

**WATER QUALITY AND STRESS INDICATORS
IN MARINE AND FRESHWATER ECOSYSTEMS:
LINKING LEVELS OF ORGANISATION
(INDIVIDUALS, POPULATIONS, COMMUNITIES)**

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From the individual to the community and beyond: water quality, stress indicators and key species in coastal ecosystems

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This review examines water quality and stress indicators at levels of organisation from the individual to the community and beyond by means of three case studies concentrating on rocky shores within the north-east Atlantic.

Responses of dogwhelks (*Nucella*) to tributyltin pollution from antifouling paints is examined as the main case study. There are effects at the individual level (development of male sexual characteristics in the female leading to effective sterility) and population level (reduction in juveniles, few females and eventual population disappearance of dogwhelks in badly contaminated areas) but information on community level effects of dogwhelk demise is sparse. Such effects were simulated by dogwhelk removal experiments on well studied, moderately exposed ledges on shores on the Isle of Man. The removal of dogwhelks reduced the size and longevity of newly established *Fucus* clumps that had escaped grazing. Removal of dogwhelks also increased the likelihood of algal escapes. In a factorial experiment dogwhelks were shown to be less important than limpets (*Patella*) in structuring communities but still had a significant modifying effect by increasing the probability of algal escapes.

Community level responses to stress on rocky shores are then explored by reference to catastrophic impacts such as oil spills, using the Torrey Canyon as a case study. Recovery of the system in response to this major perturbation took between 10-15 years through a series of damped oscillations.

The final case study is that of indicators of ecosystem level change in response to climate fluctuations, using ratios of northern (*Semibalanus balanoides*) and southern (*Chthamalus* spp.) barnacles. Indices derived from counts on the shore show good correlations with inshore sea-water temperatures after a 2-year lag phase. The use of barnacles to measure offshore changes is reviewed.

The discussion considers the use of bioindicators at various levels of organisation. Species which are good at the cellular or individual level are not useful at the population or community level – particularly if they have a planktonic stage leading to recruitment fluctuations. The lack of community level responses to tributyltin is discussed and the need for further experimental work on rocky shore interactions, particularly on *Mytilus*-dominated shores, is highlighted. The importance of monitoring recovery of perturbed systems as a means of cross-calibrating and integrating bioindicators at different levels of organisation is emphasised.

Introduction

In any aquatic community certain species are more susceptible than others to water quality problems. These species have the potential to be indicators of pollution or “bioindicators”,

particularly if detectable sub-lethal effects are expressed in an obvious manner or accumulation from the environment occurs in response to very low levels of pollution (Phillips 1977, 1980; Bryan *et al.* 1980; Bryan 1984). Thus if body concentrations increase or if responses can be detected at the individual or sub-individual level (i.e. cellular and tissue levels) then an early warning can be given for possible significant effects at the population, community or ecosystem level of organisation. Additionally, responses to stress (see Underwood 1989 for definitions) at the sub-individual and individual levels of organisation can be used to trace the furthest extent of influence of point sources of pollution.

Effects at the individual level will express themselves at the population level if reproduction and hence recruitment is impaired. In organisms with a pelagic phase recruitment varies considerably so that advected propagules from elsewhere may mask any localised reductions in reproductive output. Population level effects will also manifest themselves if the risk of mortality is enhanced or if direct mortality occurs due to pulses of pollutants or episodic events such as anoxia in response to eutrophication. Again some species may be especially susceptible, lacking the behavioural or physiological responses needed to avoid exposure or due simply to being less tolerant. Community level effects will only be apparent if several species are affected or if a particularly sensitive species is important in structuring the community (e.g. a "keystone species" *sensu* Paine 1966).

To avoid undue generalisation this paper focuses mostly on north-east Atlantic rocky shores (see Hawkins *et al.* 1992a for review). It uses the responses of the dogwhelk *Nucella lapillus* to organotin leachates from antifouling paints as a case study. Effects at the sub-individual, individual, and population level are reviewed to illustrate the usefulness of this species as an indicator. The consequences of the individual and population level changes on communities are then explored using some unpublished examples of manipulative field experiments designed to investigate the role of predation by *Nucella* on British rocky shore communities. The subtle community level effects of dogwhelk demise on rocky shores are compared with the dramatic effects of kills of limpets (*Patella*) following oil spills and red tides. On a broader scale, rocky shore indicators of the effects of decadal-scale global climatic change are briefly touched upon.

In the final section the use of bioindicators at different levels of organisation on rocky shores is discussed. The reasons for the lack of expression of community level effects of tributyltin pollution on rocky shores are considered. Hence the case is argued for studies of the population dynamics and community role of current and potential indicator species. We also emphasise the need for long-term observations, made in parallel with manipulative experiments, if community level responses are to be detected and understood against the background of natural variation. A plea is made for the study of recovery of polluted systems at all levels of organisation.

Case study 1. The effect of tributyltin on *Nucella lapillus*

From the individual to the population

Since the early 1980s many studies have highlighted the environmental impact of pollution caused by the biocide tributyltin (tributyl tin, TBT) when used in antifouling paints (see Rexrode 1987 and Bryan & Gibbs 1991 for reviews). The magnitude of these effects was first realised when the collapse of the French oyster fishery in Arcachon Bay was attributed to the increased usage of tributyltin on the boats in the harbours nearby (Alzieu *et al.* 1986). Previously it had been thought that, due to the large dilution factors involved, the concentrations of TBT present in the water posed no direct threat to marine organisms (Bellinger & Benham 1978).

Although a multitude of organisms have been shown to be susceptible to pollution from TBT (Fig. 1), none are as sensitive or have such clearly defined responses as those which are seen in

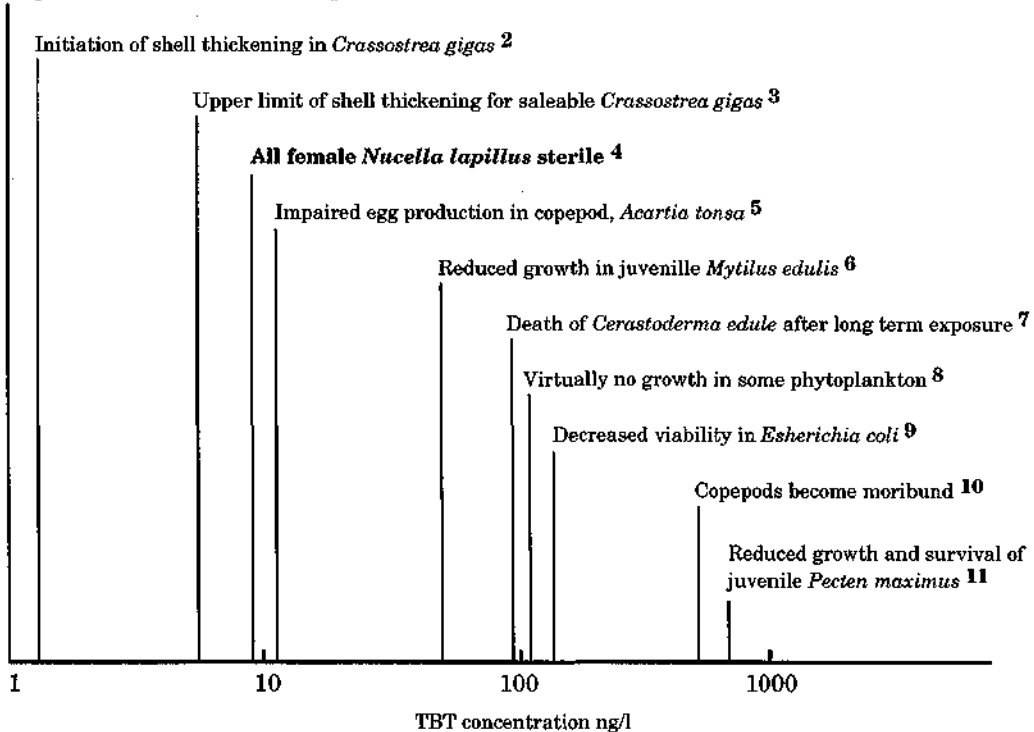
Imposex initiated in *Nucella lapillus*¹

Figure 1. Sensitivity to tributyltin contamination (ng l^{-1}) of various marine organisms. The responses range from subtle effects on individuals to acute effects directly affecting populations. Note the use of a logarithmic scale. Superscript numbers refer to references (¹Gibbs *et al.* 1988; ²Chagot *et al.* 1990; ³Thain *et al.* 1987; ⁴Gibbs *et al.* 1988; ⁵Johansen & Møhlenburg 1987; ⁶Salazar & Salazar 1991; ⁷Beaumont 1988; ⁸Beaumont & Newman 1986; ⁹Pettibone & Cooney 1986; ¹⁰U'ren 1983; ¹¹Paul & Davies 1986 and Davies *et al.* 1986).

stenoglossan gastropods (Gibbs *et al.* 1991a). The common dogwhelk *Nucella lapillus*, which occurs on both sides of the North Atlantic, is particularly vulnerable. Tributyltin induces the development of male sexual characteristics in female dogwhelks (Bryan *et al.* 1986, 1988) a phenomenon termed "imposex" (Smith 1980). The link between imposex and TBT was first described in *Nassarius obsoletus* (Smith 1981) but has now been reported in up to 45 species of stenoglossan gastropods world-wide (Ellis & Pattisina 1990). In the case of *Nucella lapillus* imposex development is initiated at environmental concentrations of TBT below 0.5 ng Sn l^{-1} and is expressed in a concentration dependent manner (Gibbs *et al.* 1988).

The effects of TBT on *Nucella lapillus* are now well documented at the sub-cellular, individual and population levels (see Fig. 2). The biochemical changes responsible for the development of imposex are thought to be a consequence of an increase in the steroid hormone testosterone in the female. It is possible that on exposure to TBT the cytochrome P-540 dependent aromatase responsible for the conversion of testosterone to oestradiol 17β is inhibited, increasing the testosterone titre in the individual (Gibbs *et al.* 1991b). The direct injection of testosterone into female dogwhelks in the absence of TBT causes an increased expression of imposex (Spooner *et al.* 1991).

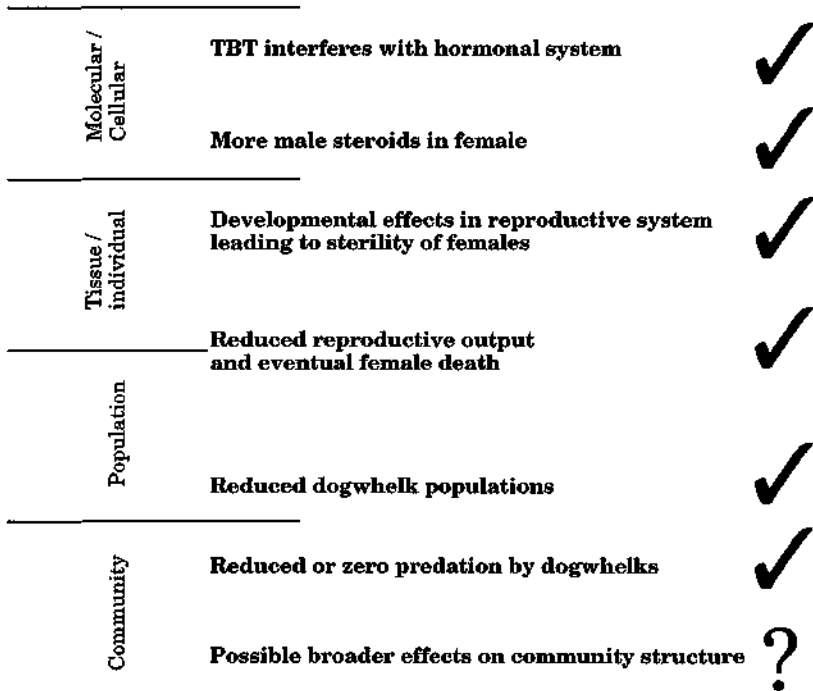


Figure 2. Summary diagram of the known effects of tributyltin at different levels of organisation.

Table 1. Summary of the effects of tributyltin (TBT) exposure on the reproductive system of female *Nucella lapillus*. Effects are expressed as measurements of TBT contamination in water (ng Sn l^{-1}), relative penis size (RPS, per cent) and vas deferens sequence (VDS) (Gibbs *et al.* 1988).

TBT in water	RPS index	VDS index	Effect on reproductive system
< 0.5	< 5	< 4	Breeding normal. Development of penis and vas deferens.
1–2	40+	4–5 (+)	Breeding capacity retained by some females; others sterilised by oviduct blockage. Aborted capsules in capsule gland.
3–5	90+	5 (+)	Virtually all females sterilised. Oogenesis apparently normal.
10+	90+	5	Oogenesis suppressed. Oocytes resorbed. Spermatogenesis initiated.
20	90+	5	Testis developed to variable extent. Vesicula seminalis with ripe sperm in the most affected animals.
100	90+	5	Sperm-ingesting gland undeveloped in some 'females'.

The extent of imposex development can be measured by two indices: relative penis size (RPS) and vas deferens sequence (VDS), between which there is a significant relationship (Gibbs *et al.* 1987). The RPS compares the bulk of the female penis to that of the male within the same population. The VDS index consists of six stages (Fig. 3; Gibbs & Bryan 1987). These categorise the development of the penis and vas deferens in affected females from their initial appearance and growth (stages 1–4). The continual development of the vas deferens subsequently leads to occlusion of the genital papilla (stage 5); this in turn prevents the release

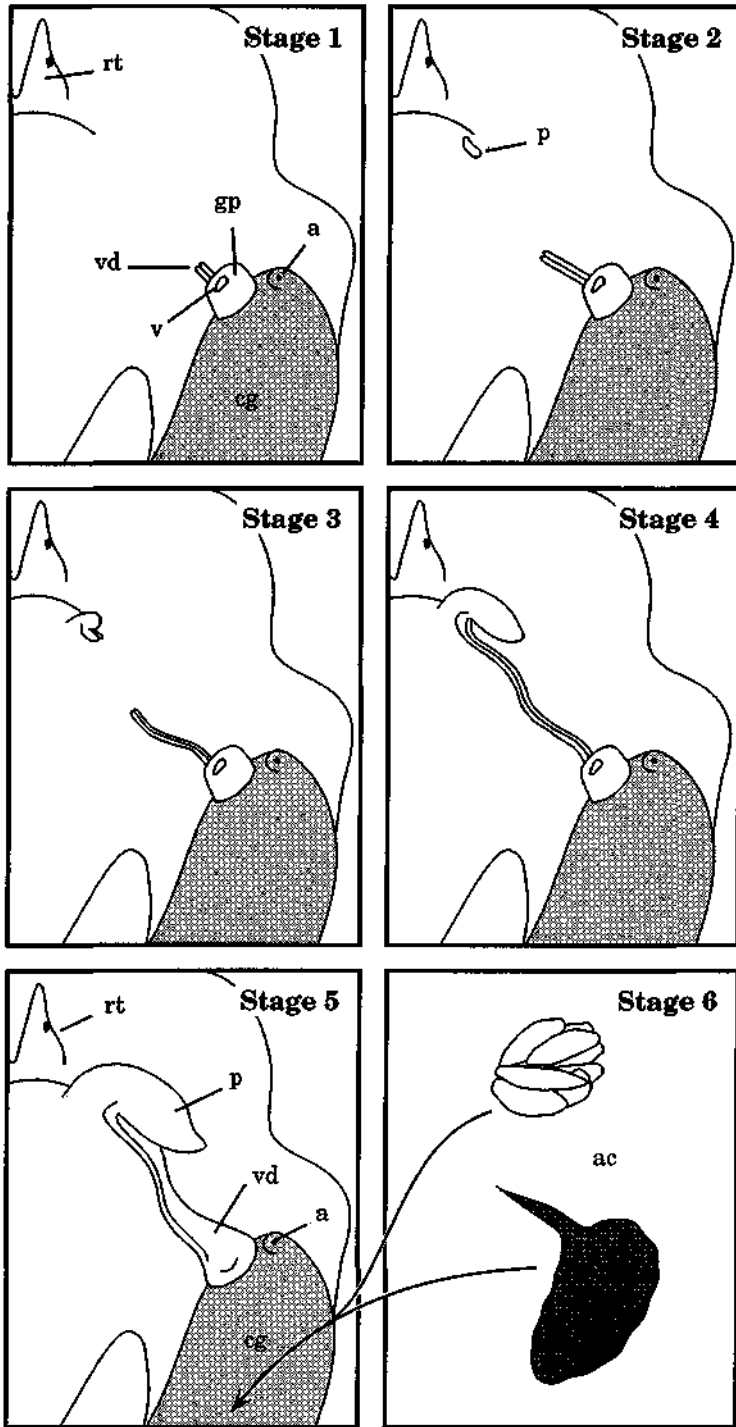


Figure 3. Six stages in the development of imposex from its initiation (stage 1) to sterilisation (stage 5) and subsequent accumulation of aborted capsules in the capsule gland (stage 6). Abbreviations: a, anus; ac, aborted capsule masses; cg, capsule gland; gp, genital papilla; p, penis; v, vulva; vd, vas deferens. (Redrawn from Gibbs & Bryan 1987).

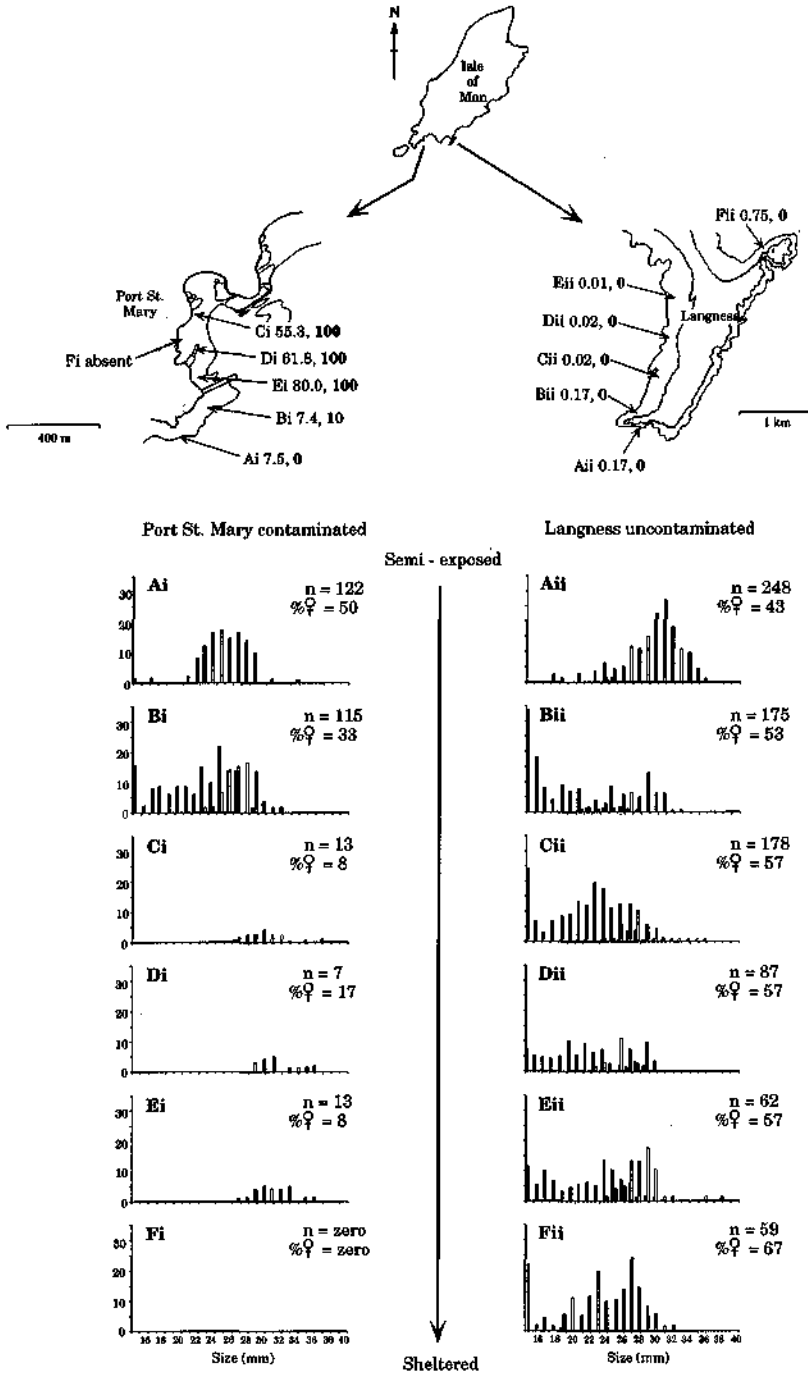


Figure 4. Comparing dogwhelk populations along a tributyltin-contaminated (Port St Mary) and uncontaminated (Langness) gradient of wave exposure on the Isle of Man. Sites of similar wave exposure have been compared from A (semi-exposed) to F (sheltered). Imposex (Relative Penis Size values) and the percentage of sterile females (in bold) in the population are shown at Port St Mary (left) and Langness (right). The histograms denote population structure on shores of similar wave exposure (Ai to Fi and Aii to Fii) and indicate the percentage of females in the samples collected. (Modified from Spence *et al.* 1990a).

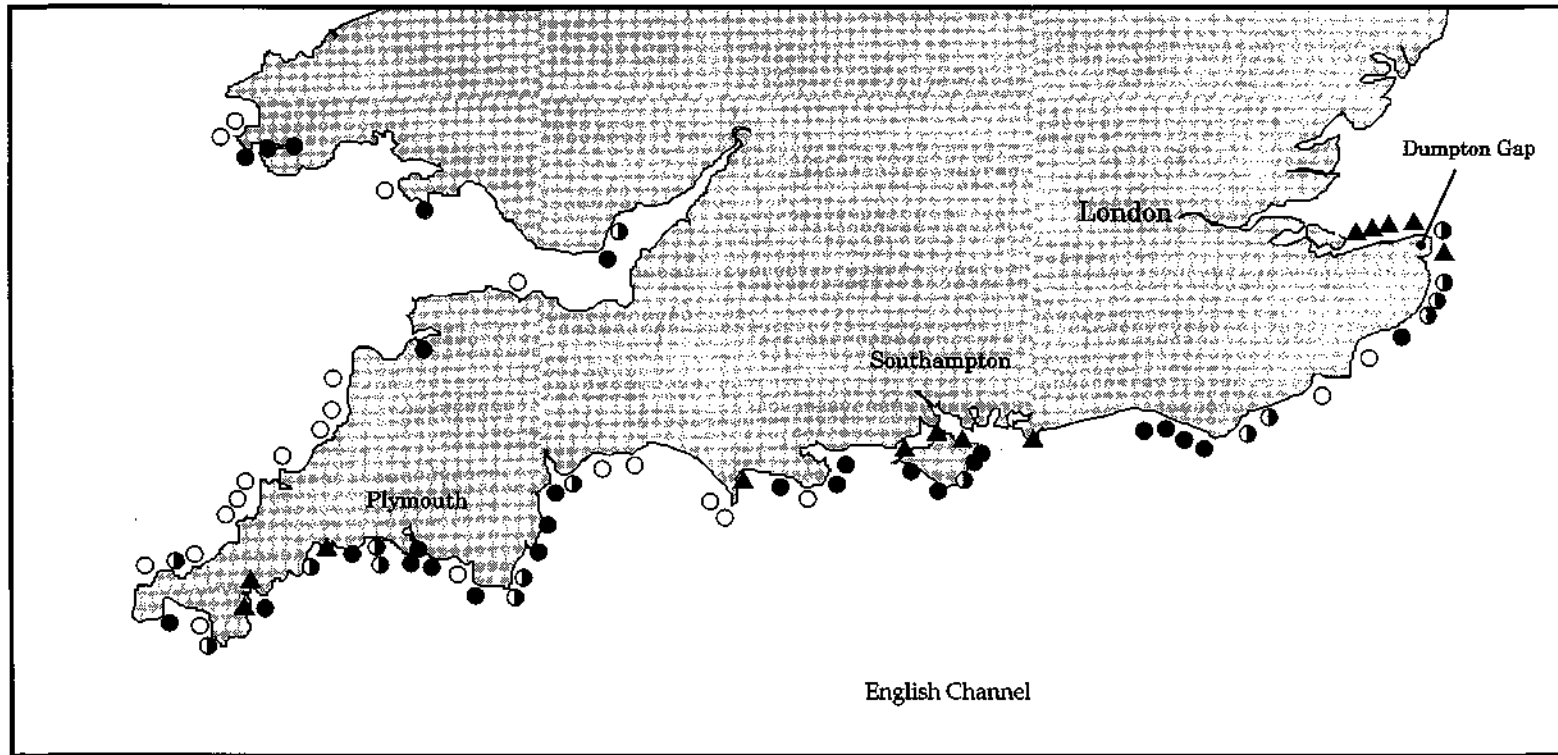


Figure 5. Incidence of sterility in female *Nucella lapillus* around southern Britain (1986–1989). (○) zero %; (◐) less than 50%; (●) over 50%; triangles indicate a population absent where previously recorded (from Bryan & Gibbs 1991). The position of Dumpton Gap is also marked on the map.

of egg capsules which subsequently build up in the capsule gland (stage 6). These latter stages (5 and 6) render the female effectively sterile. The build-up of aborted capsules eventually ruptures the capsule gland of the female, leading to the death of the individual.

Imposex has been found in populations of *Nucella* throughout the British Isles (Bryan *et al.* 1986; Bailey & Davies 1988; Spence *et al.* 1990a) and Europe (Fioroni *et al.* 1991; Oehlmann *et al.* 1993). The level of sensitivity and development of imposex in *Nucella* in response to TBT is uniform throughout its range (Gibbs *et al.* 1991a). Only at a few isolated sites do populations exist where no effects are seen (Bailey & Davies 1989; Spence *et al.* 1990a).

At environmental concentrations of 1–2 ng Sn l⁻¹ some females become sterilised (Table 1). When environmental levels reach 4 ng Sn l⁻¹ most females in the population are unable to breed (Gibbs *et al.* 1988). At highly contaminated sites juvenile *Nucella* may become effectively sterile before ever being able to breed (Gibbs & Bryan 1987). As a consequence of the direct development of *Nucella*, which lacks a planktonic larval stage, and the relative immobility of adults, there is a scarcity of juveniles at affected sites. The structure of the population is thereby altered (Bryan *et al.* 1986), subsequently becoming dominated by adult males before it disappears altogether (Fig. 4; Spence *et al.* 1990a). Effectively, *Nucella* has been exterminated from many areas throughout its European range (Norway to Portugal: Gibbs *et al.* 1991a), most notably on shores adjacent to harbours or marinas where TBT levels have extended above the critical 2 ng Sn l⁻¹, often by several orders of magnitude (Cleary & Stebbing 1985). This situation has been especially severe on the south coast of England (Gibbs *et al.* 1991c) where virtually all dogwhelk populations have been affected to some degree (Fig. 5; Bryan & Gibbs 1991).

In the UK a ban has been imposed on the use of organotin paints on boats less than 25 metres in length, and on equipment used in mariculture since 1987 (Duff 1987). Evidence suggests that water concentrations of TBT have decreased in some areas since 1987 (Bryan *et al.* 1993), as has the degree of imposex expression in some populations (Evans *et al.* 1991). Although imposex itself is irreversible (Bryan *et al.* 1987), juveniles entering the population are less affected as environmental concentrations drop (Bailey & Davies 1991). Measurement of the degree of imposex in immature females that have yet to breed provides the best gauge to short-term exposure to TBT levels (Gibbs *et al.* 1987). The process of recovery is likely to be slow. In French waters the use of antifouling paints was restricted by legislation in 1982 (Alzieu 1986). Seven years later, in 1989, the levels of TBT in south-west Brittany were still sufficient to cause a high level of imposex in *Nucella* populations (Gibbs *et al.* 1991a). Observations from dogwhelk populations on the south coast of England show a slow rate of recovery (Spence & Proud unpublished); in some areas any chance of recovery is likely to be inhibited due to the continued legal use of TBT on ships greater than 25 metres in length (Davies & Bailey 1991).

One enclave at Dumpton Gap, Kent (Fig. 5), has survived despite those surrounding being wiped out. This population appears to have a genetic disorder which leads to the incomplete development of the male genital system, the "Dumpton syndrome". It is estimated that around 10% of the males in this population are affected, with non-development or under-development of the penis. This deficiency is also reflected in the development of imposex in females. The result is that the females express a variable response to TBT pollution and as a consequence the sterilising effect is lessened and breeding continues in some females (Gibbs 1993).

Since the initial visible stages of imposex in *Nucella* develop at levels of TBT < 0.5 ng Sn l⁻¹, imposex can be used as a sensitive bioindicator of TBT pollution (Gibbs *et al.* 1987). The monitoring of imposex in other stenoglossan gastropods now provides not only a local but a world-wide indicator of TBT pollution (Bright & Ellis 1990; Ellis & Pattisina 1990; Spence

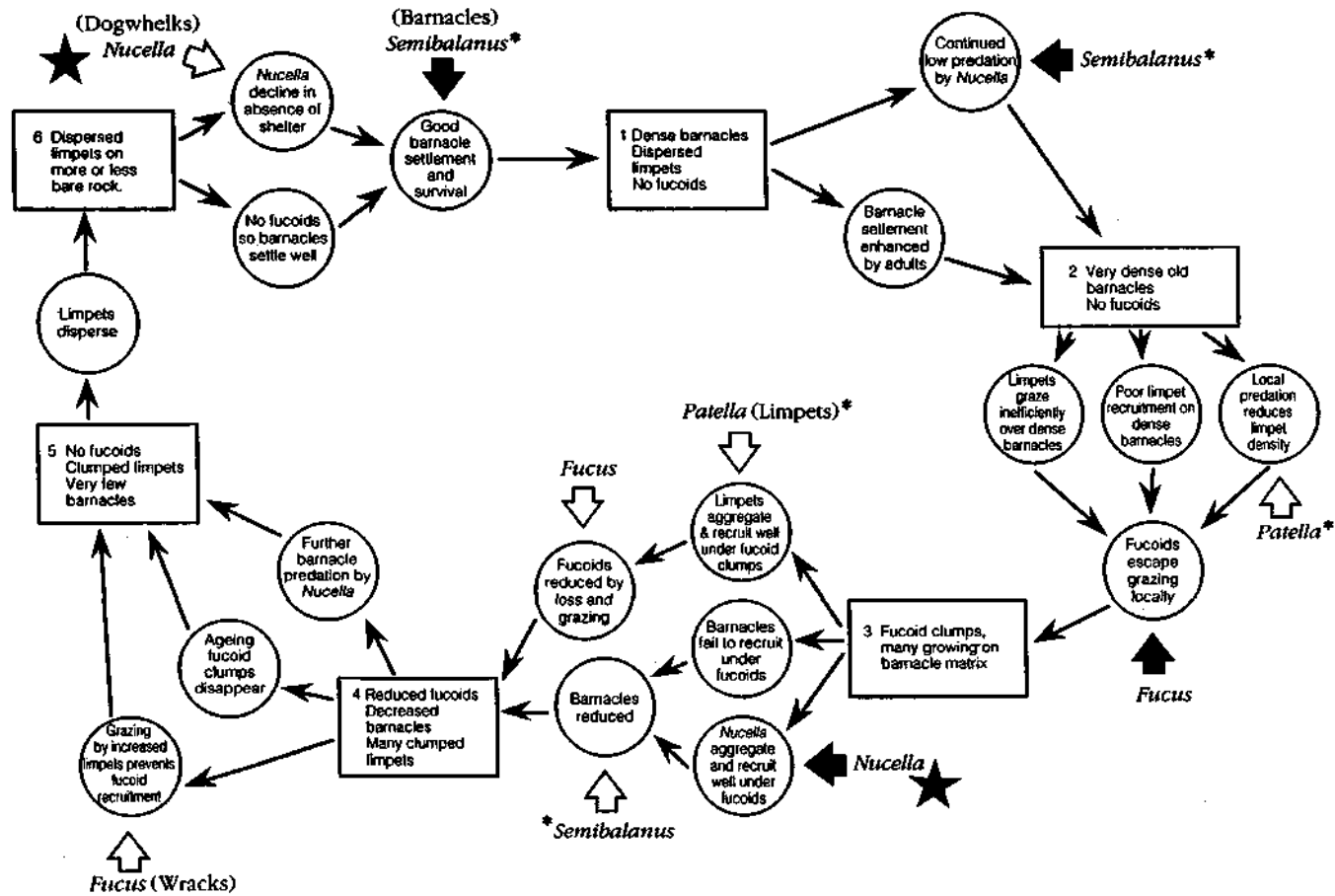


Figure 6. A simplified flow chart to represent the sequence of events in the mid-tide level of a moderately exposed shore on the Isle of Man over several years. The six numbered rectangles are changes in the cycle. The circles are intrinsic biological processes generating and maintaining the cycle. The heavy arrows are where very good recruitment of the named species either promotes (solid arrows) or inhibits (open arrows) the progress of the cycle. The asterisks indicate where settlement is from a highly variable planktonic phase (modified from Hartnoll & Hawkins 1985). The large stars indicate where *Nucella* are important and have been examined experimentally in this study.

et al. 1990b; Smith & McVeagh 1991). In addition to the clear responses to TBT and world-wide distribution, their accessibility, commonness and ease of identification makes these gastropods ideal bioindicators for contamination studies (Bryan *et al.* 1980, 1985; Bryan 1984).

Whelks have been shown to be important predators in rocky shore communities world-wide (Connell 1961, 1970; Dayton 1971; Menge 1976, 1978; Menge & Sutherland 1976; Underwood 1978; Fairweather *et al.* 1984; Fairweather 1987, 1988a,b). Despite speculation (Spence *et al.* 1990a; Bryan & Gibbs 1991; Hughes & Burrows 1993) no studies have so far shown a clear community effect as a consequence of TBT-induced dogwhelk decline. The following section addresses the problem by experimental manipulation of dogwhelk densities.

Experimental investigations into the role of Nucella lapillus in shore communities

On moderately exposed rocky shores in Britain a natural cycle of barnacle–fucoid dominance exists, mediated by the grazing of patellid limpets (Fig. 6) (Burrows & Lodge 1950; Southward 1956, 1964; Hawkins & Hartnoll 1983; Hartnoll & Hawkins 1985; Hawkins *et al.* 1992a; [summarised in Hawkins & Jones 1992]). This cycle of dominance is generated in part by stochastic recruitment fluctuations but also by deterministic cyclical events following escapes of fucoids from grazing by limpets (*Patella vulgata*) (Hartnoll & Hawkins 1985; Hawkins *et al.* 1992a). High barnacle densities reduce the foraging efficiency of *Patella*, allowing vulnerable algal germlings to “escape” from grazing and form an algal clump on the barnacle matrix (Hawkins 1981a,b). These clumps create a valuable resource as food and shelter for many intertidal organisms. With time the *Fucus* canopy thins and the sheltering organisms disperse; the bare area left is then recolonised by barnacles (Hawkins & Hartnoll 1983). *Nucella* is an important predator on barnacles (Connell 1961) and uses the shelter of the *Fucus* clump from which to forage: as a result it would be expected to play an important role in this cycle. The extent of this role was investigated in a series of manipulative field experiments at Kallow Point, Port St Mary, Isle of Man.

Rather than using the traditional experimental approach of caged controls and treatments, dogwhelks were removed from experimental areas every 1–2 days. This created a control with dogwhelks present, and treatment areas with reduced numbers of dogwhelks, akin to shores with very small or absent populations of dogwhelks.

The first set of experiments involved determining the influence of dogwhelks on the survival of newly established *Fucus* clumps. Dogwhelks were continually removed from replicate clumps of *Fucus vesiculosus* between January and September 1993. Those clumps from which the dogwhelks had been regularly removed were found to grow larger (Fig. 7a) and denser and remain attached longer compared to those clumps where the dogwhelks had been allowed to shelter and feed. The reason for this result was that the dogwhelks, by eating the barnacles to which the *Fucus* plants were attached, effectively undermined the foundations of the algal clump.

Other experiments examined the importance of *Nucella* in initiating the *Fucus* cycle. Owing to the low numbers of *Nucella* actively feeding on the barnacle-dominated horizontal areas, these experiments were conducted on vertical faces of ledges at Kallow Point. The removal of dogwhelks over an 18-month period from replicated areas on this shore produced dense patches of barnacles compared to the control areas on which the dogwhelks were allowed to feed. As a consequence the foraging efficiency of *Patella vulgata* in these areas was reduced and *Fucus* escapes occurred amongst the barnacles. A third set of experiments investigated the combined effect of the removal of *Nucella* and *Patella* in a factorial experiment. After one year the areas where the dogwhelks had been removed, but limpets remained, were covered in densely packed barnacles compared to a less dense cover in the control areas (Fig. 7b). All of the areas where

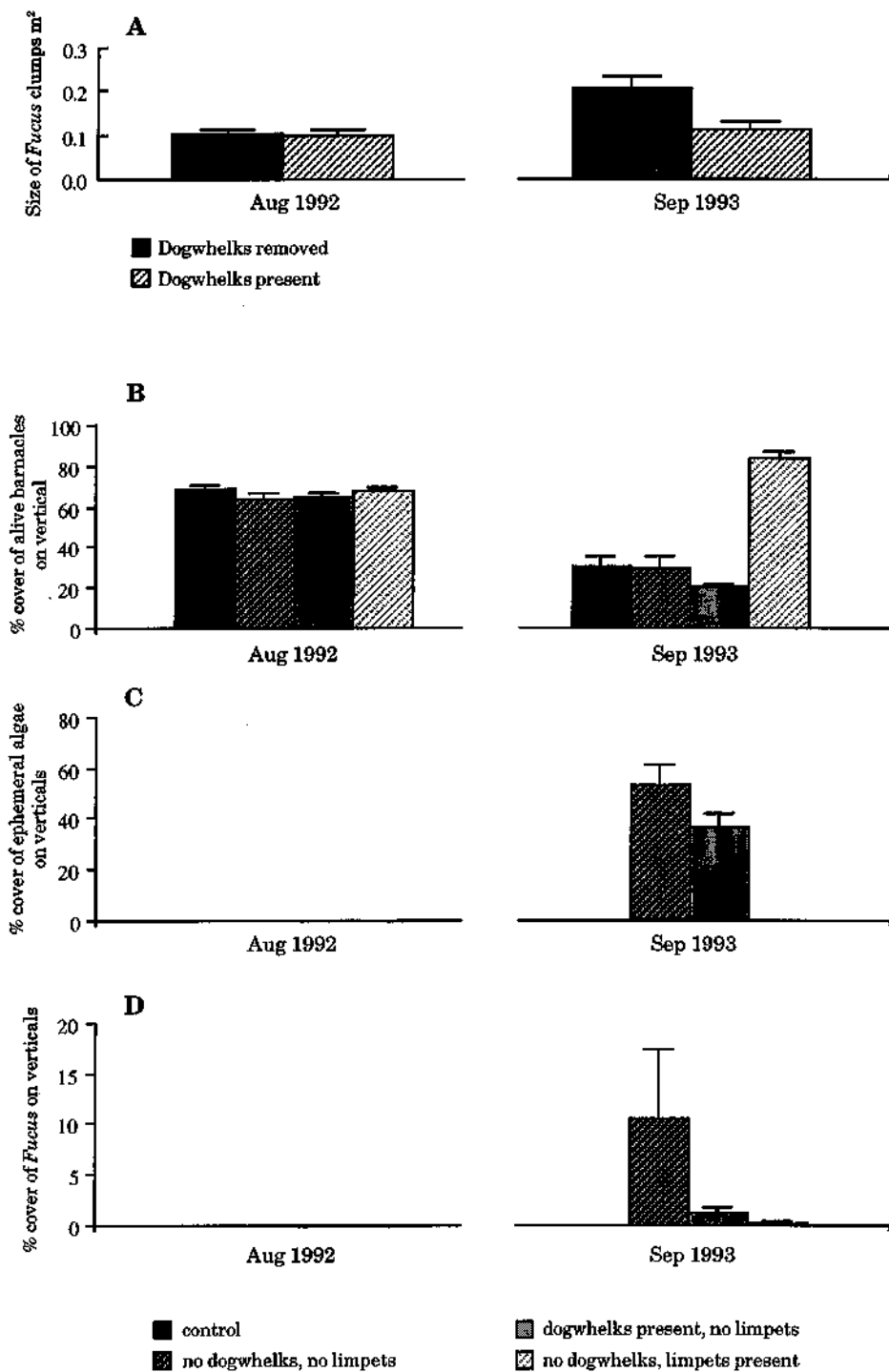


Figure 7. Effects of the experimental manipulation of dogwhelk and limpet densities at Kallow Point, Port St Mary. The size of *Fucus* clumps before and after dogwhelk removal (7A) and the percentage cover of barnacles (7B), ephemeral algae (7C) and *Fucus* (7D) on vertical ledges are shown before and after a factorial dogwhelks and limpet removal experiment.

limpets were removed had a cover of algae (Fig. 7c). This was greater where dogwhelks had also been removed, and consisted of green algae plus small clumps of *Fucus* (Fig. 7d).

Although less important than limpets, dogwhelks clearly modify the effectiveness of limpet grazing. Denser barnacles in the absence of limpet grazing increase the likelihood of algal settlement and escapes from grazing, thus initiating the formation of *Fucus* clumps. These escapes are less likely if dogwhelks are present. In the presence of dogwhelks the longevity of these clumps is reduced. In the absence of dogwhelks, escapes are more likely and will persist longer.

Case study 2. Community level stress – impacts of oil spills

The difficulties in detecting low-level chronic stress at the community level on rocky shores have been appreciated for a long time (Lewis 1976, 1977; Hawkins & Hartnoll 1983; Hiscock 1985). In most cases for community level effects to be expressed, and to be detected, either the stress must come from a point source (e.g. a large effluent), a catastrophic event (e.g. an oil spill or the aftermath of a red tide), or it must be a gradual effect measured over a long period of time (e.g. climatic changes). Recently the need for properly designed impact assessments with replicated spatial and temporal control areas has been re-emphasised (Underwood 1992).

Surprisingly few studies have been published on the effects of point sources on rocky shore communities. In general there is a tendency for shorter-lived ephemeral algal species to dominate the community near such outfalls or point sources of pollution. This can be due to direct enrichment by nutrients (e.g. from sewers; Burrows 1971; Borowitzka 1972) or because grazing species, space-occupying animals, and perennial algae, are rarer (e.g. Littler & Murray 1975). It is also possible that ephemeral green algae can out-compete perennial algal turfs in these areas, smothering them (see Cox & Norton in this volume).

The best-recorded community level impacts are from oil spills. These have been well-documented on rocky shores (Clark 1989). We focus here on the Torrey Canyon oil spill and clean-up from which we now have over 20 years of observations on the recovery of the affected rocky shores. We also have a good background knowledge of spatial and temporal variation of these systems to put the results into context (see Hawkins *et al.* 1992a for review). The short-term effects of the Torrey Canyon oil spill were well recorded at the time (Smith 1968). It was soon very apparent that the major damage was not caused by the oil itself but a massive and excessive treatment of the shores with toxic "first generation" dispersants. These were later shown to be very toxic to marine life (Corner *et al.* 1968). Over 14,000 tons of dispersant were poured onto the 10,000 tons of oil that came ashore in Cornwall.

The following summary is based largely upon Southward & Southward (1978) and Hawkins & Southward (1992). The dispersants killed the grazer *Patella vulgata* as well as other herbivores (e.g. *Monodonta lineata* and *Littorina* spp.) to a lesser extent. This reduction led to dense swards of ephemeral green algae followed by an equally dense growth of fucoids (Fig. 8a). This proliferation of fucoids occurred on many of the exposed and moderately exposed shores of south-west Cornwall – coincidentally showing the importance of limpet grazing in preventing the extension of fucoids on to exposed shores and confirming earlier experiments on the Isle of Man (Jones 1948; Lodge 1948; Burrows & Lodge 1950; Southward 1956; summarised in Southward 1964). Some dogwhelks survived the spill and were able to reproduce locally under the shelter of the fucoid canopy (Bryan 1969). Barnacles were not greatly affected by either the oil or the dispersants used, except in areas cleaned repeatedly. However, they succumbed to smothering by algae over the next few years plus predation from the now dense populations of dogwhelks. Of greatest significance was the highly favourable environment created by the fucoids for the settlement and early survival of *Patella vulgata*

(Fig. 8b,c,f). A huge recruitment occurred and these limpets grew rapidly, preventing any further algal recruitment (Fig. 8a). When food became scarce they abandoned their usual homing habits and migrated, lemming-like, along the shore in a front before, in many cases, dying. This heavy grazing pressure led to an unusual bare phase on the shore in the late 1970s (Southward & Southward 1978; Hawkins *et al.* 1983). Subsequently there was a smaller increase in fucoid cover which then fluctuated throughout the 1980s at a level more typical of a shore of this exposure (Fig. 8a). The shore had returned by then to small-scale spatial and temporal fluctuations typical of rocky shores on the west coast of Britain (Hawkins *et al.* 1983; Hartmoll & Hawkins 1985; Hawkins & Southward 1992; Hawkins *et al.* 1992a).

Counts of barnacles were available for 10 years before the oil spill and during the subsequent recovery (Fig. 9). Due to small-scale spatial variation, and recruitment fluctuations, these counts showed considerable changes during the recovery time. Numbers on the high shore took 20 years to reach pre-spill abundance. This slow build-up from successive years of settlement, with relatively low adult mortality, has been confirmed by experiments and observations on other rocky shores in the southwest (Southward unpublished). On the mid-shore, abundance reached previous levels after 10 to 15 years, but numbers have fluctuated considerably since. On the low shore the population increased during the first few years and reached higher numbers than previously, but there has since been much fluctuation, perhaps an effect of changes in predation, settlement of *Mytilus* and variations in the low-water algal mosaic as the ecosystem matured.

Patella depressa did not reappear in any numbers on the studied area until the mid 1980s, partly reflecting climatic change. *P. depressa*, a southern species, became rarer during the late 1970s before increasing in numbers in the mid 1980s; a pattern that has been seen at a variety of sites in the south-west (Southward & Hawkins unpublished observations). It is also possible that the initial dense seaweed phase during re-colonisation did not favour *P. depressa* settlement since this species is rarely found associated with fucoids (Hawkins unpublished). A dense covering of fucoids would also smother the shallow lithothamnia-covered rock pools which typically form its nursery ground (Bowman 1981). At another site nearby, where the rocks are scoured by sand and gravel, preventing a build up of *Fucus*, there was an initial settlement of *P. depressa* in 1968 and 1969 (the end of the warm period), but this was reduced in later years.

By monitoring key species, recovery to normal levels of spatial and temporal variation was found to have occurred within 10–15 years. This recovery was through a series of damped oscillations (Hawkins *et al.* 1983; Hawkins & Southward 1992). Disruption of the community to this vast extent was primarily by widespread killing of the grazer *Patella*, the “keystone” species on these shores.

Similar dramatic disruption of communities can occur after “red tides” of toxic algal species. These have long been known as natural events but in recent years suspicion has grown about their frequency, which may have increased due to coastal eutrophication (Hallegraeff 1993). Southgate *et al.* (1984) documented the effects of a dinoflagellate bloom on the coast of Ireland and its effect on the shore community. Recently, attention has focused on the effects of massive kills off the Swedish west coast caused by a bloom of *Chrysochromulina polyplepis*. This killed up to 99% of the dogwhelks from some areas of the coast and affected the reproductive output of the survivors in the following year (Robertson 1991).

Case study 3. Indicators of ecosystem level change

Barnacles have long been known to respond to climatic change on both geographic (Moore & Kitching 1939; Fischer-Piette & Prenant 1956; see Lewis 1964 for a summary) and temporal scales in the same region (Southward & Crisp 1954, 1956). Continuation of these early surveys

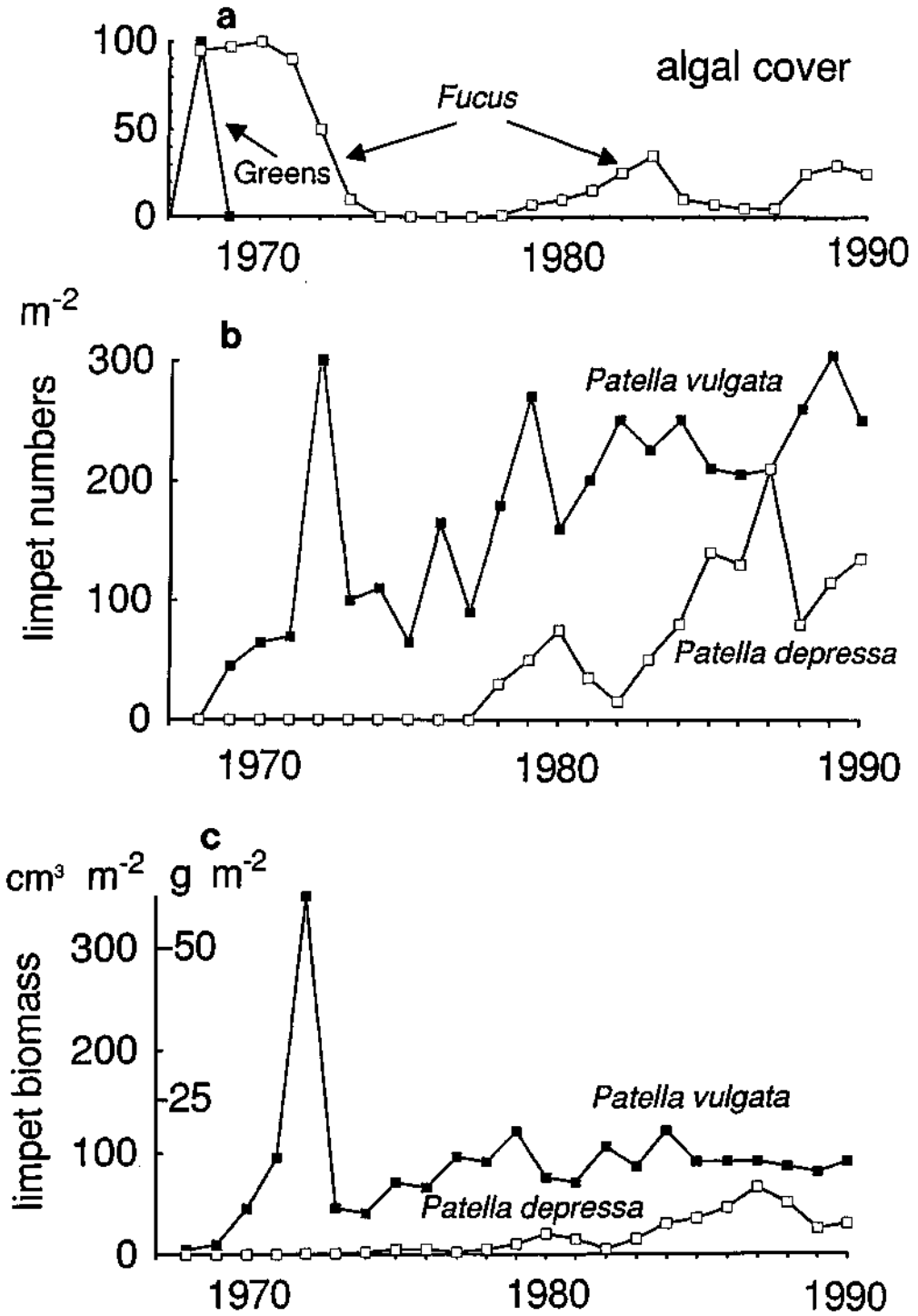
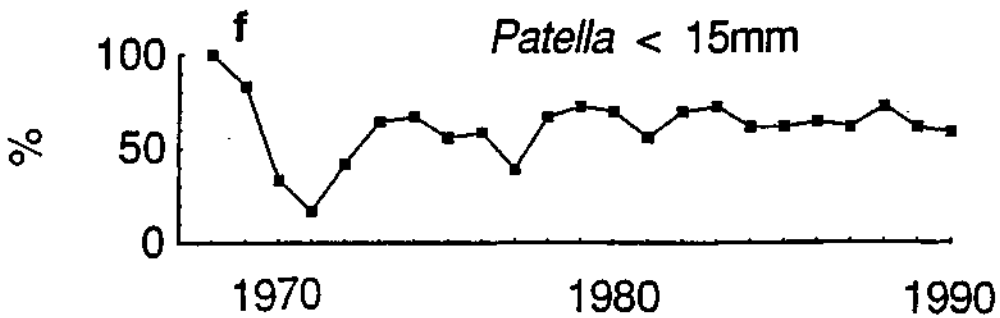
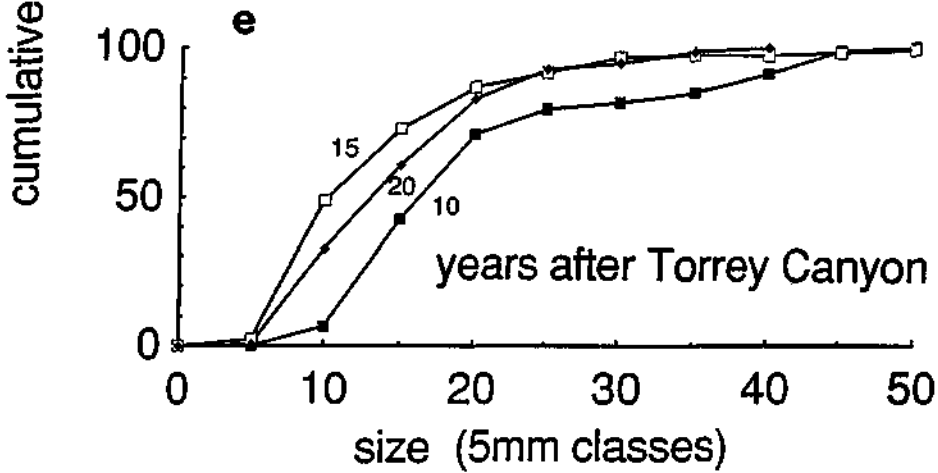
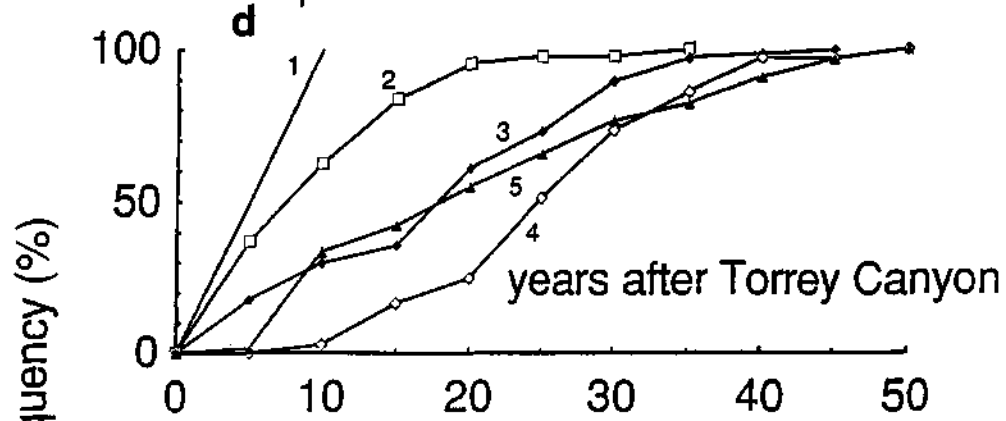


Figure 8. Changes in the abundance of algae (8a), limpet numbers (8b) and limpet biomass (8c), and in the population structure of *Patella vulgata* (8d, 8e) and the percentage of new recruits in the population (8f) at Porthleven, Cornwall, since the Torrey Canyon oil spill. (Redrawn from Hawkins & Southward 1992).

Population structure of *Patella*



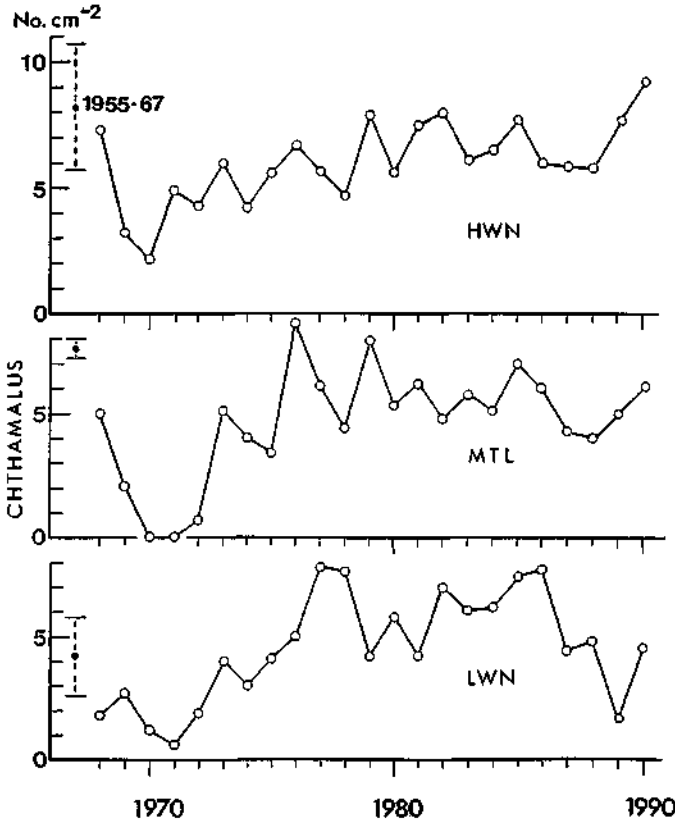


Figure 9. Density of barnacles (*Chthamalus* spp.) at three shore levels at Porthleven, Cornwall. HWN high water neaps, MTL mid tide level, LWN low water neaps. The mean and standard deviation of the counts made before the spill (1955–1967) are shown. (Redrawn from Hawkins & Southward 1992).

in the south-west has produced clear evidence of responses of southern (*Chthamalus* spp.) and northern species (*Semibalanus balanoides*) to climate on decadal scales (Southward 1967, 1980; Southward *et al.* 1975). During warm periods *Chthamalus* spp. predominate, whilst *S. balanoides* does better during colder spells. This relationship can be expressed by various indices (summarised in Table 2). The barnacle indices of warm conditions correlate well with inshore sea-water temperatures after a 2-year time lag (see Table 2 and Fig. 10). This reflects the response time needed for successful reproduction, settlement and recruitment to the adult (counted) population.

Of greater importance is the observation that changes in easily quantified shore animals, such as barnacles, reflect changes that are also occurring offshore. During warm periods (1935–1962) with increased *Chthamalus* numbers, the offshore assemblage in the western English Channel off Plymouth was characterised by pilchard *Sardina pilchardus* and zooplankton indicators such as *Sagitta setosa* (Southward 1984). Zooplankton numbers, including larval fish, were low during this period as were phosphate levels (Southward 1963) whilst warm-water fish (e.g. red mullet *Mullus surmuletus* and red sea-bream *Pagellus bogaraveo*) were commoner (Southward & Boalch 1993).

Prior to the early 1930s and since 1963 a different offshore assemblage was present off Plymouth; this coincided with higher numbers of *Semibalanus balanoides* on the shore. Pre-1930s there was a herring *Clupea harengus* fishery off Plymouth: the chaetognath *Sagitta elegans* and the trachymedusan *Aglantha digitalis* were dominant zooplankton indicator species, zooplankton biomass was an order of magnitude higher than in the intervening period, and winter- and spring-spawning fish larvae were commoner in the plankton. The main fish species were northern gadoids and pleuronectids. Between 1963 and 1972 the system switched back to this assemblage, except that herring never fully returned, instead being replaced by mackerel *Scomber scombrus*, perhaps because of overfishing elsewhere in their range. *Sagitta elegans* and *Aglantha* were abundant again in the zooplankton and penetrated further up the Channel. Phosphate levels eventually declined somewhat, and winter- and spring-spawning fish larvae again became common. Even very northern species of fish, such as the Norway pout *Trisopterus esmarki* and the blue whiting *Micromesistius poutassou*, were caught off Plymouth in some numbers (Southward 1980; Southward & Mattacola 1980).

Table 2. Values of the correlation coefficient (r) between annual mean sea temperatures (Plymouth Sound) and changes in the proportion of the barnacle species (expressed as indices) on the transect near Cellar Beach, River Yealm.

The indices used are given below (from Southward 1991).
 Barnacle index (BI) = $CT/(CT+SB+EM)$,
 Warm index (WI) = $CT/(CT+SB)$,
 Cold or Boreal index (CI) = $SB/(CT+SB+EM)$,
 Neritic index (NI) = $EM/(CT+SB+EM)$,
 where CT = total *Chthamalus* (*C. montagui* + *C. stellatus*),
 SB = *Semibalanus balanoides*,
 EM = *Elminius modestus*.
 The best correlations are shown in **bold** type.

Time periods	Mean sea temperature	
	Annual	5-year smoothed
Same year	Barnacle index	0.55
	Warm index	0.50
	Neritic index	-0.27
	Cold index	-0.47
1-year lag	Barnacle index	0.62
	Warm index	0.58
	Neritic index	-0.27
	Cold index	-0.54
2-year lag	Barnacle index	0.67
	Warm index	0.63
	Neritic index	-0.25
	Cold index	-0.60
3-year lag	Barnacle index	0.64
	Warm index	0.59
	Neritic index	-0.30
	Cold index	-0.55

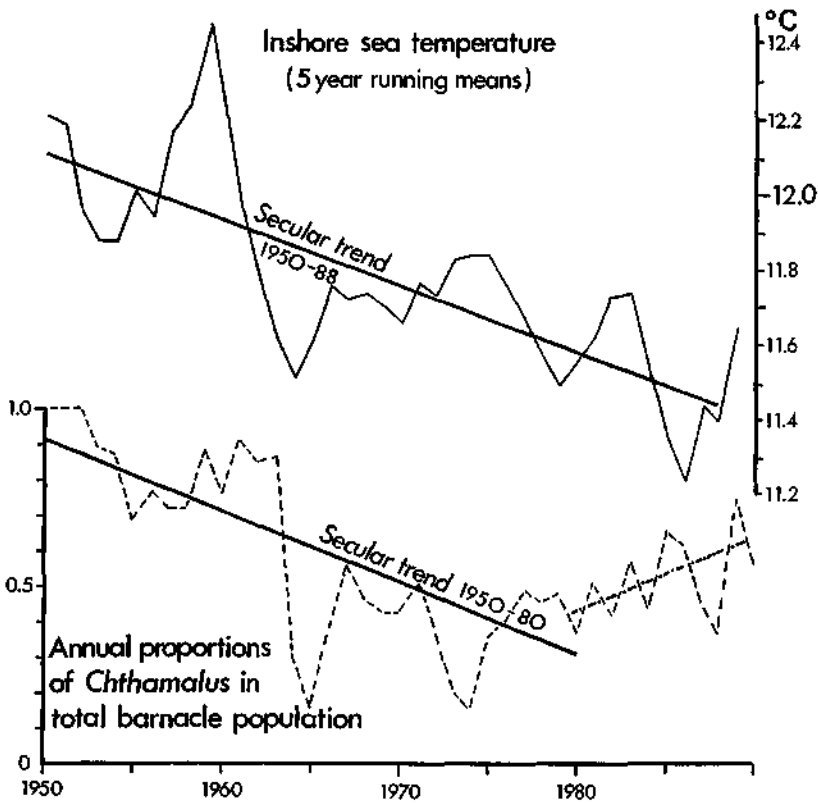


Figure 10. Comparison of changes in inshore sea temperature (upper graph) and fluctuations in the barnacle index (lower graph). The temperature for Plymouth Sound is shown as 5-year running means of the annual means, with the long-term ('secular') trend shown as a linear regression of the annual means against time. The barnacle index is the annual value for all levels on the Cellar Beach transect; the long-term trend from 1950 to the 1970s agrees with the temperature trend, but has diverged since. (Redrawn from Southward 1991).

After 1980 the planktonic ecosystem began to change back towards the warm-water type, with increases in spawning of pilchard (Southward *et al.* 1988). Unfortunately the observations were not continued after 1987, when the Marine Biological Association's environmental responsibilities were taken over by the Natural Environment Research Council's Plymouth Laboratory in 1988, and all long-term monitoring was immediately stopped. The barnacle series at Cellar Beach (Southward 1991) has been maintained as a private venture. It will be interesting to see if this set of observations continues to show increases in *Chthamalus* spp. over the next few years, to levels exceeding those in the 1950s. If it does, then broadscale climatic changes in response to rises of atmospheric levels of carbon dioxide can be invoked. If it does not, then we have just seen another warm phase within a natural cyclical fluctuation. By tracing historical fishing records it is possible to show an alternation between herring and pilchard stretching back over several centuries, to a period before the first regular records of temperatures were made in England (Southward *et al.* 1988). Barnacles are a cheap and effective indicator of such ecosystem level changes.

Discussion

Bioindicators and levels of organisation on rocky shores

Clearly, bioindicators at lower levels of organisation correlate more directly with environmental levels of a known stress than do those at a higher levels. Many rocky shore organisms have been used as bioindicators (Bryan 1984; Bryan *et al.* 1985). In addition they have been used as sources of bioindicator molecules such as metallothioneins (e.g. *Littorina littorea*; Langston & Zhou 1986), as providers of cellular indices (e.g. *L. littorea*; Moore *et al.* 1982; *Mytilus*; Moore 1991), or as individual level indicators (e.g. scope for growth in *Mytilus*; Widdows *et al.* 1980; Willows in this volume). Approaches to the study of stress and pollution at these levels are reviewed by Bayne *et al.* (1985). In contrast, difficulties abound at the population or community level. This is especially so in species with recruitment by planktonic larvae, such as *Mytilus* or *Littorina littorea*, which can colonise contaminated sites from unaffected populations (see comments in Underwood 1989; Underwood & Fairweather 1989). That such a marked population level effect of tributyltin (TBT) can be seen in *Nucella* is due to the nature of the individual level effect which interferes with the reproductive system and the inability of populations to recruit much from elsewhere due to the direct developmental mode exhibited.

From the foregoing account it is clear that at least on rocky shores different bioindicators perform best at different levels of organisation. Also certain organisms (e.g. dogwhelks) can be very sensitive indicators of particular contaminants (e.g. TBT) but not others (e.g. arsenic, which they regulate; Klumpp 1980). Broad-scale larval dispersers (e.g. mussels, *Littorina littorea* and *Patella vulgata*) are often excellent at the sub-individual and individual level but the unpredictability of recruitment makes population level monitoring difficult. In communities where these species occur, recruitment variation makes it very difficult to separate natural fluctuations from any pollution effects – unless the impacts are gross, such as in massive oil spills. Ironically, barnacles showed themselves to be good indicators of global change but have shown little discernible response to *Nucella* decline along the south coast (Southward 1991).

At present considerable effort has gone into developing evermore sensitive sub-individual indicators of contamination (e.g. Dixon & Pascoe, George & Langston and Pulsford *et al.*, all in this volume). These are superb early warning systems and can give an idea of the furthest extent of sub-lethal effects of a point source or a generalised contaminated area (e.g. Liverpool Bay or the southern North Sea). Expression of effects at the individual level are also well documented. These sensitive indices are often criticised (the “so what” syndrome). For a lay person it is easy to accept an ecological impact if there are fewer of a species (population level) or if species composition changes (community level). At the population level the best documented example on rocky shores is the response of the dogwhelk to TBT – a species with direct development. No similar effects have been found in other marine systems with an effect so specific as to affect the reproduction of one species over such a wide geographical area.

In soft benthos the organisms are surrounded by sediments which act as sinks to pollutants. The amount of organic enrichment of the sediment will affect deposit-feeding infauna and in extreme cases render the sediments and the surface layer of the water anoxic. Effects on organisms tend to be direct. In freshwater streams most pollution comes from point sources. It is easy to have an upstream control and look at dilution effects downstream from the source. The species used as indicators have a unidirectional medium flowing over them or live amongst sediments, and are exposed in a more predictable manner. They are also generally short-lived and many are larval stages of insects, thus making very good community level bioassay organisms (Hynes 1960; Wright *et al.* in this volume). Rocky shore communities, in

contrast, typically have multidimensional water movement with mixing and dispersal. Compared to fresh water there is often a change in the chemical state of the contaminant. Large fluctuations in recruitment and a community structured by intense interactions between organisms results in a variable community, often making pollution effects difficult to predict (Lewis 1976; Hawkins & Hartnoll 1983; Underwood 1989).

Why were no community effects detected in response to TBT?

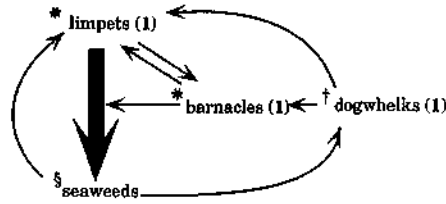
The most badly-affected dogwhelk populations were on sheltered shores where dogwhelks may have a lesser ecological effect. Dogwhelk abundance changes naturally along an exposure gradient, becoming rarer at sheltered sites (Moyses & Nelson Smith 1963; Lewis 1964). Consequently where the TBT contamination has generally been greatest (sheltered sites and harbours) pollution effects have been acting at the edge of the dogwhelk's natural range (Spence *et al.* 1990a). Barnacles are often rare here anyway, and the few dogwhelks present seem to feed on *Littorina obtusata* and *L. mariae* where *Mytilus* is not present. Sheltered shores are characterised by being inherently stable (Hartnoll & Hawkins 1985; Hawkins *et al.* 1985). Only on moderately exposed shores are dogwhelks likely to have much of an effect, particularly if the shore is broken or fissured (Hughes & Burrows 1993). It is on the south coast of England where dogwhelks have been reduced to the greatest extent that we would expect the widespread effects on the community to be seen. That these effects were not detected can be partly attributed to the lack of long-term observations of dogwhelks in the context of the whole community on such shores.

An explanation also lies in the nature of the communities themselves. On the Isle of Man, experimental removal of dogwhelks showed that effects were significant but less than those of limpets. The removal of dogwhelks also enhanced the effects of limpet removal. This was within a reasonably simple interaction web (Fig. 11a) and a species of barnacle capable of heavy settlement to produce a dense population in one year (e.g. *Semibalanus balanoides*). With the more diverse communities on the south coast of England, the removal of any one species is likely to have lesser effects (Fig. 11b), especially as space is rarely saturated by relatively slow-growing *Chthamalus* species (Burrows 1988; Southward 1991). Similarly, on mussel-dominated shores, complex interactions are likely (Fig. 11c). Unfortunately no experimental work in Europe has, so far, teased out the interactions on the types of community illustrated in Figure 11c, which would enable predictions to be made – unlike the moderately exposed shores on the Isle of Man. We feel that research on the patch dynamics of mussel shores is urgently needed. They differ markedly from other mussel-dominated shores that have been investigated (e.g. Dayton 1971; Menge 1976), in that limpets are likely to play a more important role in the north-east Atlantic.

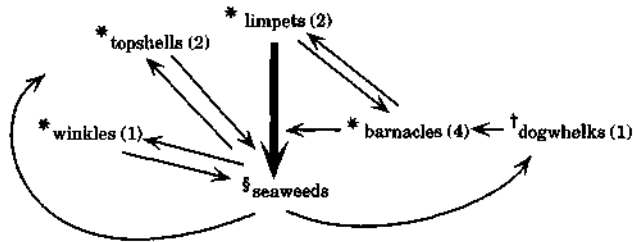
Recovery

A prime use of bioindicators is for the monitoring of recovery, a fact that is often ignored. Studies of recovery are needed after legislation (e.g. banning of sale and use of organotin paints: Duff 1987), decommissioning of effluent outfalls, instigation of a higher standard of treatment or after catastrophic environmental disasters. Such studies are often neglected or are not funded for long enough. They are best done at as high a level of organisation as possible – at the ecosystem or community levels. As an effect becomes more subtle, population or individual level responses can be monitored in selected bioindicators. Studies of recovery provide a superb way of integrating and cross-calibrating the use of bioindicators at different levels of organisation. To use an example from a mostly sediment shore region: the Mersey estuary is improving, due to the de-industrialisation of north-west England, a tightening of

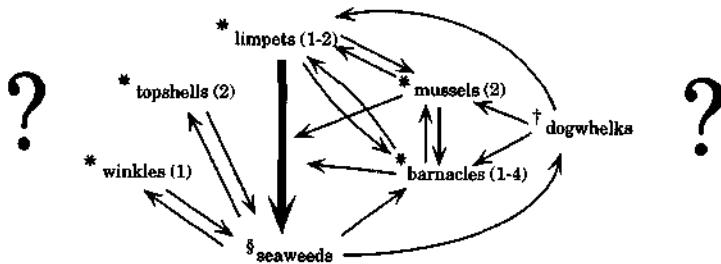
a) Isle of Man: midshore moderately exposed ledges with limpet-fucoid-barnacle mosaics



b) Southwest: midshore barnacles, limpets, fucoids



c) Mussel Dominated Shores: midshore (Scotland, S. west, N. Wales, west coast of Isle of Man)



* stochastic recruitment from plankton

§ variable recruitment

† direct development

Figure 11. Interaction webs on various British rocky shores. Moderately exposed fucoid/barnacle/limpet mosaics at Port St Mary, Isle of Man (a), south-west coasts of Britain (b) and mussel-dominated shores (c). Numbers in parentheses refer to the number of species involved (e.g. 4 species of barnacles, etc.). Both positive and negative interactions are shown.

environmental legislation, and the introduction of clean technologies. Long periods of anoxia no longer exist. There have been no recent bird kills (Bull *et al.* 1983) and fish and invertebrates are now returning to the estuary (Wilson *et al.* 1988) and to the docks (see Hawkins *et al.* 1992b for review). Dense flocks of over-wintering shorebirds and waterfowl feed upon the mud-flat invertebrates (e.g. Rees & Tasker 1990). Nevertheless, worrying levels of various contaminants are still found in some organisms that now live long enough in the Mersey for bioaccumulation to occur (Langston 1988) although, most importantly, at least they are recolonising.

Conclusions

Population level bioindicators, although cheap and attractive in that tangible effects can be demonstrated, are rare in coastal ecosystems – particularly on rocky shores. At the community level rocky shores are particularly variable and hence often unsuitable for monitoring subtle effects. They do have distinct advantages when monitoring recovery from catastrophic events – they are easy to sample non-destructively and the interactions within the community are reasonably well understood. In the UK there are still some major gaps in knowledge, particularly in communities dominated by *Mytilus edulis* on wave-beaten rocky shores. Offshore or intertidal soft benthos are better communities for showing community level effects probably because the impacts, whether they are organic enrichment or toxic compounds, end up in the sediments which act like a sink of some form. Hence the infauna is affected. On the rocky shores the lack of sediment and the mixing of the water column mean that the impacts are less direct – except at the catastrophic level or where effluents of chronic pollution fan out over the rocks at low tide.

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References

- Alzieu, C. (1986). TBT detrimental effects on oyster culture in France – evolution since antifouling paint regulation. In *Oceans '86 Proceedings, Volume 4: International Organotin Symposium*, pp. 1130–1134. Institute of Electrical and Electronic Engineers, New York.
- Alzieu, C., Sanjuan, J., Deltreil, J. P. & Borel, M. (1986). Tin contamination in Arcachon Bay: effects on oyster shell anomalies. *Marine Pollution Bulletin*, **17**, 494–498.
- Bailey, S. K. & Davies, I. M. (1988). Tributyltin contamination in the Firth of Forth (1975–87). *The Science of the Total Environment*, **76**, 185–192.
- Bailey, S. K. & Davies, I. M. (1989). The effects of tributyltin on dogwhelks (*Nucella lapillus*) from Scottish coastal waters. *Journal of the Marine Biological Association of the United Kingdom*, **69**, 335–354.
- Bailey, S. K. & Davies, I. M. (1991). Continuing impact of TBT, previously used in mariculture, on dogwhelk (*Nucella lapillus* L.) populations in a Scottish sea loch. *Marine Environmental Research*, **32**, 187–199.
- Bayne, B. L., Brown, D. W., Burns, K., Dixon, D. R., Ivanovici, A., Livingstone, D. R., Lowe, D. M., Moore, M. N., Stebbing, A. R. D. & Widdows, J. (1985). *The Effects of Stress and Pollution on Marine Animals*. Praeger, New York. 384 pp.
- Beaumont, A. R. (1988). Some ecological consequences of the use of anti-fouling paints containing tributyltin. *Advances in Underwater Technology, Ocean Science and Offshore Engineering*, **16**, 291–298.

- Beaumont, A. R. & Newman, P. B. (1986). Low levels of tributyltin reduce growth of marine microalgae. *Marine Pollution Bulletin*, **17**, 457-461.
- Bellinger, E. G. & Benham, B. R. (1978). The levels of metals in dock yard sediments with particular reference to the contributions from ship-bottom paints. *Environmental Pollution*, **15**, 71-81.
- Borowitzka, S. (1972). Intertidal algal species diversity and the effect of pollution. *Australian Journal of Marine and Freshwater Research*, **23**, 73-84.
- Bowman, R. S. (1981). The morphology of *Patella* spp. juveniles in Britain, and some phylogenetic influences. *Journal of the Marine Biological Association of the United Kingdom*, **61**, 647-666.
- Bright, D. A. & Ellis, D. V. (1990). A comparative survey of imposex in NE Pacific neogastropods (Prosobranchia) related to tributyltin contamination and choice of a suitable bioindicator. *Canadian Journal of Zoology*, **68**, 1915-1924.
- Bryan, G. W. (1969). The effects of oil spill removers ('detergents') on the gastropod *Nucella lapillus* on a rocky shore and in the laboratory. *Journal of the Marine Biological Association of the United Kingdom*, **49**, 1067-1092.
- Bryan, G. W. (1984). Pollution due to heavy metals and their compounds. In *Marine Ecology* (ed. O. Kinne), pp. 1289-1431. John Wiley and Sons, Chichester.
- Bryan, G. W. & Gibbs, P. E. (1991). Impact of low concentrations of tributyltin (TBT) on marine organisms: a review. In *Metal Ecotoxicology: Concepts and Applications* (eds M. C. Newman & A. W. McIntosh), pp. 323-361. Lewis Publishers, Boston.
- Bryan, G. W., Gibbs, P. E. & Burt, G. R. (1988). A comparison of the effectiveness of tri-n-butyltin chloride and five other organotin compounds in promoting the development of imposex in the dogwhelk, *Nucella lapillus*. *Journal of the Marine Biological Association of the United Kingdom*, **68**, 733-744.
- Bryan, G. W., Langston, W. J. & Hummerstone, L. G. (1980). The use of biological indicators of heavy metal contamination in estuaries with special reference to an assessment of the biological availability of metals in estuarine sediments from south-west Britain. *Journal of the Marine Biological Association of the United Kingdom, Occasional Publication*, No. 1, 1-73.
- Bryan, G. W., Burt, G. R., Gibbs, P. E. & Pascoe, P. L. (1993). *Nassarius reticulatus* (Nassariidae: gastropoda) as an indicator of tributyltin pollution before and after TBT restrictions. *Journal of the Marine Biological Association of the United Kingdom*, **73**, 913-929.
- Bryan, G. W., Gibbs, P. E., Burt, G. R. & Hummerstone, L. G. (1987). The effects of tributyltin (TBT) accumulation on adult dogwhelks *Nucella lapillus*: long term field and laboratory studies. *Journal of the Marine Biological Association of the United Kingdom*, **67**, 525-544.
- Bryan, G. W., Gibbs, P. E., Hummerstone, L. G. & Burt, G. R. (1986). The decline of the gastropod *Nucella lapillus* around south-west England: evidence for the effect of tributyltin from antifouling paints. *Journal of the Marine Biological Association of the United Kingdom*, **66**, 611-640.
- Bryan, G. W., Langston, W. J., Hummerstone, L. G., & Burt, G. R. (1985). A guide to the assessment of heavy metal contamination in estuaries using biological indicators. *Journal of the Marine Biological Association of the United Kingdom, Occasional Publication*, No. 4, 1-92.
- Bull, K. R., Every, J., Freestone, P., Hall, J. R., Osborne, D., Cooke, A. S. & Stowe, T. J. (1983). Alkyl lead pollution and bird mortalities on the Mersey Estuary, UK (1979-81). *Environmental Pollution*, **31**, 239-260.
- Burrows, E. M. (1971). Assessment of pollution effects by the use of algae. *Proceedings of the Royal Society of London*, **B177**, 295-306.
- Burrows, E. M. & Lodge, S. M. (1950). A note on the inter-relationships of *Patella*, *Balanus* and *Fucus* on a semi-exposed coast. *Report of the Marine Biological Station, Port Erin*, **62**, 30-34.
- Burrows, M. T. (1988). *The comparative biology of Chthamalus stellatus Poli and Chthamalus montagui Southward*. Unpublished Ph.D. thesis, University of Manchester.
- Clark, R. B. (1989). *Marine Pollution*. Second edition. Clarendon Press, Oxford. 220 pp.
- Cleary, J. J. & Stebbing, A. R. D. (1985). Organotin and total tin in coastal waters of south-west England. *Marine Pollution Bulletin*, **16**, 350-355.
- Chagot, D., Alzieu, J., Sanjuan, J. & Grizel, H. (1990). Sublethal and histopathological effects of trace levels of tributyltin fluoride on adult oysters *Crassostrea gigas*. *Aquatic Living Resources*, **3**, 121-130.

- Connell, J. H. (1961). Effects of competition, predation by *Thais lapillus* and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs*, **31**, 61-104.
- Connell, J. H. (1970). A predator prey system in the marine intertidal region, in *Balanus glandula* and several predatory species of *Thais*. *Ecological Monographs*, **40**, 49-78.
- Corer, A. D., Southward, A. J. & Southward, E. C. (1968). Toxicity of oil-spill removers ('detergents') to marine life: an assessment using the intertidal barnacle *Elminius modestus*. *Journal of the Marine Biological Association of the United Kingdom*, **48**, 29-47.
- Davies, I. M. & Bailey, S. K. (1991). The impact of tributyltin from large vessels on the dogwhelk (*Nucella lapillus*) populations around Scottish oil ports. *Marine Environmental Research*, **32**, 201-211.
- Davies, I. M., McKie, J. C. & Paul, J. D. (1986). Accumulation of tin and tributyltin from antifouling paint by cultivated scallops (*Pecten maximus*) and Pacific oysters (*Crassostrea gigas*). *Aquaculture*, **55**, 103-144.
- Dayton, P. K. (1971). Competition, disturbance and community organisation: the provision and subsequent utilisation of the space in a rocky intertidal community. *Ecological Monographs*, **41**, 351-389.
- Duff, A. (1987). TBT ban. *Marine Pollution Bulletin*, **18**, 146.
- Ellis, D. V. & Pattisina, L. A. (1990). Widespread neogastropod imposex: a biological indicator of global TBT pollution. *Marine Pollution Bulletin*, **21**, 248-253.
- Evans, S. M., Hutton, A., Kendall, M. A. & Samosir, A. M. (1991). Recovery in populations of dogwhelks *Nucella lapillus* (L.) suffering from imposex. *Marine Pollution Bulletin*, **22**, 331-333.
- Fairweather, P. G. (1987). Experiments on the interaction between predation and the availability of different prey on rocky shores. *Journal of Experimental Marine Biology and Ecology*, **114**, 261-273.
- Fairweather, P. G. (1988a). Correlations of predatory whelks with intertidal prey at several scales of space and time. *Marine Ecology Progress Series*, **45**, 237-243.
- Fairweather, P. G. (1988b). Predation can increase variability in the abundance of prey on seashores. *Oikos*, **53**, 87-92.
- Fairweather, P. G., Underwood, A. J. & Moran, M. J. (1984). Preliminary investigations of predation by the whelk *Morula marginalba*. *Marine Ecology Progress Series*, **17**, 143-156.
- Fioroni, P., Oehlmann, J. & Stroben, E. (1991). The pseudohermaphroditism of prosobranchs; morphological aspects. *Zoologischer Anzeiger*, **226**, 1-26.
- Fischer-Piette, E. & Prenant, M. (1956). Distribution des Cirripèdes inter côtiaux d'Espagne septentrionale. *Bulletin du Centre d'Études et de Recherches Scientifiques, Biarritz*, **1**, 7-19.
- Gibbs, P. E. (1993). A male genital defect in the dogwhelk, *Nucella lapillus* (Neogastropoda) favoring survival in a TBT-polluted area. *Journal of the Marine Biological Association of the United Kingdom*, **73**, 667-678.
- Gibbs, P. E., & Bryan, G. W. (1987). TBT paints and the demise of the dogwhelk, *Nucella lapillus* (Gastropoda). In *Oceans '87 Proceedings, Volume 4: International Organotin Symposium*, pp. 1482-1487. Institute of Electrical and Electronic Engineers, New York.
- Gibbs, P. E., Bryan, G. W. & Pascoe, P. L. (1991a). TBT-induced imposex in the dogwhelk, *Nucella lapillus*: geographical uniformity of the response and effects. *Marine Environmental Research*, **32**, 79-87.
- Gibbs, P. E., Bryan, G. W. & Spence, S. K. (1991c). The impact of tributyltin (TBT) pollution on the *Nucella lapillus* (Gastropoda) populations around the coast of south-east England. *Oceanologica Acta, Proceedings of the International Colloquium on the Environment of Epicontinental Seas, Lille, 20-22 March, 1990; Special volume*, **11**, 257-261.
- Gibbs, P. E., Pascoe, P. L. & Bryan, G. W. (1991b). Tributyltin induced imposex in stenoglossan gastropods: pathological effects on the female reproductive system. *Comparative Biochemistry and Physiology*, **100C**, 231-235.
- Gibbs, P. E., Pascoe, P. L. & Burt, G. R. (1988). Sex change in the female dogwhelk *Nucella lapillus*, induced by TBT from antifouling paints. *Journal of the Marine Biological Association of the United Kingdom*, **68**, 715-732.
- Gibbs, P. E., Bryan, G. W., Pascoe, P. L. & Burt, G. R. (1987). The use of the dogwhelk *Nucella lapillus* as an indicator of TBT contamination. *Journal of the Marine Biological Association of the United Kingdom*, **67**, 507-523.

- Hallegraeff, G. M. (1993). A review of harmful algal blooms and their apparent global increase. *Phycologia*, **32**, 79-99.
- Hartnoll, R. G. & Hawkins, S. J. (1985). Patchiness and fluctuations on moderately exposed rocky shores. *Ophelia*, **24**, 53-63.
- Hawkins, S. J. (1981a). The influence of *Patella* grazing on the fucoid/barnacle mosaic on moderately exposed rocky shores. *Kieler Meeresforschungen*, **5**, 537-543.
- Hawkins, S. J. (1981b). The influence of season and barnacles on the algal colonization of *Patella vulgata* exclusion areas. *Journal of the Marine Biological Association of the United Kingdom*, **61**, 1-15.
- Hawkins, S. J., Allen, J. R., Russell, G., White, K. N., Conlan, K., Hendry, K. & Jones, H. D. (1992b). Restoring and managing disused docks in inner city areas. In *Restoring the Nation's Environment* (ed. G. W. Thayer), pp. 473-542. Maryland Sea Grant, Maryland.
- Hawkins, S. J. & Hartnoll, R. G. (1982). The influence of barnacle cover on the numbers, growth and behaviour of *Patella vulgata* on a vertical pier. *Journal of the Marine Biological Association of the United Kingdom*, **62**, 855-867.
- Hawkins, S. J. & Hartnoll, R. G. (1983). Changes in a rocky shore community: an evaluation of monitoring. *Marine Environmental Research*, **9**, 131-181.
- Hawkins, S. J., Hartnoll, R. G., Kain, J. M. & Norton, T. A. (1992a). Plant-animal interactions on hard substrata in the north-east Atlantic. In *Plant-Animal Interactions in the Marine Benthos* (eds D. M. John, S. J. Hawkins & J. H. Price), pp. 1-32. Clarendon Press, Oxford.
- Hawkins, S. J., Hartnoll, R. G. & Southward, A. J. (1985). On stability and fluctuations in rocky shore communities in relation to pollution monitoring. In *Rocky Shore Survey and Monitoring Workshop. May 1st-4th 1984* (ed. K. Hiscock), pp. 13-22. British Petroleum International Ltd., London.
- Hawkins, S. J. & Jones, H. D. (1992). *Rocky Shores, Marine Field Course Guide 1*. IMMEL Publishing, London. 144 pp.
- Hawkins, S. J. & Southward, A. J. (1992). The Torrey Canyon oil spill: recovery of rocky shore communities. In *Restoring the Nation's Environment* (ed. G. W. Thayer), pp. 583-631. Maryland Sea Grant, Maryland.
- Hawkins, S. J., Southward, A. J. & Barrett, R. L. (1983). Population structure of *Patella vulgata* during succession on rocky shores in south-west England. In *Oceanologica Acta, Proceedings of the 17th European Marine Biology Symposium, Brest, France, 27 September-1 October 1982, Special Volume*, pp. 103-107.
- Hiscock, K. (1985). *Rocky Shore Survey and Monitoring Workshop. May 1-4 1984*. British Petroleum International Ltd., London. 136 pp.
- Hughes, R. N., & Burrows, M. T. (1993). Predatory behaviour of the intertidal snail, *Nucella lapillus*, and its effects on community structure. In *Mutualism and Community Organisation. Behavioural, Theoretical and Food Web Approaches* (eds H. Kawanabe, J. E. Cohen & K. Iwasaki), pp. 63-83. Oxford University Press, Oxford.
- Hynes, H. B. N. (1960). *The Biology of Polluted Waters*. Liverpool University Press, Liverpool. 202 pp.
- Johansen, K. & Møhlenberg, F. (1987). Impairment of egg production in *Acartia tonsa* exposed to tributyltin oxide. *Ophelia*, **27**, 137-141.
- Jones, N. S. (1948). Observations and experiments on the biology of *Patella vulgata* at Port St. Mary, Isle of Man. *Proceedings and Transactions of the Liverpool Biological Society*, **56**, 60-77.
- Klumpp, D. W. (1980). Accumulation of arsenic from water and food by *Littorina littoralis* and *Nucella lapillus*. *Marine Biology*, **58**, 265-274.
- Langston, W. J. (1988). A survey of trace metals in biota from the Mersey Estuary. *Marine Biological Association of the United Kingdom*. 124 pp.
- Langston, W. J. & Zhou, M. (1986). Evaluation of the significance of metal binding proteins in the gastropod *Littorina littorea*. *Marine Biology*, **92**, 505-515.
- Lewis, J. R. (1964). *The Ecology of Rocky Shores*. English Universities Press, London. 323 pp.
- Lewis, J. R. (1976). Long-term ecological surveillance: practical realities in the rocky littoral. *Oceanography and Marine Biology Annual Review*, **14**, 371-390.
- Lewis, J. R. (1977). The role of physical and biological factors in the distribution and stability of rocky shore communities. In *Biology of Benthic Organisms* (eds B. F. Keegan, P. O. Ceidigh & P. J. S.

- Boaden), pp. 417-424. Pergamon Press, Oxford.
- Littler, M. M. & Murray, S. N. (1975). Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro organisms. *Marine Biology*, **30**, 277-291.
- Lodge, S. M. (1948). Algal growth in the absence of *Patella* on an experimental strip of foreshore, Port St. Mary, Isle of Man. *Proceedings and Transactions of the Liverpool Biological Society*, **56**, 78-84.
- Menge, B. A. (1976). Organisation of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs*, **46**, 355-393.
- Menge, B. A. (1978). Predation intensity in a rocky intertidal community. Relationship between predator foraging activity and environmental harshness. *Oecologica (Berlin)*, **34**, 1-16.
- Menge, B. A. & Sutherland, J. P. (1976). Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist*, **110**, 351-369.
- Moore, H. B. & Kitching, J. A. (1939). The biology of *Chthamalus stellatus* (Poli). *Journal of the Marine Biological Association of the United Kingdom*, **23**, 521-541.
- Moore, M. N. (1991). Lysosomal changes in the response of molluscan hepatopancreatic cells to extracellular signals. *Histochemical Journal*, **23**, 495-500.
- Moore, M. N., Pipe, R. K. & Farrar, S. V. (1982). Lysosomal and microsomal responses to environmental factors in *Littorina littorea* from Sullom Voe. *Marine Pollution Bulletin*, **13**, 340-345.
- Moyse, J. & Nelson-Smith, A. (1963). Zonation of animals and plants on rocky shores around Dale, Pembrokeshire. *Field Studies*, **1**, 1-31.
- Oehlmann, J., Stroben, E. & Fioroni, P. (1993). Fréquence et degré d'expression du pseudo-hermaphrodisme chez quelques Prosobranches Sténoglosses des côtes françaises (surtout de la baie de Morlaix et de la Manche) 2. Situation jusqu'au printemps de 1992. *Cahiers de Biologie Marine*, **34**, 343-362.
- Paine, R. T. (1966). Food web complexity and species diversity. *American Naturalist*, **100**, 65-75.
- Paul, J. D. & Davies, I. M. (1986). Effects of copper and tin based anti-fouling compounds on the growth of scallops (*Pecten maximus*) and oysters (*Crassostrea gigas*). *Aquaculture*, **54**, 191-203.
- Pettibone, G. W. & Cooney, J. J. (1986). Effect of organotins on fecal pollution indicator organisms. *Applied and Environmental Microbiology*, **52**, 562-566.
- Phillips, D. J. H. (1977). The use of biological indicator organisms to monitor trace metal pollution in marine and estuarine environments - a review. *Environmental Pollution*, **13**, 281-317.
- Phillips, D. J. H. (1980). *Quantitative Aquatic Biological Indicators*. Applied Science Publishers Ltd, London. 488 pp.
- Rees, E. I. S. & Tasker, M. L. (1990). Birds of the Irish Sea and its shores: a conservation evaluation. In *The Irish Sea: An Environmental Review. Part 1: Nature Conservation*, pp. 219-291. Liverpool University Press, Liverpool.
- Rexrode, M. (1987). Ecotoxicity of tributyltin. In *Oceans '87 Proceedings, Volume 4: International Organotin Symposium*, pp. 1443-1455. Institute of Electrical and Electronic Engineers, New York.
- Robertson, A. (1991). Effects of a toxic bloom of *Chrysochromulina polylepis* on the common dogwhelk, *Nucella lapillus*, on the Swedish west coast. *Journal of the Marine Biological Association of the United Kingdom*, **71**, 569-578.
- Salazar, M. H. & Salazar, S. M. (1991). Assessing the effects of TBT contamination with mussel growth rates. *Marine Environmental Research*, **32**, 131-150.
- Smith, B. S. (1980). The estuarine mud snail, *Nassarius obsoletus*: abnormalities in the reproductive system. *Journal of Molluscan Studies*, **46**, 247-256.
- Smith, B. S. (1981). Tributyltin compounds induce male characteristics on female mud snails *Nassarius obsoletus* = *Ilyanassa obsoleta*. *Journal of Applied Toxicology*, **1**, 141-144.
- Smith, D. J. & McVeagh, M. (1991). Widespread organotin pollution in New Zealand coastal waters as indicated by imposex in dogwhelks. *Marine Pollution Bulletin*, **22**, 409-413.
- Smith, J. E. (1968). *Torrey Canyon Pollution and Marine Life*. Cambridge University Press, London. 196 pp.
- Southgate, T. K., Wilson, K., Cross, T. F. & Myers, A. A. (1984). Recolonisation of a rocky shore in south-west Ireland following a toxic bloom of the dinoflagellate *Gyrodinium aureolum*. *Journal of the Marine Biological Association of the United Kingdom*, **64**, 485-492.

- Southward, A. J. (1956). The population balance between limpets and seaweeds on wave beaten rocky shores. *Report of the Marine Biological Station, Port Erin*, **68**, 20-29.
- Southward, A. J. (1963). The distribution of some planktonic animals in the English Channel and approaches. III. Theories about long term biological changes including fish. *Journal of the Marine Biological Association of the United Kingdom*, **42**, 431-429.
- Southward, A. J. (1964). Limpet grazing and the control of vegetation on rocky shores. In *Grazing in Terrestrial and Marine Environments* (ed. D. J. Crisp), pp. 265-273. Blackwell, Oxford.
- Southward, A. J. (1967). Recent changes in abundance of intertidal barnacles in south-west England: a possible effect of climatic deterioration. *Journal of the Marine Biological Association of the United Kingdom*, **47**, 81-97.
- Southward, A. J. (1979). Cyclic fluctuations in population density during 11 years recolonisation of rocky shores in West Cornwall following the Torrey Canyon oil spill in 1967. In *Cyclic Phenomena in Marine Plants and Animals* (eds E. Naylor & R. G. Hartnoll), pp. 85-92. Pergamon Press, Oxford.
- Southward, A. J. (1980). The Western English Channel – an inconsistent ecosystem. *Nature, London*, **285**, 361-366.
- Southward, A. J. (1984). Fluctuations in the 'indicator' chaetognaths *Sagitta elegans* and *Sagitta setosa* in the Western Channel. *Oceanologica Acta*, **7**, 229-239.
- Southward, A. J. (1991). Forty year changes in species composition and population density of barnacles on a rocky shore near Plymouth. *Journal of the Marine Biological Association of the United Kingdom*, **71**, 495-513.
- Southward, A. J. & Boalch, G. T. (1993). The marine resources of Devon's coastal waters. In *The New Maritime History of Devon, Volume 1* (eds M. Duffy, S. Fisher, B. Greenhill, D. J. Starkey & J. Youngs), pp 51-61. Conway Maritime Press, London.
- Southward, A. J., Boalch, G. T. & Maddock, L. (1988). Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16th century. *Journal of the Marine Biological Association of the United Kingdom*, **68**, 423-446.
- Southward, A. J., Butler, E. I. & Pennycuik, L. (1975). Recent cyclic changes in climate and in abundance of marine life. *Nature, London*, **253**, 714-717.
- Southward, A. J. & Mattacola, A. D. (1980). Occurrence of Norway pout, *Trisopterus esmarki* (Nilsson) and blue whiting, *Micromesistius poutassou* (Risso), in the Western English Channel off Plymouth. *Journal of the Marine Biological Association of the United Kingdom*, **60**, 39-44.
- Southward, A. J. & Crisp, D. J. (1954). Recent changes in the distribution of the intertidal barnacles *Chthamalus stellatus* Poli and *Balanus balanoides* L. in the British Isles. *Journal of Animal Ecology*, **23**, 163-177.
- Southward, A. J. & Crisp, D. J. (1956). Fluctuations in the distribution and abundance of intertidal barnacles. *Journal of the Marine Biological Association of the United Kingdom*, **35**, 211-229.
- Southward, A. J. & Southward, E. C. (1978). Recolonisation of rocky shores in Cornwall after use of toxic dispersants to clean up the Torrey Canyon spill. *Journal of the Fisheries Research Board of Canada*, **35**, 682-706.
- Spence, S. K., Bryan, G. W., Gibbs, P. E., Masters, D., Morris, L. & Hawkins, S. J. (1990a). Effects of TBT contamination on *Nucella* populations. *Functional Ecology*, **4**, 425-432.
- Spence, S. K., Hawkins, S. J. & Santos, R. S. (1990b). The mollusc *Thyas haemastoma* – an exhibitor of 'imposex' and potential biological indicator of tributyltin pollution. *Marine Ecology*, **11**, 147-156.
- Spooner, N., Gibbs, P. E., Bryan, G. W. & Goad, L. J. (1991). The effect of tributyltin upon steroid titres in the female dogwhelk, *Nucella lapillus*, and the development of imposex. *Marine Environmental Research*, **32**, 37-49.
- Thain, J., Waldock, M. J. & Waite, M. E. (1987). Toxicity and degradation studies of tributyltin (TBT) and dibutyltin (DBT) in the aquatic environment. In *Oceans '87 Proceedings, Volume 4: International Organotin Symposium*, pp. 1398-1404. Institute of Electrical and Electronic Engineers, New York.
- Underwood, A. J. (1978). An experimental evaluation of competition between three species of intertidal prosobranch gastropods. *Oecologica (Berlin)*, **33**, 185-202.
- Underwood, A. J. (1989). The analysis of stress in natural populations. *Biological Journal of the Linnean Society*, **37**, 51-78.

- Underwood, A. J. (1992). Beyond BACI: the detection of environmental impacts on populations in the real but variable world. *Journal of Experimental Marine Biology and Ecology*, **161**, 145-178.
- Underwood, A. J. & Fairweather, P. G. (1989). Supply-side ecology and benthic marine assemblages. *Trends in Ecology and Evolution*, **4**, 16-20.
- U'ren, S. C. (1983). Acute toxicity of bis(tributyltin) oxide to a marine copepod. *Marine Pollution Bulletin*, **14**, 303-306.
- Widdows, J., Phelps, D. K. & Galloway, W. (1980). Measurements of physiological condition of mussels transplanted along a pollution gradient in Narragansett Bay. *Marine Environmental Research*, **4**, 181-194.
- Wilson, K. W., D'Arcy, B. J. & Taylor, S. (1988). The return of fish to the Mersey. *Journal of Fish Biology (Supplement A)*, **33**, 235-238.