REVIEW

Temporal scale of field experiments in benthic ecology

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

KEY WORDS: Field experiments · Long term · Perturbation · Scaling up · Temporal scale

INTRODUCTION

Our understanding of ecological processes in the marine benthic environment has been built on a foundation of manipulative experiments over the past half century or so in a range of intertidal and shallow subtidal systems. Both soft and hard substrata habitats have been utilised by experimental ecologists intent on understanding the processes structuring marine assemblages and hence explaining patterns in abundance, distribution and diversity of species (see Raffaelli & Hawkins 1996 for a review). Marine ecological experiments have also contributed

to important advances in ecological theory (e.g. Connell 1961, Paine 1966, Dayton 1975, Menge & Sutherland 1976, Bertness & Callaway 1994). The intertidal zone is favoured by experimental ecologists owing to the logistical ease of working on marine communities when the tide is out, combined with a sharp marine/ terrestrial environmental gradient which is conducive to investigations of the interaction of physical and biological processes. Additionally, the intertidal is inhabited by organisms which are generally small and sessile/slow moving and hence amenable to experimental manipulation (Connell 1972, Paine 1977, Underwood 2000), and in the case of hard substrate,

the environment is 2-dimensional in nature. Subtidal work is more challenging, but there is still a vast body of experimental research undertaken in this environment, either through the use of SCUBA or by suspending experiments from floating or fixed structures. Focal habitats for experimental research in the coastal zone include coral reefs, seagrass beds, subtidal rocky reefs, intertidal rocky shores, mudflats and beaches and subtidal soft-sediment systems.

The development of experimental ecology in marine systems and the advances made over the past 50 yr or so are well documented (see Paine 1994, Castilla 2000, Underwood 2000 for reviews). One area which has received increasing attention, in marine as well as terrestrial and freshwater habitats, is the issue of scale (Wiens 1989, Levin 1992, Schneider 2001, Ellis & Schneider 2008). Schneider (2001) neatly summarised 3 components for the problem of scale: problems in ecology often exist at decadal time scales over large ecosystems; most variables can only be measured in small areas over short time scales; and patterns and processes observed at small scales do not necessarily hold at large scales. It is increasingly recognised that environmental drivers and ecological processes operate over a range of different spatial and temporal scales, and over the past 2 decades, scale, in a quantitative sense, has been increasingly incorporated into experimental work (Ellis & Schneider 2008).

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

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

Consideration of temporal scale also clearly needs to take account of the duration of any particular manipulative experiment. Underwood (2000), based on the assertion of Connell & Sousa (1983) that studies should encompass a period as long as the turnover of individuals in resident species, suggests that on Australian rocky shores, a period of between 5 and 7 yr might be appropriate but also considers that studies may need to be much longer to allow analyses of equilibria. Yodzis (1988) considered that for the impact of a press perturbation to be known, a long-term approach is required. He recommended adopting a rule of thumb such that the time scale of observation should approximate 2 times the sum of the generation times of a pressed species (i.e. one whose density has been modified) and the potentially impacted species of interest. It is debatable whether all experiments require such duration, and clearly there are specific questions which can be addressed by much shorter studies. For example, by determining the relationship between duration of experiment and the importance of indirect effects using 23 rocky intertidal interaction webs, Menge (1997) tested the assertion that indirect effects may take longer to become apparent following a manipulation than direct effects. He concluded that in the case studies examined, which ranged in length from 0.5 to 156 mo, 'interpretations of community dynamics are not likely to be distorted because experiments were

too brief' (Menge 1997, p. 812). Thus, based on addressing a very specific goal, that of quantifying indirect effects in community dynamics, Menge (1997) considered the experiments he reviewed as being sufficiently long.

In most fields of marine benthic ecology, there has been a lack of explicit consideration of experimental duration. A field of burgeoning research that has recently recognised the serious implications of a short-term approach is in biodiversity and ecosystem functioning (BEF) work (Hooper et al. 2005, O'Connor & Crowe 2005, Raffaelli 2006, Crowe et al. 2012, Duffy et al. 2012). Crowe et al. (2012) used existing meta-analyses (Cardinale et al. 2007, Stachowicz et al. 2007) to review the temporal scale of BEF studies conducted in both laboratory and field settings (in marine, terrestrial and freshwater environments). The authors argue that limiting the temporal extent of experiments has a marked effect on the conclusions regarding the importance of biodiversity in ecosystems and the mechanism by which biodiversity may exert an effect; short-term experiments will overemphasise the importance of dominant species (a species identity effect) relative to complementarity among species. Stachowicz et al. (2008) examined the effect of seaweed diversity on cover over a period of 3 yr. They showed that seaweed cover in diverse treatments only exceeded that in the best performing monoculture after a period of 18 mo, a period much longer than many biodiversity studies (Crowe et al. 2012). These observations might reasonably be seen as strong arguments for lengthening the duration of BEF experiments (although doing so in any multi-trophic manner incorporating large, mobile, long-lived consumers will be enormously challenging [Raffaelli 2006]).

Although many aspects of temporal scale have been addressed through ecological experiments in recent decades, it is debatable whether the scaling-up approach, so prevalent in considerations of spatial scale, has been applied to temporal scale. Thus, it is unclear whether the overall length of experimental study (i.e. scaling up in time) has increased, despite numerous publications tentatively expressing concern at the paucity of longer-term experimentation (e.g. Connell & Sousa 1983, Underwood 2000, Raffaelli 2006). Such calls have no doubt been influenced by the perceived benefits of long-term experimentation (Underwood 2000, Crowe et al. 2012). Here, we examine the temporal scale at which ecological experiments (which apply some form of perturbation) are undertaken in intertidal and shallow sublittoral environments before reviewing the literature to highlight the range of insights gained from

long-term experiments. We finish by considering the challenges associated with increasing the temporal extent of marine benthic experiments and the way in which these may be addressed.

REVIEW OF EXPERIMENTAL DURATION

As outlined above, there have been a number of calls for longer-term experimentation, but a factor which may act to counter such a move is the increasing pressure on scientists to publish their work. While publication of research in a vibrant international literature is the lifeblood of science, the pressure to publish could be argued to lead to a short-term approach, with researchers rushing to publish each new piece of research. It is very easy to see how this short-term approach can influence our approach to experimental ecology. Why spend 5 yr undertaking an experiment when a paper can be published on the basis of results collected over a period of 18 mo? By reviewing the literature (including both marine-focused and general ecological journals), we hope to determine what range of temporal scales experimental marine ecologists are working at and whether the approach to experimental duration has changed over a 33 yr period.

Methods

We examined literature published over a 33 yr period in 2 of the leading marine ecological journals, *Marine Ecology Progress Series* (*MEPS*) *and Journal of Experimental Marine Biology and Ecology* (*JEMBE*), and 3 general ecological journals, *Ecology*, *Oikos* and *Oecologia*, to examine the temporal scale and sampling frequency of field perturbation experiments in shallow subtidal and intertidal benthic environments. In selecting publications, all types of pulse and press perturbations were included, from manipulations which simulate some form of natural or anthropogenic disturbance event to those in which the density or presence of one or more particular species is altered. In addition to manipulation of biota, we included perturbations to the physical environment, for example modification of the nutrient or light regime. One very common type of study was one in which new substrata (often simple PVC panels) were introduced into the environment. Such perturbations may be considered analogous to clearance of biota in natural communities, since both provide bare space, free from competitors.

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

In addition to manipulative experiments implemented by the experimenter, numerous studies examine the consequences of events or implementation of management structures not under the control of the experimenter. These include investigations of natural disturbances such as extreme weather events (e.g. Tegner et al. 1997) or human-induced perturbations such as pollution (e.g. Jacobs 1980), the exclusion of humans from marine protected areas (MPAs) (Castilla & Bustamante 1989) and managed realignment of coastal limits through intentional flooding (Hughes et al. 2009). These natural experiments were included in our review of literature whenever data were available prior to the perturbation taking place, such that a true temporal control existed.

Using the criteria outlined above, all publications in *MEPS*, *JEMBE*, *Ecology*, *Oikos* and *Oecologia* at 4-yearly intervals from 1981 to 2013 were initially reviewed by examination of the title and abstract. Following identification of potential papers, the full text was read and then either rejected or the appropriate information extracted. This approach was taken rather than performing a search based on key words because of the difficulty of creating suitable search terms which would highlight appropriate papers without bias. Our search through 12 557 titles (6940 in general ecological journals; 5617 in marine ecological journals) identified 263 publications containing 322 independent experiments over the 9 publication years. These represented an average of 3.5 and 1.3 % of the studies published in marine and general ecological journals, respectively (or 15.9 % of the marine-related papers published in general journals). Although there was no obvious directional change over the 33 yr of review in the proportion of appropriate studies selected in each year in either journal type, there was a general increase in the number of studies from which data were extracted; this was due to the huge increase in the number of publications in all journals over time (from 299 and 564 in 1981 to 823 and 831 in 2013 for marine and general ecological journals, respectively). To allow good representation of experimental work in earlier years, additional publications were sought for the earliest 5 dates by examining studies published up to 2 yr before (and in the case of 1981, 2 yr after). This approach was taken in the same way as described earlier in this section until a minimum of 10 independent experiments in both marine ecological and general ecological journals were identified for each of the 4-yearly periods. This resulted in 293 publications containing 352 studies being reviewed (see details of all studies in Table S1 in the Supplement at www.int-res.com/articles/suppl/m547p273_supp.pdf).

The temporal scale of experiments in all 352 studies was determined as the length of time from initial sampling, immediately prior to the perturbation, to the final sampling event. Where multiple experiments within a single publication were conducted with the aim of examining a single goal or hypothesis, the maximum length of experimentation was documented. In determining the sampling interval (i.e. length of time between each sampling event), an average value over the period of the study was calculated. For example, in a 10 mo study examining the influence of bivalve shell material introduced to a mudflat on colonisation by burrowing thalassinidean shrimp, Feldman et al. (1997) made observations 1 and 10 mo after the perturbation. Hence, the average sampling interval was recorded as 5 mo. The habitats in which experiments were undertaken were classified as intertidal or subtidal. In microtidal regimes such as the Mediterranean (e.g. Maggi et al. 2009) and Baltic (e.g. Lindegarth et al. 2001), studies undertaken in areas frequently exposed to air through variations in pressure and wind were classified as intertidal. The Caribbean fringing reef studied by Kilar & McLachlan (1989) is exposed to air

only during particular conditions, at certain times of the year, and was therefore considered subtidal. The classification of habitat type (rock, soft sediment, seagrass, coral, mangrove, saltmarsh, artificial substrate) was generally clear cut. Cobble and boulder habitat were considered simply as rock rather than creating a novel category.

Classification of experiments as pulse or press was clear cut in most cases. Pulse experiments were defined as those receiving a one-off perturbation which was generally short in temporal extent compared to the temporal scale of the study. The introduction of artificial substrata such as PVC panels (e.g. Valdivia et al. 2005) or newly quarried boulders (e.g. Chapman 2013) was considered a pulse disturbance, analogous in many ways to the creation of bare space by a single disturbance event. In cases where both pulse and press perturbations were implemented, the experiments were invariably classified as press. For example, in numerous studies, novel substrata were introduced to examine the consequences of a particular press manipulation, such as light and sediment (Connell 2005) or herbivores (Kaehler & Williams 1997). Other studies (e.g. Russell & Connell 2005) combined pulse manipulations such as the one-off removal of a particular species with continued press perturbations such as the addition of nutrients. Rather than class

these as a combination of both pulse and press, they were classed as press. In some studies, multiple perturbations were applied through time (Jewett et al. 2005, Incera et al. 2009, Minchinton & Fels 2013), and again here it was considered that the principle of an ongoing perturbation (although not continuous) justified categorisation as press.

Results and Discussion

Of the 352 studies over the 33 yr, 64% were from marine journals (*MEPS*, *JEMBE*), whereas 36% were published in general ecological journals (*Oikos*, *Ecology*, *Oecologia*). The studies were split almost exactly equally between the intertidal (49.7%) and the subtidal (50.3%) zones. Of the 11 different habitats identified, the most common was intertidal rocky shore (31% of studies) followed by subtidal rocky reef (14%) and then subtidal artificial substrate and subtidal coral reef (9% each). Sixty-two percent of the studies were categorised as press (217 studies), while the rest were considered as pulse (135).

Examination of the frequency distribution of study length across 33 yr showed a clear skew to a shorter time frame (Fig. 1). The highest proportions (24 and 33% for marine and general ecological journals, respectively) were very short (between 0 and 3 mo), with obvious peaks at 9 to 12 and 21 to 24 mo for marine journals (presumably due to the logical attraction of terminating experiments at 1 and 2 yr, respectively) (Fig. 1). Most studies (85% for marine and 82% for general ecological journals) lasted 2 yr or less, and only 39 of the 352 studies were conducted over a period of 3 yr or more. Of these, 17 studies were of a period of 5 yr or more. The median length of study over the period reviewed was 11 mo in marine journals, 9 mo in general ecological journals and 10 mo overall (Fig. 2). Although the median study length varied among years for marine journals (Kruskal-Wallis test, chi-square = 19.427; df = 8; p = 0.013), there was no apparent trend in study length with time.

Study length showed differences between habitat (intertidal versus subtidal) and between perturbation type (pulse versus press) (Fig. 3). The median length of intertidal studies (12 mo) was significantly longer than that of subtidal studies (8 mo) (Mann-Whitney *U* test: $Z = -2.407$; p = 0.016 (Fig. 3A). In the intertidal zone, 30% of studies were conducted over 2 yr or more, approximately double that in the sub-
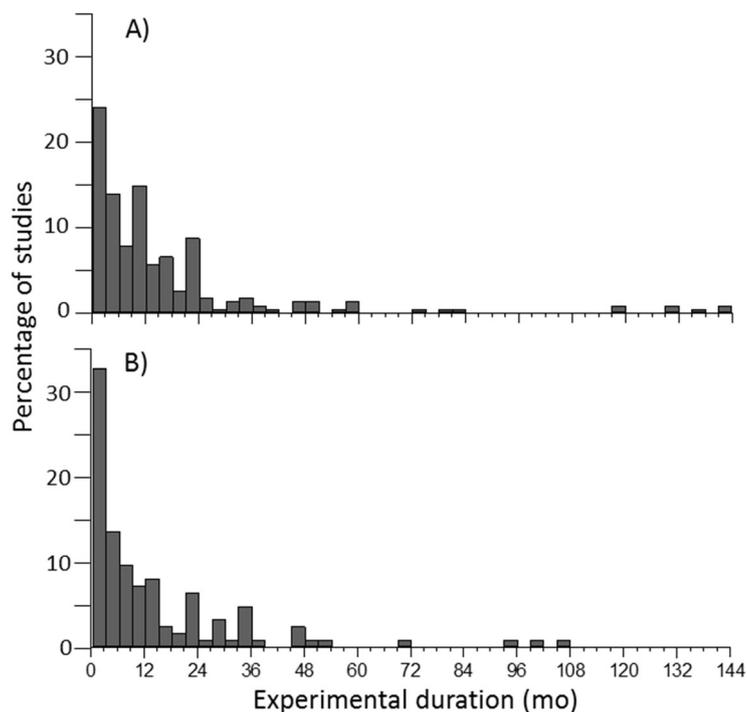

Fig. 1. Distribution of experimental study duration in (A) marine journals and (B) ecological journals over the period 1980 to 2013
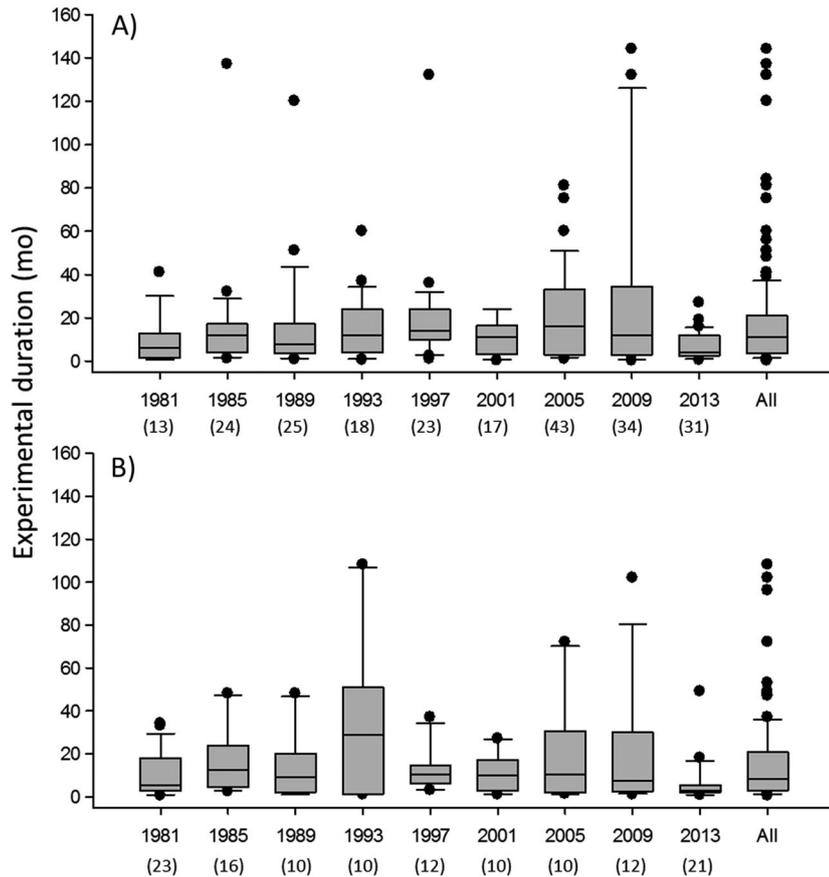
Fig. 2. Duration of manipulative experiments over the 9 periods examined and for all periods combined in (A) marine journals and (B) ecological journals. Boxes indicate the median (horizontal line) and the 25th and 75th percentiles; whiskers indicate the 10th and 90th percentiles; black dots indicate the outliers. Number of independent experiments included in the analysis indicated in parentheses beneath each year
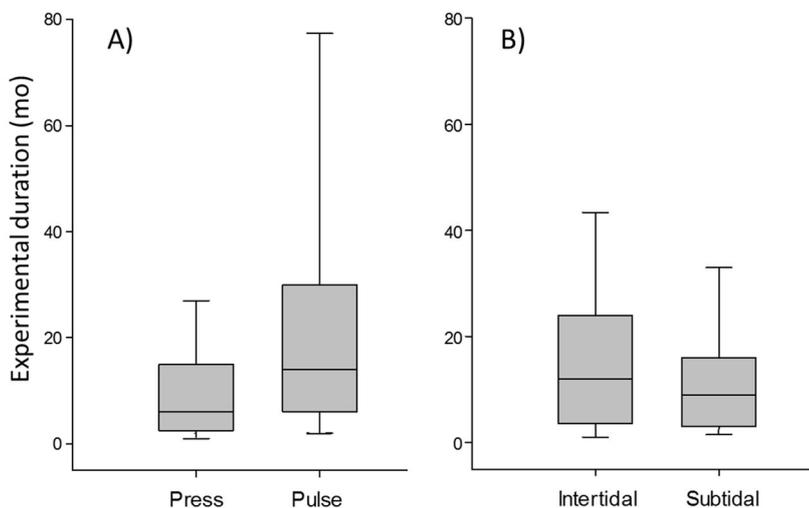

Fig. 3. Median study duration (and 10th, 25th, 75th and 90th percentiles) for comparisons among (A) press (n = 219) and pulse (n = 133) studies and (B) intertidal (n = 175) and subtidal (n = 177) studies

tidal. The median study duration of pulse experiments (14 mo) was significantly longer than that of press experiments (6 mo) (Mann-Whitney U test: Z = −4.762; p < 0.001) (Fig. 3A), and a far greater proportion lasted 2 yr or longer (35% of pulse compared to only 16% of press studies).

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

In discussing the need for a longer-term approach, Underwood (2000, p. 68) states that 'the majority of ecological studies are quite short, usually three to five years'. In fact, our analysis of 352 studies over 33 yr shows that for experiments (i.e. where some form of manipulation or perturbation has taken place, as opposed to purely observational work), the median length of study was only 10 mo, and only 12% of published work was over a period greater than 3 yr. Patterns were similar irrespective of the type of journal (marine specific versus general ecological) in which papers were published. These results were quite clear in indicating that calls for an increase in the temporal scale of studies have not led to any general increase in experimental duration over the past 3 decades. This is true whether considering the median duration of studies or the proportions which are longer than 24 or 36 mo.

Different approaches can be taken to make an argument for the benefits of longer-term experimental duration. One is in demonstrating that longer-term experiments reveal, for example, differences in effect sizes compared to

shorter-term experiments. Such an approach is fraught with problems in designing a non-biased analysis, since often the benefits of long-term experimentation are revealed not in a single bigger outcome but in multi-faceted results which provide greater insight into ecological complexities. In the following, we address such complexity by reviewing a range of longer-term studies (generally greater than 3 yr) which have revealed greater insight than could be achieved by equivalent short-term work.

INSIGHTS FROM LONG-TERM EXPERIMENTS

Controlled manipulations

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

In polar regions, disturbance can have a profound effect on community structure owing to very slow

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

One argument for conducting long-term experiments is that they can reveal quite unexpected results. Jenkins et al. (1999a,b, 2004) report the results of factorial manipulations of the long-lived canopy species *Ascophyllum nodosum* and the keystone grazer *Patella vulgata* on sheltered canopy-dominated shores of the Isle of Man. Short-term results over a period of 1 to 2 yr included the dieback of understorey turfing algae, opening up of bare space and replacement of the *Ascophyllum* canopy with alternative more opportunistic, shorter-lived fucoid species, *Fucus vesiculosus* and *F. serratus*. However, it was the longer-term observations over 6 yr (Jenkins et al. 1999a) and then 12 yr (Jenkins et al. 2004) which revealed the importance of *Ascophyllum* in limiting patellid limpet populations: loss of the facilitatory function of the canopy on understorey turfing algae, and hence the opening up of bare space, resulted in enhancement of limpet recruitment, leading to populations up to 6 times greater in abundance over a decade after canopy loss. Here, experimental work demonstrated the stabilising function of turfing algae in the undisturbed community. Other work has recognised how the dense, low-lying nature of turfing algae, combined with sediment trapping ability (Connell et al. 2014), contributes to stability or slow succession (e.g. Cervin et al. 2005, Schiel & Lilley 2011).

It is frequently stated that coastal marine systems are ideal environments in which to conduct manipulative experiments because dominant organisms have relatively short generation times; hence, experiments may be conducted over short time scales. However, it is debatable whether generation times in primary producers, key consumers and dominant

space occupiers (which are often a number of years) are short enough to justify this view (Beuchel & Gulliksen 2008). Species life-history traits are important determinants for the recovery of communities following disturbance in a range of different ecosystems including saltmarshes (e.g. Bertness 1991), mangroves (e.g. Clarke & Allaway 1993) and rocky shores (e.g. Methratta & Petraitis 2008), and species longevity, as well as mode and rate of colonisation, has clear implications for experimental duration. Methratta & Petraitis (2008) examined recovery from disturbance on rocky shores focusing on species with contrasting longevities, barnacles and fucoid algae. They showed that differences in life-history traits of dominant species modified successional trajectories at different spatial scales over a 5 yr period. Understanding of the population dynamics and community structuring role of long-lived species will invariably require longer-term studies than investigation into species with short generation times, as clearly demonstrated by the 9 yr study of Clarke & Allaway (1993) on mangrove regeneration and the 3 yr study of Bertness (1991) on *Spartina* competitive interactions. On rocky shores, *A. nodosum*, a dioecious, long-lived species (Åberg 1992) with low rates of recruitment rate and slow growth rate (Åberg & Pavia 1997, Cervin et al. 2005), has been the focus of a number of long-term studies in the NE and NW Atlantic (e.g. Jenkins et al. 1999a,b, 2004, Cervin et al. 2005, Ingólfsson & Hawkins 2008, Araújo et al. 2012). Araújo et al. (2012) showed that the impacts of human trampling can have long-term (5 yr) effects on understorey community structure in stands of *A. nodosum*. Even small-scale (25 × 25 cm) disturbance events can have long-lasting effects on *Ascophyllum* understorey communities (Cervin et al. 2005); small-scale loss of *Ascophyllum* canopy led to a change in community structure still apparent after 7 yr. Such effects can occur despite recovery of the long-lived biomass dominants. Schiel & Lilley (2011) showed differences between disturbed and control understorey communities 8 yr after removal of the *Hormosira* canopy even though this dominant fucoid returned to a nearly closed canopy.

Communities composed of long-lived individuals are often described as stable but in reality may only be stable as a consequence of the long-lived nature of their components (Connell & Sousa 1983). Long-term observations following perturbations, especially where dominant biota are long lived, are essential to judge the stability of communities and consequent properties of ecosystems (Farrell 1988, Hooper et al. 2005). Hooper et al. (2005) point out that theoretical

work on stability has outpaced the ability of empirical work to test predictions, essentially because of the time and resource requirements of the long-term experimental work required to determine the fate of all adults over at least one complete turnover (Connell & Sousa 1983). The problem of time scale is one which has dogged the sometimes vigorous debate surrounding the existence, or otherwise, of alternate stable states (see Petraitis & Dudgeon 2004 for review). The question of whether systems can occupy more than one equilibrium point and hence support different stable communities in the same habitat (Lewontin 1969, Connell & Sousa 1983, Peterson 1984, Petraitis & Latham 1999, Petraitis et al. 2009) has been addressed in a number of different marine coastal assemblages, including coral reefs (Scheffer et al. 2001), rocky shores (Paine et al. 1985, Petraitis & Latham 1999), subtidal rocky reefs (Simenstad et al. 1978) and soft sediments (van de Koppel et al. 2001). Part of the problem in answering what at first sight seems a relatively simple question is that spatial and temporal scale are an intractable part of defining stability. Connell & Sousa (1983, p. 808) argued that experimental tests of stability require long-term experiments where 'the fate of all adults of the population or community must either be followed for a minimal period of at least one complete turnover, or their replacement probabilities estimated'. Others disagree (Peterson 1984, Sutherland 1990), and over the last decade or so, Petraitis and co-workers (e.g. Petraitis & Latham 1999, Petraitis & Dudgeon 2005, Petraitis et al. 2009) have implemented manipulations which, although long term by the standards of this review, do not reach the temporal standards defined by Connell & Sousa (1983). The possibility that mussel beds and stands of *A. nodosum* represent alternate states in sheltered bays of the Gulf of Maine was tested through initiating pulse disturbances (clearance of the *Ascophyllum* canopy) of different sizes and monitoring successional pathways over a 9 yr period (Petraitis et al. 2009). The shift from *Ascophyllum* assemblage to mussel bed in 37% of large clearances 9 yr after disturbance is argued by Petraitis et al. (2009) to show that these communities represent multiple stable states on the intertidal shore of the Gulf of Maine. They go on to present a conceptual framework which combines this view with the prevailing paradigm of environmentally driven consumer control (Lubchenco & Menge 1978, Bertness et al. 2002). Irrespective of tests of ecological theory, investigation of how the scale of disturbance affects successional trajectory clearly requires a long-term approach in this environment at least, as

evidenced by the diversity of successional responses among clearing sizes and sites over a 6 yr period (Petraitis & Dudgeon 2005).

Natural perturbations and Marine Protected Areas (MPAs)

The majority of ecological experimentation involves small-scale, controlled manipulation, which, if of sufficient duration, may give insight into the time scale of recovery of marine communities following perturbation. However, Schiel & Lilley (2011) point out the limitation of such approaches in understanding recovery at coast-wide scales, where propagule supply may be limiting. Underwood (1998, p. 292) makes a cogent argument to 'grab opportunities afforded by dramatic events, such as unusually severe weather and large-scale changes brought about by natural agents' to enable a longer-term and larger-scale approach to ecology. Observations over temporal and spatial scales well beyond standard controlled experiments following mass die-offs (Levitan 1988, Linares et al. 2005), large disturbance events such as ice scour (McCook & Chapman 1997), storms (Hughes 1989, Underwood 1998), earthquakes (Castilla 1988), human management intervention (Hughes et al. 2009) and pollution (Southward & Southward 1978) have created insight into ecological processes. McCook & Chapman (1997) assessed the impacts of large-scale ice scouring on exposed rocky shores in Nova Scotia over a 5 yr period and showed that many experimental effects noted over shorter time scales (McCook & Chapman 1991, 1992) were not apparent after longer periods, suggesting that much of the variation within the exposed shore habitat is temporary. They also argue that the temporal dominance of *Fucus* observed over mussels over a 5 yr period, and no evidence of competitive superiority by mussels, should lead to caution in assuming any general applicability of previously stated general models of community structure based on the work of Menge & Sutherland (1976, 1987). Such conclusions, based on long-term observations following large-scale perturbations, present a cautionary note to basing environmental management advice on a theoretical framework based predominantly on the short term and small scale. Underwood (1998) makes the point that observations following disturbance can give rise to hypotheses regarding mechanisms which can then be tested through small-scale, shorter-term experiments. He observed variable rates of recovery in the canopy

alga *H. banksii* over a 7 yr period following an extremely large storm and then used short-term experimental manipulations to test 2 alternative models: (1) that the rate of recovery was a function of the severity of disturbance and (2) that recovery was determined by the activities of grazers. A similar combined approach was taken by Carroll & Highsmith (1996). A severe freeze in Alaska coincided with a spring low tide series, leading to high levels of mussel mortality but little effect on the mussels' principal predator, *Nucella lima*, which winters in the subtidal. A combination of observations over 3 yr and experimental manipulations demonstrated that the extreme event 'set the framework for a shift in balance of the interaction' between predator and prey (Carroll & Highsmith 1996, p. 130). In the presence of high numbers of *N. lima*, mussels were unable to recover over a 3 yr period despite annual recruitment events.

One type of experiment in coastal marine environments which by its nature tends to be long term is the implementation of MPAs. By totally or partially excluding the extractive activities of humans (Sciberras et al. 2015), MPAs establish a (usually) large-scale experiment (Castilla 1999, Diaz et al. 2003) which can be used for understanding long-term dynamics (Castilla 2000) and which has led to enormous ecological insight in coastal marine systems, particularly into the prevalence, time scale and magnitude of trophic cascades (reviewed by Castilla 1999). For example, in Chile, Durán & Castilla (1989) report the results of a 5 yr study of the consequences of exclusion of human food gatherers from the rocky intertidal and shallow subtidal at Las Cruces in central Chile. The cessation of human exploitation of the carnivorous muricid gastropod *Concholepas concholepas* ('loco') led to significant enhancement of its density and consequent strong predatory control of previously dominating mussels. These cascading effects resulted in an elevation of intertidal diversity and subsequent domination by barnacles.

The majority of marine reserves or protected areas are established to protect fisheries-targeted species, including benthic organisms such as lobsters, scallops, abalone and the Chilean loco. Such organisms are generally long lived relative to the majority of benthic organisms studied in perturbation experiments. Because the focus of MPA studies has often been to establish effects on these relatively long-lived target species (e.g. Durán & Castilla 1989, Hoskin et al. 2011) and because the temporal scale of the press manipulation (reduction or elimination of human disturbance) is not limited by the normal driv-

ers of ecological experimentation (e.g. researchers' funds), it is not surprising that published studies of MPAs are often long term. Harvested species may show a significant lag in response (e.g. Beukers-Stewart et al. 2005), but benthic prey may also take many years to respond to enhanced predation. For example, sea urchins can take many years to respond to changes in predator numbers (e.g. 13 yr in New Zealand, 7 yr in Tasmania, 15 yr in Kenya; see Babcock et al. 2010 and references therein). Thus, indirect effects on organisms that occur through cascading trophic interactions can take substantially longer to develop than direct effects (Babcock et al. 2010). This observation may explain why species assemblages in older reserves often differ from recently created reserves (Micheli et al. 2004) and could lead to failure to identify trophic cascades owing to a lack of sufficient temporal scale (Shears & Babcock 2003).

The large-scale, uncontrolled nature of MPA experiments can lead to considerable insight into the nature of the relationship between environmental and biotic drivers of community state when observations are conducted over a sufficient time scale (Babcock et al. 2010, Fraschetti et al. 2013). Fraschetti et al. (2013, p. 11) consider that a long-term approach is essential because 'ecological components may respond differently and over varying temporal scales'. They used a 9 yr series of observations inside and outside an MPA in SE Italy to examine the role of protection in determining temporal and spatial variability. They showed that protected assemblages, with relatively long-lived invertebrates and macroalgae, displayed spatial and temporal homogeneity in marked contrast to a mosaic of changing disturbed patches outside the MPA. Thus, at a local scale, protection enhanced community stability. However, there were also a number of idiosyncratic results, where the effects of protection did not match expectations. Here, it is likely that multiple processes, some derived from variation in environmental context, were acting simultaneously. Similarly, Shears & Babcock (2003) demonstrated long-term effects (25 yr) of protection in a trophic cascade in the Leigh marine reserve in New Zealand mediated through the decline of urchins. However, urchin decline was also observed over the short term (possibly as a consequence of disease) at some unprotected sites.

Studies of the effect of protection from human disturbance are often made at a single point in time through comparison of protected and unprotected sites, often many years after establishment of the protection regime. Although suffering from difficulties in firmly ascribing observed spatial differences to protection effects (Underwood 1991), these studies are logistically relatively easy to implement and can (limitations accepted) give important long-term insight. For example, Mumby et al. (2006) sampled fish and benthic assemblages of Caribbean reef systems 18 yr after implementation of a fishing ban. A net doubling of grazing pressure from parrot fishes in protected areas led to a 4-fold reduction in macroalgal cover (Mumby et al. 2006) and consequently a 2-fold increase in coral recruitment (Mumby et al. 2007). Clearly, such observations tell us nothing of the rate of change in fish or benthic assemblages or the temporal dynamic between interacting species but do demonstrate the strong top-down control exerted by key fish consumers in supporting the health of Caribbean coral reefs. As a note of caution to accepting conclusions based on such an approach, a review of 6 time series studies showed that increases in target species following protection were not always as high as expected on the basis of studies with no temporal replication (Babcock et al. 2010). Thus, understanding how communities change through time following protection is likely to lead to a far greater mechanistic understanding of protection effects.

CONCLUSIONS

It is clear from our review of experimental duration over 33 yr that the majority of manipulative experiments in benthic systems, examining community or population responses of macro-organisms, are reasonably short (2 yr or less). It is also clear from reviewing a range of experiments operating over a longer time scale that a long-term approach can yield considerable insight and, in many cases, alter conclusions based on the same experiments conducted over shorter time scales. Thus, we argue that although many short studies will be perfectly valid, in general, increasing the period over which observations are made following experimental manipulations will yield important benefits.

Limitations on the temporal extent of marine benthic experiments are numerous and range from the logistical to considerations of motive and reward. Raffaelli & Moller (2000) showed through interviews of experimentalists that decisions regarding duration of field experiments were predominantly pragmatic. Temporal scale was often based on the time available in a studentship, or grant, or the difficulties of maintaining the experiment in a hostile environment. However, there are a number of simple, practical approaches that can be implemented to lengthen exper-

imental duration. First and foremost, when planning manipulative field experiments, Diaz et al. (2003) stress the need for foresight and the acquisition of long-term funding where possible. However, extending sampling regimes may not necessarily be costly. A common approach where the temporal scale has been extended is to sample at regular intervals over the first year or so of an experiment and then sample at much lower frequencies over a number of years (e.g. Jenkins et al. 2004, Viejo 2009). Extending an experiment over multiple years generally requires some foresight in experimental establishment (e.g. use of secure, non-corrosive, preferably stainless steel markers and a mapping system of spatial replicates which can be utilised by persons other than the original experimenter) plus the motivation to revisit experimental sites over multiple years. This can be achieved long after the original experimenter (e.g. student, post-doctoral scientist) has moved on to new pastures.

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

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