*  
735 *antillarum* Philippi at Saint John, U.S. Virgin Islands. *J Exp Mar Biol Ecol*  
736 119:167-178
- 737 Lewontin RC (1969) The meaning of stability. In: Woodwell G, Smith H (eds) *Diversity and*  
738 *stability in ecological systems*. Brookhaven National Laboratory, Upton, NY., p 12-24
- 739 Linares C, Coma R, Diaz D, Zabala M, Hereu B, Dantart L (2005) Immediate and delayed  
740 effects of a mass mortality event on gorgonian population dynamics and benthic  
741 community structure in the NW Mediterranean Sea. *Mar Ecol Prog Ser* 305:127-137
- 742 Lindegarth M, Aberg P, Cervin G, Nilsson PG (2001) Effects of grazing on the structure of  
743 mid-shore, inter-tidal assemblages on moderately exposed rocky shores of the  
744 Swedish west coast. *Mar Ecol Prog Ser* 212:29-38
- 745 Lubchenco J, Menge BA (1978) Community development and persistence in a low rocky  
746 intertidal zone. *Ecol Monogr* 48:67-94
- 747 Maggi E, Bertocci I, Vaselli S, Benedetti-Cecchi L (2009) Effects of changes in number,  
748 identity and abundance of habitat-forming species on assemblages of rocky seashores.  
749 *Mar Ecol Prog Ser* 381:39-49
- 750 Maggi E, Bulleri F, Bertocci I, Benedetti-Cecchi L (2012) Competitive ability of macroalgal  
751 canopies overwhelms the effects of variable regimes of disturbance. *Mar Ecol Prog*  
752 *Ser* 465:99-109
- 753 McCook, LJ Chapman ARO (1991) Community succession following massive ice scour on  
754 an exposed rocky shore : effects of *Fucus* canopy algae and of mussels during late  
755 succession. *J Exp Mar Biol Ecol* 154:137-169
- 756 McCook LJ, Chapman ARO (1992) Vegetative regeneration of *Fucus* rockweed canopy as a  
757 mechanism of secondary succession on an exposed rocky shore. *Bot Mar* 35:35-
- 758 McCook LJ, Chapman ARO (1997) Patterns and variations in natural succession following  
759 massive ice-scour of a rocky intertidal seashore. *J Exp Mar Biol Ecol* 214:121-147
- 760 Menge BA (1997) Detection of direct versus indirect effects: Were experiments long enough?  
761 *Am Nat* 149:801-823
- 762 Menge BA, Daley BA, Wheeler PA, Dahlhoff E, Sanford E, Strub PT (1997) Benthic-pelagic  
763 links and rocky intertidal communities: Bottom-up effects on top-down control? *Proc*  
764 *Natl Acad Sci USA* 94:14530-14535
- 765 Menge BA, Lubchenco J, Bracken MES, Chan F, Foley MM, Freidenburg TL, Gaines SD,  
766 Hudson G, Krenz C, Leslie H, Menge DNL, Russell R, Webster MS (2003) Coastal



767 oceanography sets the pace of rocky intertidal community dynamics. *Proc Natl Acad*  
768 *Sci USA* 100:12229-12234

769 Menge BA, Sanford E, Daley BA, Freidenburg TL, Hudson G, Lubchenco J (2002) Inter-  
770 hemispheric comparison of bottom-up effects on community structure: Insights  
771 revealed using the comparative-experimental approach. *Ecol Res* 17:1-16

772 Menge BA, Sutherland JP (1976) Species diversity gradients: synthesis of the roles of  
773 predation, competition and temporal heterogeneity. *Am Nat* 110:351-369

774 Menge BA, Sutherland JP (1987) Community regulation: Variation in disturbance,  
775 competition and predation in relation to environmental stress and recruitment. *Am Nat*  
776 130:730-757

777 Methratta ET, Petraitis PS (2008) Propagation of scale-dependent effects from recruits to  
778 adults in barnacles and seaweeds. *Ecology* 89:3128-3137

779 Micheli F, Halpern BS, Botsford LW, Warner RR (2004) Trajectories and correlates of  
780 community change in no-take marine reserves. *Ecol Appl* 14:1709–1723

781 Miller MW, Valdivia A, Kramer KL, Mason B, Williams DE, Johnston L (2009) Alternate  
782 benthic assemblages on reef restoration structures and cascading effects on coral  
783 settlement. *Mar Ecol Prog Ser* 387:147-156

784 Minchinton TE, Fels KJ (2013) Sediment disturbance associated with trampling by humans  
785 alters species assemblages on a rocky intertidal seashore. *Mar Ecol Prog Ser* 472:129-  
786 140

787 Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE,  
788 Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB (2006)  
789 Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98-  
790 101

791 Mumby PJ, Harborne AR, Williams J, Kappel CV, Brumbaugh DR, Micheli F, Holmes KE,  
792 Dahlgren CP, Paris CB, Blackwell PG (2007) Trophic cascade facilitates coral  
793 recruitment in a marine reserve. *Proc Natl Acad Sci USA* 104:8362-8367

794 Naeem S (2008) Advancing realism in biodiversity research. *Trends in Ecology and*  
795 *Evolution* 23:414-416

796 Nelson WG (1981) Experimental studies of decapod and fish predation on seagrass  
797 macrobenthos. *Mar Ecol Prog Ser* 5:141-149

798 O'Connor NE, Crowe TP (2005) Biodiversity loss and ecosystem functioning: Distinguishing  
799 between number and identity of species. *Ecology* 86:1783-1796

800 Oliveira JP, Sousa-Pinto I, Weber GM, Bertocci I (2014) Interplay of experimental harvesting  
801 and climate-related disturbance on benthic assemblages of rocky seashores. *Mar Ecol*  
802 *Prog Ser* 495:131-142

803 Paine RT (1966) Food web complexity and species diversity. *Am Nat* 100:65-75

804 Paine, R. (1977). Controlled manipulations in the marine intertidal zone and their  
805 contributions to ecological theory. In: Goulden CE (ed) *Changing scenes in natural*  
806 *sciences 1776-1976*. Academy of Natural Sciences, Philadelphia, PA, 245-270.

807 Paine RT (1994) Marine rocky shores and community ecology: an experimentalist's  
808 perspective. In: Kinne O. (ed.) *Excellence in Ecology 4*. Ecology Institute, D-21385  
809 Oldendorf/Luhe, Germany

810 Paine RT, Castillo JC, Cancino J (1985) Perturbation and recovery patterns of starfish-  
811 dominated intertidal assemblages in Chile, New Zealand, and Washington State. *Am*  
812 *Nat* 125:679-691

- 813 Peterson CH (1984) Does a rigorous criterion for environmental identity preclude the  
814 existence of multiple stable points? *Am Nat* 124:127-133
- 815 Petraitis PS, Dudgeon SR (2004) Detection of alternative stable states in marine communities.  
816 *J Exp Mar Biol Ecol* 300:343- 371
- 817 Petraitis PS, Dudgeon SR (2005) Divergent succession and implications for alternative states  
818 on rocky intertidal shores. *J Exp Mar Biol Ecol* 326:14 – 26
- 819 Petraitis PS, Latham RE (1999) The importance of scale in testing the origins of alternative  
820 community states. *Ecology* 80: 429 - 442
- 821 Petraitis PS, Methratta ET, Rhile EC, Vidargas NA, Dudgeon SR (2009) Experimental  
822 confirmation of multiple community states in a marine ecosystem. *Oecologia* 161:139-  
823 148
- 824 Raffaelli DG (2006) Biodiversity and ecosystem functioning: issues of scale and trophic  
825 complexity. *Mar Ecol Prog Ser* 311:285-294
- 826 Raffaelli DG, Hawkins SJ (1996) *Intertidal ecology*. Chapman and Hall, London
- 827 Raffaelli DG, Moller H (2000) Manipulative experiments in animal ecology-Do they promise  
828 more than they can deliver? *Adv Ecol Res* 30:299-330
- 829 Reinhardt JF, Whitlatch RB, Osman RW (2013) Effects of temperature on the recruitment  
830 phenology and niche overlap of shallow epifaunal assemblages in southern New  
831 England. *Mar Ecol Prog Ser* 489:61-74
- 832 Ruiz JM, Romero J (2001) Effects of in situ experimental shading on the Mediterranean  
833 seagrass *Posidonia oceanica*. *Mar Ecol Prog Ser* 215:107-120
- 834 Russell BD, Connell SD (2005) A novel interaction between nutrients and grazers alters  
835 relative dominance of marine habitats. *Mar Ecol Prog Ser* 289:5-11
- 836 Sanford E (1999) Regulation of keystone predation by small changes in ocean temperature.  
837 *Science* 283:2095-2097
- 838 Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in  
839 ecosystems. *Nature* 413:591 - 596
- 840 Schiel DR, Lilley SA (2011) Impacts and negative feedbacks in community recovery over  
841 eight years following removal of habitat-forming macroalgae. *J Exp Mar Biol Ecol*  
842 407:108-115
- 843 Schneider DC (2001) The rise of the concept of scale in ecology. *Bioscience* 51:545-553
- 844 Sciberras M, Jenkins SR, Kaiser MJ, Hawkins SJ, Pullin AS (2015) Evaluating the relative  
845 conservation value of partially and fully protected marine reserves. *Fish and Fisheries*  
846 16: 58–77
- 847 Shears NT, Babcock RC (2003) Continuing trophic cascade effects after 25 years of no take  
848 marine reserve protection. *Mar Ecol Prog Ser* 246:1-16
- 849 Simenstad CA, Estes JA, Kenyon KW (1978) Aleuts, sea otters, and alternate stable state  
850 communities. *Science* 200:403-411
- 851 Southward AJ, Southward EC (1978) Recolonization of rocky shores in Cornwall after use of  
852 toxic dispersants to clean up the Torrey Canyon spill. *J Fish Res Board Can* 35:682-  
853 706
- 854 Spivak AC, Canuel EA, Duffy JE, Douglass JG, Richardson JP (2009) Epifaunal community  
855 composition and nutrient addition alter sediment organic matter composition in a  
856 natural eelgrass *Zostera marina* bed: a field experiment. *Mar Ecol Prog Ser* 376:55-67

- 857 Stachowicz JJ, Bracken MES, Graham M (2008b) Complementarity in marine biodiversity  
858 manipulations: reconciling divergent evidence from field and mesocosm experiments.  
859 Proc Natl Acad Sci 105:18842-18847
- 860 Stachowicz JJ, Graham M, Bracken MES, Szoboszlai AI (2008a) Diversity enhances cover  
861 and stability of seaweed assemblages: the role of heterogeneity and time. Ecology  
862 89:3008–3019
- 863 Sutherland JP (1990) Perturbations, resistance and alternative views of the existence of  
864 multiple stable points in nature. Am Nat 136:270-275
- 865 Sutherland JP, Karlson RH (1977) Development and stability of fouling community at  
866 Beaufort, North-Carolina. Ecol Monogr 47:425-446
- 867 Tait LW, Schiel DR (2011) Legacy effects of canopy disturbance on ecosystem functioning in  
868 macroalgal assemblages. PloS ONE DOI: 10.1371/journal.pone.0026986
- 869 Tegner MJ, Dayton PK, Edwards PB, Riser KL (1997) Large-scale, low-frequency  
870 oceanographic effects on kelp forest succession: A tale of two cohorts. Mar Ecol Prog  
871 Ser 146:117-134
- 872 Underwood AJ (1991) Beyond BACI: Experimental designs for detecting human  
873 environmental impacts on temporal variations in natural populations. Aust J Mar  
874 Freshwat Res 42:569-587
- 875 Underwood AJ (1998) Grazing and disturbance: an experimental analysis of patchiness in  
876 recovery from a severe storm by the intertidal alga *Hormosira banksii* on rocky shores  
877 in New South Wales. J Exp Mar Biol Ecol 231:291-306
- 878 Underwood AJ (2000) Experimental ecology of rocky intertidal habitats: what are we  
879 learning? J Exp Mar Biol Ecol 250:51-76
- 880 Valdivia N, Heidemann A, Thiel M, Molis M, Wahl M (2005) Effects of disturbance on the  
881 diversity of hard-bottom macrobenthic communities on the coast of Chile. Mar Ecol  
882 Prog Ser 299:45-54
- 883 Van De Koppel J, Herman PMJ, Thoolen P, Heip CHR (2001) Do alternate stable states occur  
884 in natural ecosystems? Evidence from a tidal flat. Ecology 82:3449 - 3461
- 885 Viejo RM (2009) Resilience in intertidal rocky shore assemblages across the stress gradient  
886 created by emersion times. Mar Ecol Prog Ser 390:55-65
- 887 Wiens JA (1989) Spatial scaling in ecology Func Ecol 3:385-397
- 888 Yodzis P (1988) The indeterminacy of ecological interactions as perceived through  
889 perturbation experiments Ecology 69:508-515

890

891

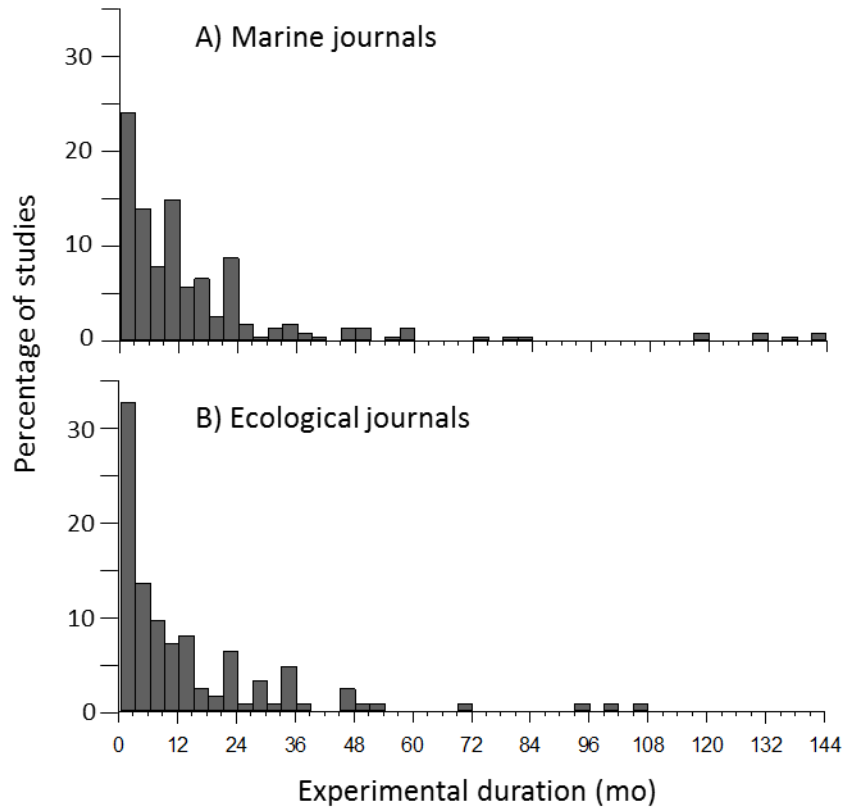
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899 Figure 1 Frequency histogram indicating the distribution of experimental study duration in  
900 (A) marine journals and (B) ecological journals over the period 1980 to 2013.

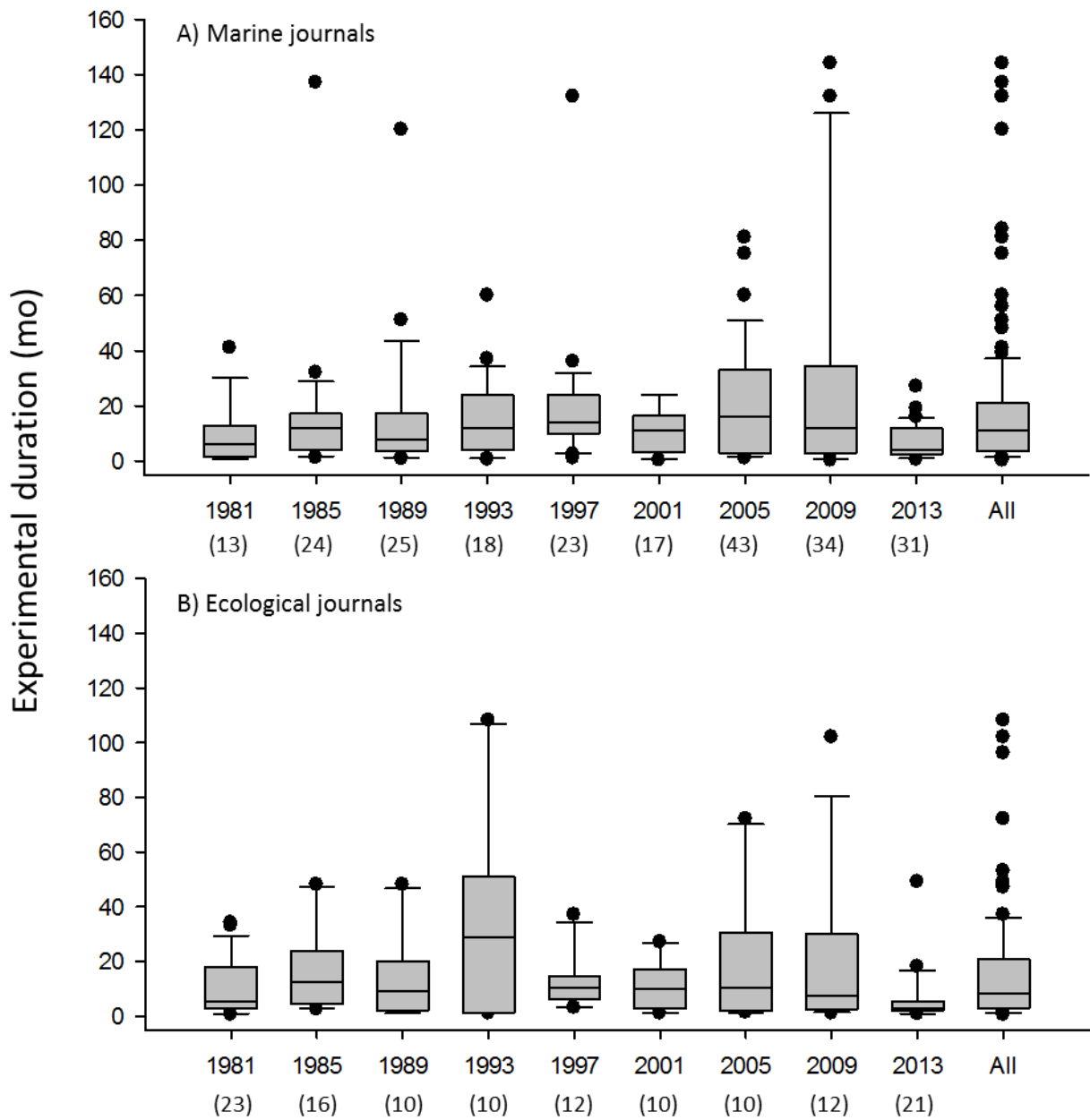
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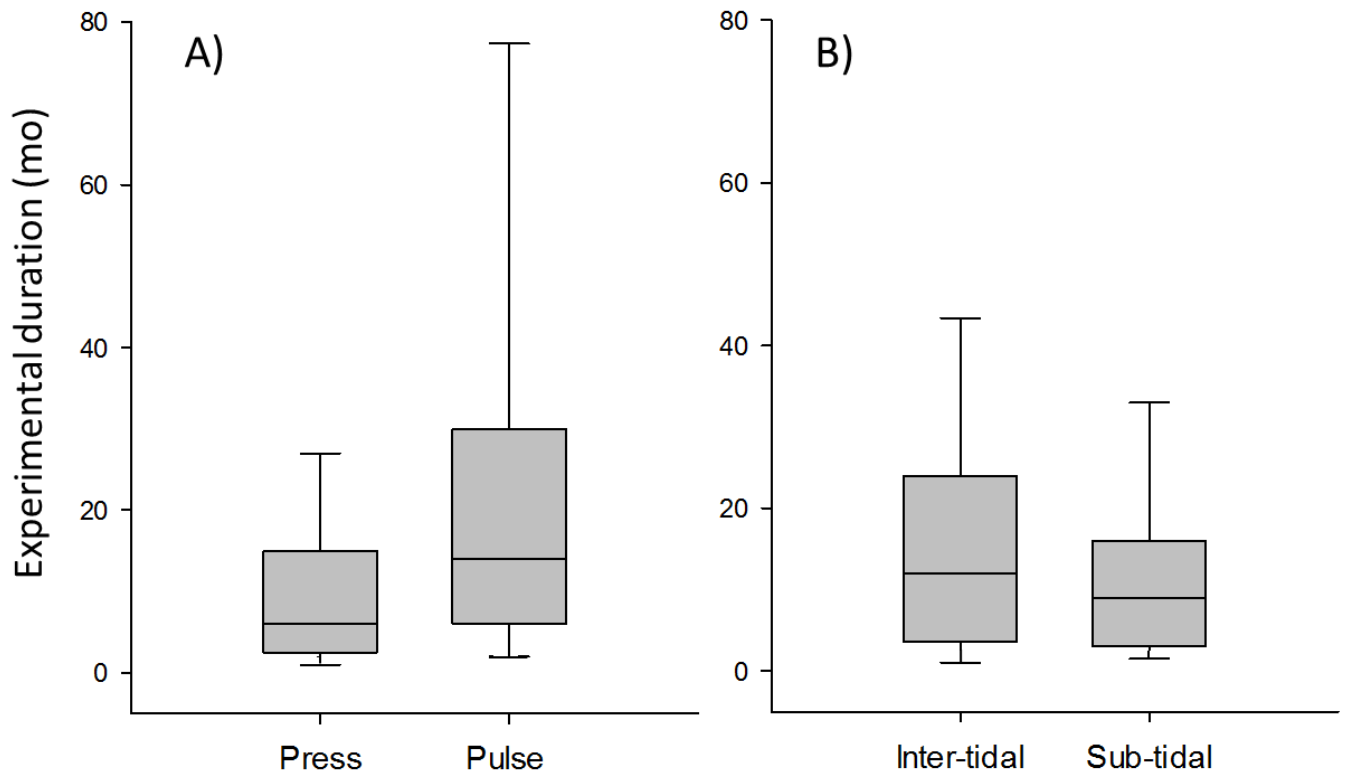


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908 Figure 2 Box plot showing the duration of manipulative experiments over the nine periods  
 909 examined and for all periods combined in (A) marine journals and (B) ecological journals.  
 910 Boxes indicate the median (horizontal line) and the 25<sup>th</sup> and 75<sup>th</sup> percentiles; whiskers indicate  
 911 the 10<sup>th</sup> and 90<sup>th</sup> percentile and black dots the outliers. Number of independent experiments  
 912 included in the analysis indicated in brackets beneath each year.

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916 Figure 3 Box plots showing median study duration (and 10<sup>th</sup>, 25<sup>th</sup>, 75<sup>th</sup> and 90<sup>th</sup> percentiles)  
 917 for comparisons among A) press (n=219) and pulse (n=133) studies and B) intertidal (n= 175)  
 918 and sub-tidal (n=177) studies

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