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Scale- and intensity-dependent disturbance determines the magnitude of opportunistic response

Alf Norkko [a,*], Rutger Rosenberg [b], Simon F. Thrush [c], Robert B. Whitlatch [d]

[a] *Department of Biological Oceanography, Finnish Institute of Marine Research, PB 2, 00561 Helsinki, Finland*
[b] *Department of Marine Ecology, Göteborg University, Kristineberg Marine Research Station, 450 34 Fiskebäckskil, Sweden*
[c] *National Institute of Water and Atmospheric Research, PO Box 11-115, Hamilton, New Zealand*
[d] *Department of Marine Sciences, University of Connecticut, 1080 Shennecossett Road, Groton, CT 06340, USA*

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Abstract

Opportunistic, fugitive or pioneer species are species that posses life-history characteristics that allow them to respond quickly to disturbances. Their abundance during the early stages of succession is central to ecological models of benthic soft-sediment succession and these species can play important roles in affecting subsequent successional trajectories. Nevertheless, numerous studies have demonstrated seemingly random patterns of opportunistic responses following disturbance, questioning the generality of currently accepted successional models. In this paper we provide examples from two case studies and argue that the spatial scale or magnitude of disturbance is key to the development of opportunistic responses, and that the scale of disturbance may be particularly important in determining (a) the levels of resources made available and (b) the magnitude of release from competitive interactions, which permit opportunists to flourish.
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1. Introduction

The nature and predictability of successional trajectories of communities following disturbance have been debated since the early days of ecology as a science (e.g. Clements, 1916, Gleason, 1926). Succession is inextricably linked to disturbance events that, depending upon their magnitude, frequency and extent, may reverse or reset the successional process. Natural disturbances operate over a variety of time and space scales, and are key processes defining the organisation of natural communities (e.g. Kitching, 1937, Dayton, 1971, Connell, 1978, Pickett and White, 1985, Sousa, 2001). With broad-scale habitat degradation, however, continuing at an unprecedented rate due to human impacts, developing an understanding of how the nature and magnitude of disturbance affects communities and trajectories of succession is as relevant as ever, and is at the heart of efforts aimed at successful habitat conservation and restoration (Jackson et al., 2001, Thrush and Dayton, 2002).

Marine soft-sediment systems are the most common habitats on earth and are increasingly being subjected to broad-scale anthropogenic disturbances due to, for example, eutrophication, hypoxia, fishing, sedimentation

* Corresponding author.
E-mail address: alf.norkko@fimr.fi (A. Norkko).

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and pollution (Diaz and Rosenberg, 1995, Gray, 1997, Zajac et al., 1998, Ellis et al., 2000, Jackson et al., 2001, Thrush and Dayton, 2002, Thrush et al., 2004). Although the impact of such large-scale disturbances is relatively well studied, our knowledge of ecosystem resilience and recovery remains relatively limited. While much empirical evidence suggests that the succession of disturbed patches gradually converge towards local undisturbed resident assemblages (Sousa, 2001, Hall et al., 1994, Rosenberg et al., 2002), recent work emphasizes that both the spatial scale (Petraitis and Dudgeon, 1999, Thrush and Whitlatch, 2001) and intensity (Warwick and Clarke, 1993, Platt and Connell, 2003) of disturbances have important influences on the recovery process.

In addition to the scale of disturbance, the identity, life-history and abundance of organisms that initiate and facilitate the early stages of recovery are predicted to have far reaching implications for the outcome of successional processes (Rhoads et al., 1977, Whitlatch et al., 1998), and are likely of particular importance in understanding the recovery potential after broad-scale disturbances (Thrush and Whitlatch, 2001). For example, Whitlatch and Zajac (1985) found that high densities of a number of different opportunistic species could arrest the successional process for periods of up to one month in a shallow-water North American temperate estuary. Opportunistic or pioneer species play a central role in prevailing models of early succession in soft-sediment systems (Pearson and Rosenberg, 1978, Rhoads et al., 1978). The Pearson and Rosenberg (P&R) model portrays a gradual succession of benthic communities along gradients of decreasing disturbance, from a 'peak of opportunists' to a 'climax-community' with deep burrowing species (Fig. 1). These early colonists often have life-history traits (e.g. small size, fast growth, high reproductive capacity, and good dispersal ability) that facilitate rapid demographic responses and large increases in abundance in recently disturbed areas. In the successional sequence, shallow sediment-dwelling opportunistic species may be important in facilitating conditions in recently defaunated sediments for subsequent colonisation by deeper-dwelling organisms with longer life-times and slower growth patterns at later successional stages (Rhoads, 1974, Pearson and Rosenberg, 1978, Gallagher et al., 1983). Further,

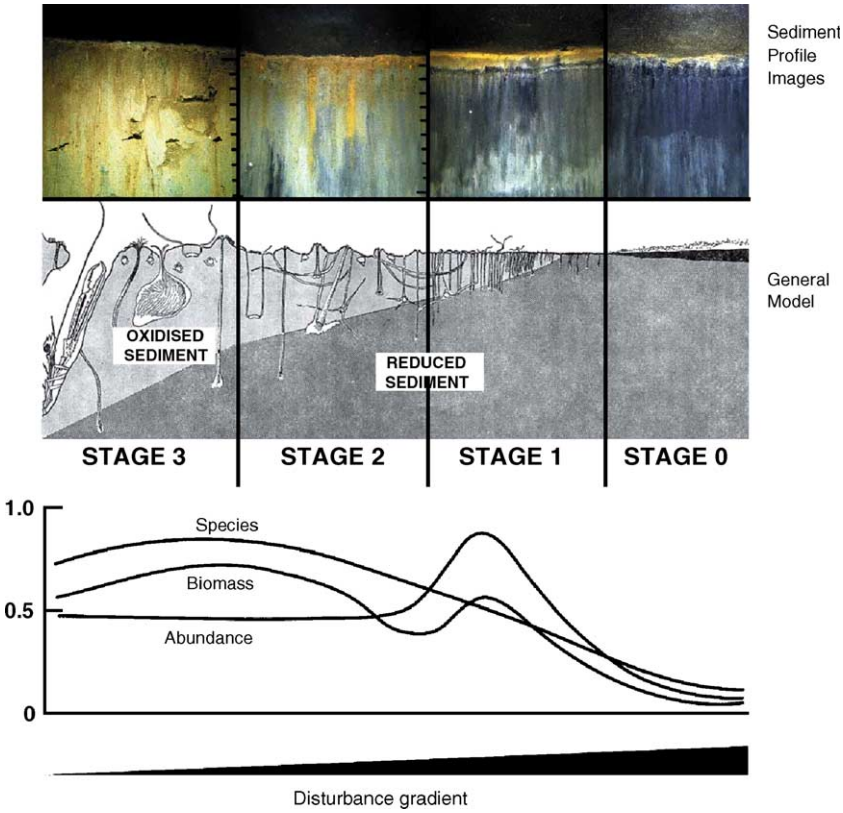

Fig. 1. The Pearson and Rosenberg (1978) model of macrobenthic succession in relation to a gradient of increasing disturbance (modified from Nilsson and Rosenberg, 2000).

McCall (1977) provided evidence that the density of opportunists was inversely related to the density of other species, suggesting that opportunists are out-competed by later colonists.

The Pearson and Rosenberg model was developed using information from broad-scale enrichment of muddy subtidal sediments and has been widely adopted. Despite its applicability and appeal as a general model describing macrobenthic succession, its application to different types of habitats and systems has yielded variable results (Thrush and Whitlatch, 2001). Many studies, and especially experimental studies, investigating succession following disturbance demonstrate (I) habitat-, species- and life-stage-dependent colonisation, (II) a variable presence of 'climax' communities, (III) mixed community types across different successional stages, and (IV) variable opportunistic responses. A lack of clearly defined opportunistic responses by early colonists may depend, for example, upon the timing of disturbance and differences in habitat type (e.g. Bonsdorff, 1980, Zajac and Whitlatch, 1982, Thrush et al., 1996, Thrush and Whitlatch, 2001), and on demographic characteristics of colonist pools (Zajac and Whitlatch, 1991, 2001). The scale of disturbance can also be particularly influential (Zajac et al., 1998, Whitlatch et al., 1998). Importantly, the characteristic peak in abundances of opportunists in the successional P&R model has not always been observed (e.g. Grant, 1981, Oliver et al., 1985, Diaz Castaneda and Frontier, 1989, Thrush et al., 1996).

General disturbance theory has recognised scale as an important component in the recovery dynamics of populations and communities (Pickett and White, 1985), and patch-size as an integral part of the patch-mosaic concept (Johnson, 1973). In soft-sediment habitats, populations and communities are patchily distributed over a range of spatial scales (Thrush, 1991), and each patch may represent a different stage of recovery from disturbance (Johnson, 1973). Colonisation in soft-sediment systems can be scale-dependent (Thrush et al., 1996), and conceptual models dictate that initial colonisation rate is governed by disturbance size and mobility of colonists (Smith and Brumsickle, 1989, Gunther, 1992, Hall et al., 1994, Thrush and Whitlatch, 2001). For example, modelling studies indicate that interactions between scale- and life-stage-dependent dispersal ability can have far-reaching implications for successional processes (Whitlatch et al., 1998, 2001). Nevertheless, spatial scale is rarely included as a factor in experiments, empirical studies of scale-dependent colonisation and succession remain scarce. Due to the obvious logistical and ethical constraints of conducting large-scale experiments, the published studies explicitly examining scale-dependence are limited in both spatial and temporal scale (Table 1). Collectively, however, these studies highlight the prime importance of spatial scale of disturbance in influencing the dynamics of recovery from disturbance.

Differences in the intensity or spatial extent of disturbance will have profound influences on successional processes and dictates the quality and quantity of habitat made available to early colonisers. To opportunists, this may entail differential levels of physical space and chances of patch encounter by colonists, varying degrees of release from interference competition, or other negative biotic interactions, and varying food availability. All of which are important in determining the nature of subsequent population and community dynamics.

In this paper we use two examples from contrasting systems to illustrate how the level of opportunistic responses may depend on the spatial extent or intensity of disturbance. More specifically, we (1) use data from a recent scale experiment on an intertidal sandflat on the Swedish west coast that demonstrates increasing opportunistic responses by the amphipod *Corophium volutator* to increasing spatial scales of disturbance (Norkko, in preparation) and (2) examine the responses of the classic opportunistic polychaete *Capitella capitata* following a history of increasingly severe disturbance due to stratification-induced hypoxia in the subtidal Gullmarsfjord (Rosenberg et al., 2002).

When discussing an "opportunistic response", we follow Thistle (1981) who defined it as an overshoot in abundance of colonists relative to ambient conditions following disturbance.

Table 1
Published experimental field studies investigating scale-dependent recovery processes in soft-sediment macrobenthic communities

Authors	Country	Habitat	Scale of disturbance	Duration of experiment
Smith and Brumsickle, 1989	USA	Intertidal sandflat	0.005 and 0.175 m^2	41 days
Ruth et al., 1994	USA	Shallow subtidal	0.005, 0.014, 0.04 and 0.102 m^2	40 days
Ragnarsson, 1995	Scotland	Intertidal mudflat	0.005, 0.16 m^2	39 days
Thrush et al., 1996	New Zealand	Intertidal sandflat	0.203, 0.81 and 3.24 m^2	9 months
This study	Sweden	Intertidal sandflat and mudflat	0.25, 1, 4 and 16 m^2	6 months

2. Case study 1: Intertidal experiment testing scale-dependent recovery processes and opportunistic responses by *Corophium volutator*

An experiment addressing the scale-dependence of macrofaunal recolonisation following disturbance was conducted at three intertidal locations on the Swedish west coast in 2003 (Norkko, in preparation). As part of this large multi-site experiment, we here utilise data from one of the locations, Finnsbovik in the Gullmarsfjord, to illustrate the spatial and temporal scale dependence of opportunistic responses exhibited by the tube-dwelling amphipod *Corophium volutator*. Finnsbovik is a microtidal (20–40 cm) shallow bay dominated by well-sorted fine sand (median grain size: 110 μm). The macrofaunal community is dominated by large bioturbating lugworms (*Arenicola marina*), cockles (*Cerastoderma edule*), soft-shell clams (*Mya arenaria*), hydrobid snails, ragworms (*Nereis diversicolor*), oligochaetes, and the tube-dwelling amphipod *Corophium*. The lugworm *Arenicola* is a major habitat modifier in the system, attaining densities of up to 20 ind m^{-2}. *Arenicola* is a deposit feeder that lives in J- or U-shaped burrows to depths of 40 cm in the sediment (Reise, 1985). *Corophium volutator* is a surface deposit-feeder common throughout Europe and northeast North America (Meadows and Reid, 1966, Möller and Rosenberg, 1982, Raffaelli et al., 1991, Flach, 1992).

The disturbance-recovery experiment was set-up at −20 cm MTL. Different-sized patches of the sediment were defaunated by covering the sediment with polyethylene sheeting which was dug into the sediment along the edges. The sheeting rapidly induced anoxia to underlying sediments resulting in more or less complete defaunation of macrofauna within 3 weeks. The plot sizes used were: 0.25, 1, 4 and 16 m^2. Five blocks containing replicates of each experimental treatment were arranged parallel to the shoreline and separated by 10–15 m. The plots were defaunated over a 3-week period in June 2003 and the experiment started by removing the plastic sheeting in early July. To track faunal recovery over time, macrofaunal community data were collected from the defaunated plots and ambient undisturbed controls on 7 occasions (i.e. 0, 1, 4, 14, 30, 66 and 152 days after removal of the plastic sheeting) until December when ice formed at the study site. The background abundance of *Arenicola* was estimated on each sampling occasion by counting the number of fecal casts in ten replicate 0.25 m^2 quadrats adjacent to each experimental block, whereas all casts were counted inside the experimental plots to monitor recovery in different treatments. Although the number of fecal casts may vary depending upon feeding activity, they provide a good proxy for estimating *Arenicola* abundance (Reise et al., 2001).

Linear regression analysis was used to model the relationship between *Corophium* abundance and spatial scale, and the relationship between *Corophium* and *Arenicola* over time. As the distribution of *Arenicola* was strongly scale-dependent and basically followed a power function, the data were log-transformed prior to the analysis of the *Corophium* and *Arenicola* relationship.

Responses of *Corophium* to the defaunated patches were rapid, positive and scale-dependent (Fig. 2). After only 4 days, some individuals had colonised the largest plots and after 14 days no differences between controls and the different treatments were observed. However, after 30 days opportunistic responses became evident as *Corophium* densities had increased markedly in the 16 m^2 plot, exhibiting a 5-fold increase compared to ambient sediments (corresponding to 11 000 and 66 000 ind m^{-2} in the control and 16 m^2 treatment, respectively; Fig. 2). *Corophium* comprised >40% of total community abundance (Table 2) and more than 40% of the amphipods in the 16 m^2 plot were newly hatched juveniles ≤1 mm in size (measured from tip of rostrum to end of telson). *Corophium* are brooders and juveniles tend to be gregarious suggesting that juveniles were hatched in situ. Indeed, on previous sampling occasions, a higher proportion of brood-carrying females was observed in the experimental plots. Following this initial opportunistic response recorded on Day 30, the general positive relationship between *Corophium* density and increasing spatial scale persisted and was strengthened throughout the experiment (Fig. 2 and Table 3).

Colonisation patterns of *Corophium* contrasted with community-wide recolonisation patterns. In terms of total community abundance, colonisation was fastest in the 0.25 m^2 plots and slowest in the 16 m^2 plots. Although all treatments had recovered in terms of total abundance by the end of the experiment, there were still marked differences in community structure and in the distribution of several individual taxa. Most taxa exhibited recolonisation patterns similar to that of *Arenicola*, although recovery of *Arenicola* was exceedingly slow in the larger plots (Fig. 2) and was mostly a diffusive process with gradual immigration of lugworms from the plot edges (Fig. 3). For example, while the 0.25 m^2 plots had recovered after 14 days, densities of *Arenicola* in the largest plots still remained at only around 50% of background values by the end of the experiment (Fig. 2).

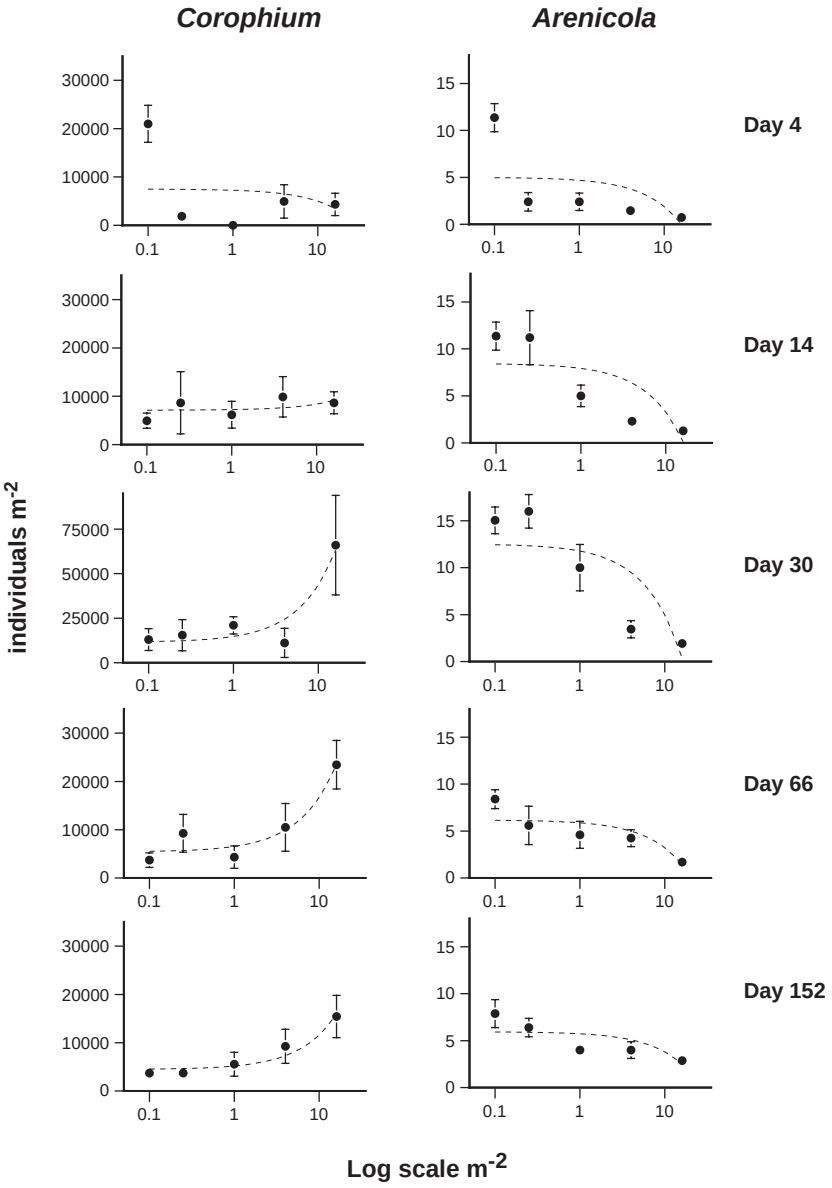

Fig. 2. Results from a scale-dependent defaunation experiment illustrating the importance of spatial and temporal scale for the development of opportunistic responses by *Corophium volutator* and the slow scale-dependent colonisation by the large bioturbating *Arenicola marina*. Curve fits are from linear regression. Note differences in scale on the *y*-axis on Day 30. Values are means ± S.E.M.

Corophium volutator is an important prey item for a variety of vertebrate and invertebrate predators. On the Swedish west coast important predators include juvenile plaice (*Pleuronectes platessa*) and brown shrimp (*Crangon crangon*) (Pihl, 1985), which can attain densities of up to 90 ind m^{-2} during the highly productive summer months (Pihl and Rosenberg, 1982). Pihl (1985) estimated that up to 57% of the annual production of *Corophium* is consumed by *Crangon* alone, highlighting the key role predators play in this system. Given the high predation pressure on *Corophium*, any factor, such as non-lethal physical disturbance events that modify prey availability may dramatically affect predator–prey relationships (e.g. Bonsdorff et al., 1995, Norkko and Bonsdorff, 1996a, Eriksson et al., 2005). For example, Flach and Debruin (1994) demonstrated that bioturbation by *Arenicola* can disrupt the burrows of *Corophium*, force them into the water column, and double their vulnerability to predation by *Crangon*. Indeed both density manipulations with

Table 2
The relative dominance (% of total community abundance) of *Corophium volutator* in different experimental treatments over time

Relative dominance	Treatments				
Time	Control	0.25 m^2	1 m^2	4 m^2	16 m^2
Day 4	**3.5**	0	2.8	0	0
Day 14	6.5	1.4	0	**16.2**	0
Day 30	8.6	17.4	26.4	13.7	**40.2**
Day 66	2.1	5.8	4.5	9.4	**28.0**
Day 152	2.6	2.2	2.7	5.6	**9.3**

Bold values indicate treatment with highest dominance on each sampling occasion.

Arenicola and field surveys show a clear negative relationship between *Corophium* and *Arenicola* density in the field (Flach and Debruin, 1993, 1994). Amensalistic interactions between *Arenicola* and *Corophium* have long been recognised (Linke, 1939) and similar local negative interactions between *Arenicola* and other dominant infaunal taxa such as *Macoma balthica* and *Pygospio elegans* have been observed (Brey, 1991). Thus, for highly mobile taxa, such as *Corophium*, capable of active habitat selection (e.g. Hughes, 1988, Lawrie and Raffaelli, 1998, Norkko, 1998), rapid colonisation into areas with low *Arenicola* density appears a favourable strategy.

We found a significant negative relationship between *Arenicola* and *Corophium*, which, although initially weak, was reinforced over time (Fig. 2 and Table 3). The scale-dependent and slow colonisation by *Arenicola* into the defaunated plots appears as the most plausible explanation for the opportunistic responses exhibited by *Corophium*, which most likely represent a scale-dependent release from *Arenicola* inhibition. Further, the absence of *Arenicola* and other larger surface deposit-feeders in the experimental plots resulted in significant 'blooms' of microphytobenthos providing surface-deposit feeding colonists with an ample food supply (Norkko, in preparation). The increased microphytobenthic biomass was clearly scale-dependent and highest in the 4 and 16 m^2 plots (Norkko, in preparation).

3. Case study 2: Role of disturbance intensity for the development of opportunistic responses: an example from the subtidal Gullmarsfjord

A large-scale hypoxic event in the Gullmarsfjord on the Swedish west coast provided the opportunity to study the effects of intensity-dependent disturbance on the development of opportunistic responses by the polychaete *Capitella capitata*. The data presented are from unpublished material additional to that reported by Rosenberg et al. (2002), which examined community level recovery following a history of increasingly severe hypoxic disturbance. Details of the hypoxic event and the sampling scheme are provided in Nilsson and Rosenberg (2000) and Rosenberg et al. (2002), and are only briefly summarised here.

The Gullmarsfjord has a maximum depth of 118 m and a 40 m sill at the entrance. The stagnant bottom water is usually renewed with cold, oxygenated deep water each spring (Nilsson and Rosenberg, 2000). In 1997, bottom-water exchange failed to occur and dissolved oxygen concentrations declined to <10% saturation at depths >80 m. These conditions prevailed until January 1998 when slight increases in oxygen saturation were recorded, which was followed by a major water exchange in April 1998. Bottom-water oxygen conditions were increasingly severe with increasing depth; in January 1998, oxygen saturation was 50%, 20%, 10%, 8% and 5% at 75, 85, 95, 105 and 118 m depth, respectively.

Replicate grab samples were obtained using a Smith–McIntyre grab (0.1 m^2) from five sites positioned at 75, 85, 95, 105 and 118 m depth, and benthic community development was followed over time (Rosenberg et al., 2002). All sites had similar sediment characteristics and macrofaunal assemblages prior to hypoxic disturbance. By the end of the study in April 2000, the macrofaunal assemblages had converged to pre-disturbance community composition (Rosenberg et al., 2002).

The successively more intense hypoxia resulted in an increasingly disturbed benthic community with increasing depth (Fig. 4). The number of individuals (excluding capitellid polychaetes) was reduced from around 360 ind $grab^{-1}$ at 75 m to 96, 50, <2 and <2 ind $grab^{-1}$ at 85, 95, 105 and 118 m depths, respectively (Fig. 4). Depth-related patterns of total number of taxa and biomass where more or less identical. These

Table 3
Results from regression analysis illustrating the relationship between *Corophium* abundance and spatial scale, and the relationship between *Corophium* and *Arenicola* over time

Time	Parameters	
	Corophium vs. Scale	*Corophium* vs. *Arenicola*
Day 4	$r^2=0.04$, $p=0.7375$ (−)	$r^2=0.43$, $p=0.2266$ (+)
Day 14	$r^2=0.18$, $p=0.4726$ (+)	$r^2=0.33$, $p=0.3082$ (−)
Day 30	$r^2=0.89$, $p=0.0162$ (+)	$r^2=0.37$, $p=0.2770$ (−)
Day 66	$r^2=0.92$, $p=0.0103$ (+)	$r^2=0.78$, $p=0.0480$ (−)
Day 152	$r^2=0.94$, $p=0.0058$ (+)	$r^2=0.81$, $p=0.0385$ (−)

(+)/(−) indicate whether relationship is positive or negative.

Fig. 3. A 4 m^2 plot on Day 66, illustrating the gradual immigration of the lugworm *Arenicola* into the defaunated plots. Note the corner pegs.

negative relationships, with reduced species, abundance and biomass increasing with depth and disturbance intensity, were significant for all parameters ($r^2 > 0.80$, $p < 0.0001$). In contrast, the abundance of *Capitella* sp. increased successively with increasing depth, increasing disturbance intensity, and the increasingly impoverished macrofaunal communities (Fig. 4). There was a strong negative relationship between *Capitella* and total macrofauna abundance ($r^2 = 0.81$, $p < 0.0001$), number of taxa ($r^2 = 0.88$, $p < 0.0001$) and community biomass ($r^2 = 0.90$, $p < 0.0001$). Although the ultimate reason(s) for the increasing opportunistic response exhibited by *Capitella* sp. after terminated hypoxic stress are uncertain, the successive reduction in the macrofaunal communities and lack of competition in the recovery process appear the most proximate reason.

At the site most severely affected by the hypoxic event (118 m), and where the opportunistic responses were strongest, the peak in *Capitella* abundance only lasted one month (Fig. 5). The subsequent rapid reduction in abundance was accompanied by the increase in abundance of other macrofauna (Fig. 5). However, initial declines in *Capitella* abundance were apparent before community recovery commenced.

Differential recruitment of *Capitella* at different depths is an alternative explanation for the 'opportunistic' patterns observed. However, prior to disturbance *Capitella* occurred in low numbers at all depths and the most plausible explanation for the increasing opportunistic response with increasing disturbance intensity, is scale-dependent increases in resources such as space and food. *Capitella* sp. has a

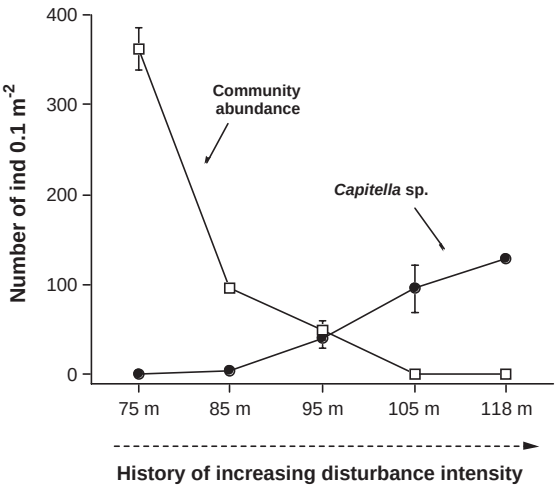

Fig. 4. Macrofaunal community abundance and increasing opportunistic responses of *Capitella* in response to increasingly severe previous hypoxic disturbance. Values are means ± S.E.M.

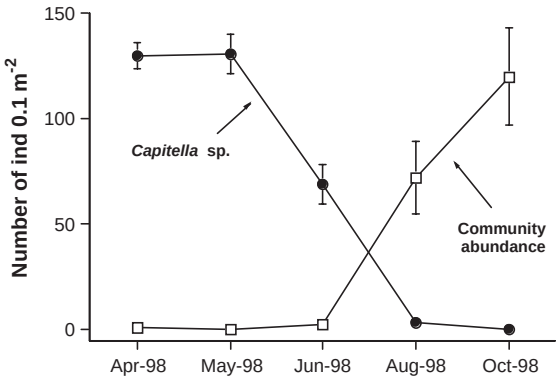

Fig. 5. Rapid decline in abundance of *Capitella* accompanied by increases in total community abundance after the disturbance event at the most severely affected study site (118 m). Values are means ± S.E.M.

classic opportunistic life history involving rapid colonisation and population increase in response to disturbances (Grassle and Grassle, 1974, McCall, 1977, Pearson and Rosenberg, 1978, Tsutsumi, 1987). *Capitella* exhibits preferential recruitment into organically enriched areas (e.g. Butman and Grassle, 1992, Grassle et al., 1992) and is known to grow fast through its efficient utilisation of nitrogen-rich organic particles (e.g. Grassle and Grassle, 1974, Phillips and Tenore, 1984, Marsh and Tenore, 1990, Linton and Taghon, 2000). Rapid increases in *Capitella* abundance are typically followed by subsequent sharp declines, which at least partly may be explained by over-exploitation of food sources (Grassle and Grassle, 1974, Chesney and Tenore, 1985). Direct experimental evidence for competitive interactions between *Capitella* and other species are sparse (although see Petraitis, 1984) and most of the literature concerns exploitation of food and population growth. Typically *Capitella* does not co-occur in high numbers with other species, but whether this may be due to direct negative interspecific interactions (Pearson and Rosenberg, 1978) or indirect competition for food remains unclear (Gray, 1981). Nevertheless, classic opportunist taxa such as *Capitella* sp. are thought to be poor competitors for food and space and lack defences against predators (Bonsdorff and Pearson, 1997), and are thus often displaced by later colonists (McCall, 1977).

Regardless of the mechanisms involved, our data suggest that the magnitude of opportunistic responses by *Capitella* depends on the scale of disturbance (in this case, the duration and intensity of hypoxic stress) that either directly or indirectly provides varying levels of opportunity for population growth.

4. General discussion

Our two case studies highlight the central role that the spatial scale or intensity of disturbance can play in the development of opportunistic responses. Although this may seem intuitive, it has not previously been emphasised probably due to the lack of studies contrasting opportunistic responses over different spatial scales or intensities of disturbance.

Results from the intertidal defaunation experiment suggest that opportunistic responses by *Corophium* are successively greater at larger spatial scales (Fig. 2) and are most likely related to the scale-dependent release from negative interactions with the lugworm *Arenicola*, which colonised the plots very slowly (Fig. 2). The opportunistic responses were potentially further facilitated by an ample supply of food through the development of microphytobenthic mats where *Arenicola* were absent. Large deep burrowing species are typical representatives of late successional stages and are generally thought to outcompete early opportunistic stages through bioturbation (biological disturbance), predation and competition (Rhoads and Young, 1970, Woodin, 1976, Pearson and Rosenberg, 1978, Thrush, 1988, Warwick et al., 1990). However, this is of course a simplistic generalisation as, depending upon species and context, effective bioturbators (e.g. crabs) may also facilitate succession and recovery by modifying the physical and chemical characteristics of the sediment and prime the habitat for colonists after disturbance events (Meadows and Tait, 1989, Wolfrath, 1992, Norkko et al., 2002, Thrush et al., 2003). The role large habitat modifiers play in communities is complex, and may shift from facilitation to inhibition depending upon scale of observation or habitat-dependent environmental conditions (Zajac et al., 1998; Norkko et al., 2006). Nevertheless, the absence of large habitat modifiers appears as a key element for the development of opportunistic responses.

Major habitat modifiers such as *Arenicola* clearly have a profound influence on benthic community dynamics exhibiting amensalistic interactions with many species sensitive to bioturbation and nearly identical effects to those described for *Arenicola marina* have been reported for the *Abarenicola pacifica* (Wilson, 1981; Woodin, 1985). The concept that opportunistic responses are scale-dependent and related to releases from amensalistic interactions with large habitat modifiers, is further corroborated by the findings of Beukema et al. (1999), who conducted unusually large-scale defaunation experiments (120 m^2 plots) in the Dutch Wadden Sea that were monitored up to 4.5 years. They found many species exhibited opportunistic responses (defined as abundance 'overshoots' by Beukema et al., 1999), including polychaetes with known opportunistic traits such as *Pygospio elegans* and *Capitella capitata*, but also by juveniles of classic late successional stage species such as *Arenicola* and *Macoma balthica* and *Mya arenaria*. In fact, more than 50% of all species in their experiment exhibited overshoots in abundance compared to controls at some stage during the course of the experiment. In contrast, recovery in their large plots by adult life stages of *Arenicola*, *Nereis*, *Macoma* and *Mya* was slow and full recovery was not observed until three or more years following the initial defaunation. Beukema et al. (1999) also suggested that the release from negative interactions with *Arenicola* and other large burrowing species might help explain the high prevalence of opportunistic responses. Thus,

although not contrasting different scales that would allow for an assessment of potential scale-dependence of opportunistic responses, experiments by Beukema et al.'s (1999) add generality to our observations that opportunistic responses are more common associated with larger-scale disturbances.

The prevailing conceptual model of macrobenthic succession following disturbance developed by Pearson and Rosenberg (1978) is indeed based on large-scale disturbances resulting from primarily organic enrichment events and describes peaks of opportunists associated with high intensity disturbance. In a similar context, described in Case study 2, we found increasing opportunistic responses by *Capitella* sp. with a history of increasing hypoxic disturbance and an increasingly degraded macrobenthic community. This was most likely a response to an abundance of food and lack of competitors, which was successively greater with higher disturbance intensity. Nevertheless, while the opportunistic responses exhibited by *Corophium* in the intertidal lasted for several months, the capitellids at the deep-water sites were transient and the populations declined after 1–2 months at the most disturbed depth. This happened before substantial recovery of other macrobenthic taxa had occurred. Thus, while the magnitude of initial response and population growth most likely was affected by the diversity and abundance of other macrofauna, competing for space and food at the time of establishment, the population crash was most likely due to natural mortality, predation and/or food limitation. Evidence for the scale dependence in opportunistic responses of *Capitella* is further supported by the findings of Ragnarsson (1995, Table 1), who conducted a scale-dependent disturbance-recovery experiment on an intertidal mudflat. Although the scales contrasted were small (0.005 and 0.16 m^2), he found significantly higher abundances of *Capitella* in the disturbed plots compared to controls and a trend for increased abundances in the large compared to small plots, with a 7- and 5-fold increase compared to the control, respectively. He also found the amphipod *Gammarus* spp. rapidly exceeded control densities, with strongest opportunistic responses recorded in the largest plots.

The spatial scale of disturbance has been identified as having a crucial role in initiating a switch between alternative community states in rocky intertidal assemblages in the western North Atlantic (Petraitis and Latham, 1999). Petraitis and Latham (1999) contend that large-scale disturbance (e.g., ice scour) provides sufficient open space to facilitate a switch from macroalgal-dominated assemblages to those dominated by mussels and barnacles. The recovery process following small-scale disturbance is more susceptible to edge effects and disturbed areas tend to be re-established with the assemblage of organisms found around the small-disturbed patches. This may imply that scale-dependent disturbance responses may be more readily inferred in systems dominated by sedentary organisms. However, even on rocky reefs, the colonising potential and rate of growth of community dominants have a strong effect on recovery across a range of scales of disturbance. Dayton and co-workers have eloquently demonstrated that in Southern California the giant kelp *Macrocystis pyrifera* will also dominate space occupancy even after large storm events, although the kelp's growth rates may be slowed by unfavourable oceanographic conditions (Dayton and Tegner, 1984a, b; Dayton et al., 1999). Thus, it is the interaction between physical factors (such as extent of disturbance) and biological factors (growth rates and species interactions) that will create the dynamics capable of generating alternate states (Van De Koppel et al., 2001).

The response of opportunistic species to disturbance depends on the magnitude or scale of disturbance and on life history traits related to the timing of reproduction, mode of development, mobility and dispersal strategies (Levin, 1984). While we argue that spatial scale and/or disturbance intensity are key for the development of opportunistic responses, in a more general sense they represent proxies for relative isolation affecting both the supply of colonists and the potential for biotic interactions or resource supply that constrain the population dynamics of opportunists within the disturbed patch. Thus, the absolute spatial scale or intensity is not necessarily important, but rather reflects the magnitude of opportunity provided to the opportunist to thrive. This opportunity and subsequent response may entail both resources, such as space and food, and the release from negative species interactions (e.g., competition, predation). The relative degree of isolation will be defined by the mobility of colonists interacting with time, space and habitat. The 'isolation' issue might serve as a plausible explanation for why some small-scale colonisation tray studies (e.g. McCall, 1977; Grassle, 1977; Bonsdorff, 1989), representing small-scale disturbances, may still exhibit opportunistic responses as they may be mimicking larger scale disturbances in terms of isolation and 'enemy-free space'.

Scale-dependent opportunistic responses are most likely influenced by a combination of extrinsic (e.g., hydrodynamic and habitat conditions) and intrinsic (e.g., life history characteristics) factors. We argue that

release from interference and exploitation competitive interactions (e.g., release from habitat modifiers such as tube-mat forming species and bio-engineers) and/or the freeing of food and space resources are important drivers for the development of scale-dependent opportunistic responses. Thus, this does not preclude transient opportunistic responses from occurring after small-scale disturbances (e.g. Norkko and Bonsdorff, 1996b; Zajac and Whitlatch, 2003), for example when involving localised increases in food sources and aggregations of mobile consumers (Norkko and Bonsdorff, 1996c). There is some evidence to suggest that the scale dependence of opportunistic responses might also be common in some widely contrasting marine and terrestrial systems, but studies explicitly contrasting different scales or intensities of disturbance are necessary for elucidating these patterns. For example, Dudgeon and Petraitis (2001) study of scale-dependent recruitment patterns on rocky shores showed strong scale-dependent patterns with increasing recruitment densities of barnacles (*Semibalanus balanoides*) as a function of experimental clearing size. A recent study examining changes in bird abundance after wildfires in mixed conifer forests demonstrated that some bird species (e.g. hairy woodpeckers) exhibited increasingly opportunistic responses with increasing previous fire severity (Smucker et al., 2005). Rydgren et al. (2004) show that the magnitude of opportunistic responses by some pioneer plant species in boreal forests was determined by disturbance severity. In a study examining spatial scale-dependent responses by colonising annual plants in prairie grasslands, McConnaughay and Bazzaz (1987) demonstrated increased species performance (survivorship, vegetative biomass, and seed biomass) for several species in response to increased gap size due to greater release of resources.

The scale and intensity of disturbance has profound influences on the magnitude of opportunistic responses and the nature of successional processes following disturbance. This has important implications for our ability to generalise models of disturbance and recovery; moreover, it emphasises the need for considering scale (and relative isolation) in the design and interpretation of experiments, especially if we want to advance our understanding of the resilience of natural communities, and highlights the value of using large-scale real-world data sets to help design and interpret experimental work, and vice versa.

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