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The regional recovery of *Nucella lapillus* populations from marine pollution, facilitated by man-made structures

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The dogwhelk Nucella lapillus *experienced localized extinction in the 1980s and 1990s due to the use of tributyltin (TBT) antifoulants, causing imposex in females. The aim of this study was to establish the extent of the return of the species across the mainland coast of central southern England as TBT use has been progressively restricted, and to quantify the extent of imposex impact on the populations present. We surveyed from Poole to Selsey where isolated populations had become extinct, and the Isle of Wight where some populations had persisted. We found evidence that since TBT restrictions, recolonization and colonization by* N. lapillus *has been rapid. By 2007–2008, of the eleven surveyed mainland sites, seven were colonized, although indications of reduced imposex impacts were mixed. Distribution had also extended on the Isle of Wight and populations were larger with less imposex impact in sites with long term populations. The lack of continuous suitable habitat blocks and the hydrodynamic complexity of the region, leads us to hypothesize that recovery has been facilitated by man-made structures which may be acting as 'stepping stones'. Populations that have become established on engineered structures such as sea walls, breakwaters and rock groynes demonstrate accelerated recovery in the region as TBT in the environment has generally declined. Sites with suitable substrates and food sources near to ports were either not recolonized or had small populations with imposex evident. For species with a short pelagic larval stage or with direct development, population connectivity between patches of harder substrata along hydrodynamically complex coastlines may be greater than previously thought.*

Keywords: imposex, tributyltin, TBT, dogwhelk *Nucella lapillus*, recolonization, sea defences, marine pollution indicator

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INTRODUCTION

There is growing interest in the reproductive connectivity of marine organism populations associated with the design of Marine Protected Area networks. Accordingly the role of man-made structures in facilitating colonization of hard substrata, and subsequent dispersal of reproductive propagules or juvenile stages, is receiving worthwhile attention (e.g. Bacchiocchi & Airoldi, 2003; Moschella *et al.*, 2005; Hawkins *et al.*, 2008, 2009). However, it may be that as many rare species have poor, or poorly understood, dispersal traits, due either to a short pelagic larval phase or direct development, the importance of artificial substrata in their persistence and movement may be underestimated.

The dogwhelk *Nucella lapillus* (L.) is a predatory gastropod inhabiting intertidal and subtidal hard structures along North Atlantic shores. The species is carnivorous, feeding preferentially on sedentary prey (e.g. barnacles, by prizing plates apart; and mussels by boring through the shell) (Moore, 1938; Morgan, 1972; Crothers, 1985), but can adapt to other prey types (Largen, 1967; Crothers, 1985). Having no recognized pelagic stage, upon emergence from capsules fully formed juvenile *N. lapillus* (crawlaways), can migrate down shore where feeding has been observed on the annelid worm *Spirorbis borealis* (Moore, 1936) or small barnacles (Crothers, 1985). Juvenile *N. lapillus* have also been observed at the same tidal level as their egg cases sheltering in empty barnacle carapaces (Feare, 1970). It may be considered that direct development may restrict dispersive abilities, but rafting (Bryan *et al.*, 1986; Martel & Chia, 1991), passive transport (Colson & Hughes, 2004) or a small amount of air trapped in the shell (Adachi & Wada, 1999), have been suggested as colonization facilitators in direct developing gastropods. In addition shells of small gastropods (*Littorina littorea*) have been noted to roll in the surf, in a similar way to saltation in sediments (Amos *et al.*, 2000).

Because of tributyltin (TBT) use as an antifoulant, many UK *N. lapillus* populations declined or became absent from shores, particularly close to ports (e.g. Spence *et al.*, 1990). Dogwhelks are highly sensitive to TBT (Evans & Nicholson, 2000) with levels as low as 1 ngl^{-1} inducing imposex

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(imposition of male sex organs on the female) (Matthiessen & Gibbs, 1998) thus the organism proved to be a sensitive and valuable indicator for marine-TBT levels. In female *N. lapillus*, imposex advances to irreversible sterility and death occurs as vas deferens growth blocks the anterior oviduct (Gibbs & Bryan, 1986).

By the 1980s *N. lapillus* became extinct in areas of high shipping and maritime activity, and, particularly along the UK south coast, many surviving populations were depleted, suffering with high imposex levels (Spence *et al.*, 1990; Bryan & Gibbs, 1991). In 1985 France was the first nation to place restrictions on TBT use and in 1987 the UK also banned the antifoulant on vessels <25 m length overall. Many other nations put in place similar bans (Champ, 2000), however, its use on larger ships continued (Bates & Benson, 1993). A global ban was finally ratified in September 2008 (Sonak *et al.*, 2009), but there are some difficulties with the legal issues (Gipperth, 2009; Kotrikla, 2009). Following progressive TBT restrictions, UK sites where *N. lapillus* was absent began to be recolonized (Evans *et al.*, 1995; Harding *et al.*, 1997; Bray & Herbert, 1998; Crothers, 1998, 2003; Birchenough *et al.*, 2002; Colson & Hughes, 2004). Some populations recovered to pre-TBT densities in just ten years (Colson & Hughes, 2004) with increasing egg production and changes in population structure documented (Morton, 2009). However, possibly due to residual and potentially continuing contamination (Kotrikla, 2009; Oliveira *et al.*, 2009), the recovery of dogwhelk populations has proved to be slow in some areas (e.g. Smith *et al.*, 2006).

One such area is the Solent region on the UK south coast: a centre for international shipping, and a focus for maritime recreation from Selsey (Sussex) to Poole Harbour (Dorset) and on the Isle of Wight. Much of the coastline is soft sediment, sand, gravel or soft chalk, with hard substrata suitable for *N. lapillus* and their prey few and far between. Isolated dogwhelk populations are believed to have existed historically on the mainland coast at Netley on Southampton Water (Langston *et al.*, 1994) and between Hurst Spit and Calshot (Moore, 1936), but they were not found in surveys in 1986–1989 (Spence *et al.*, 1990) and 1996–2002 (Bray, 2005). It seems that *N. lapillus* has been absent from much of the mainland coast of central southern England since the 1980s, potentially due to TBT pollution and unsuitable habitat. In the 1970s, large populations were present on the northern Solent coast of the Isle of Wight, mainly on piers and breakwaters. By the mid-1980s, with TBT now extensively used on all kinds of marine vessels, these populations had mostly become extinct, although those on the relatively uncontaminated rocky shores on the island's southern coast remained, albeit significantly affected by imposex (Herbert, 1988; Bray & Herbert, 1998; Herbert *et al.*, 2000).

Of the 354 km of developed North Solent coastline approximately 80% is protected from erosion with a variety of man-made structures (Williams *et al.*, 2009). Over the last two decades sea defences have changed, with combinations of rip-rap, rock armour, concrete breakwaters and rock groynes, which have often replaced wooden structures (Dong, 2004). These have created intermittent artificial 'rocky shores' which may be rapidly colonized by 'fouling organisms' (e.g. Bacchiocchi & Airoldi, 2003; Chapman & Bulleri, 2003). Yet, as *N. lapillus* has no recognized pelagic stage, it could be expected that the colonization or recolonization of these structures, would be slow, even as TBT concentrations potentially diminish (Smith *et al.*, 2006). Moreover, the Solent region has a complex hydrography and tidal regime, that together with fast offshore currents around headlands immediately east and west of the region may create barriers to colonizers from existing populations (Herbert *et al.*, 2007, 2009).

This study was prompted by initial casual observation of dogwhelks on rock groynes constructed at Highcliffe (Christchurch Bay), where *N. lapillus* were not previously documented. Subsequently the aims were to monitor and record the recovery of *N. lapillus* populations, against TBT decline, on the south coast, and in particular the colonization of man-made substrates across the Selsey–Poole coastline. As they may prove to be source sites for mainland population recovery, data from recovering populations on the Isle of Wight, on both natural and man-made substrate were also included to give a complete regional assessment.

MATERIALS AND METHODS

The Selsey–Poole coastline, including the Isle of Wight, was surveyed to identify suitable substrates (natural and man-made structures constructed of natural stone or concrete, in moderately exposed or exposed locations) that could be expected to support *N. lapillus.* The distribution of rocky structures was recorded by use of Ordnance Survey maps, data and aerial photographs.

Seven sites between Sandbanks and Calshot were surveyed in 2006. These were re-examined in 2008 in addition to the coast from east of Southampton Water to Selsey, giving a total of eleven mainland sites assessed in detail in 2008. Five sites on the Isle of Wight were surveyed in 2007. These results are compared with historic (1995 onwards) data where available (Bray, 2005).

Where *N. lapillus* were identified on mainland sites, individuals were counted over three 10-minute timed site searches conducted at low spring tides; Isle of Wight sites were searched in a single 30 minute period, so overall effort was the same. In the mainland surveys shell size was measured to the nearest 0.1 mm. Thirty-five adults were then randomly selected to undergo imposex assessment using methods as defined by Gibbs & Bryan (1986) and Gibbs *et al.* (1987) in which the vas deferens sequence (VDS) and relative penis size index (RPSI) are calculated as measures of TBT impact. The VDS in females is assessed through stages 0 (no VDS) to 6 (oviduct blocked with aborted egg capsules; stage 5 and over are sterile) and the RPSI calculated as the 'bulk' (length^3) of the average female penis length as a percentage of the average male penis length. Imposex was not assessed where low numbers were recorded (where less than 50 individuals were found, although recovering populations on the Isle of Wight were treated conservatively). VDS data have often been presented as the female population mean value (e.g. Evans *et al.*, 1998, 2000). However, as the VDS is assessed through categorical values, they are presented here as the range and median to give a representation of a population's central tendency VDS.

In terms of substrate and food resource, sites were included which appeared suitable for *N. lapillus*, but had none present: for example Hayling and Southsea were unoccupied, but had extensive suitable substrate; Sowley was occupied in 2006, but not in 2008. Food resources were not surveyed in detail in heavily industrialized estuaries such as Southampton Water and Portsmouth Harbour where no *N. lapillus* appeared to be present, apart from Netley (Southampton Water) which was monitored as part of another study (Bray, 2005) (Figure 1; Table 1). Using stratified random 0.25 m^2 quadrats, percentage cover of the main *N. lapillus* prey resources, common mussels (*Mytilus edulis*) and barnacles (*Semibalanoides balanoides* and *Elminius modestus*), was assessed in the mid to lower eulittoral zone (Lewis, 1964; Stephenson & Stephenson, 1949, 1972) as were algae, at each occupied site surveyed in 2008.

RESULTS

On the mainland coast between Sandbanks and Selsey Bill, 95 individual or grouped structures, and sub-optimal natural substrates enhanced by anthropogenic debris such as concrete blocks were recorded as having potential to support *N. lapillus*. Most are within 5 km of each other, but there is an approximately 13 km gap between Sandbanks and Hengistbury Head and only a single outfall pipe between Hurst Spit and Langley (2.5 km south-west of Calshot) (Figure 1). *Nucella lapillus* populations were recorded at eight mainland sites across the study area (in 2006 a single dogwhelk only was recorded at a ninth site, Sowley); seven of the eight populations were on man-made substrates. No dogwhelks were recorded in Southampton Water or Portsmouth Harbour despite suitable habitat in docksides, breakwaters and sea walls, and none were found at Hayling or Southsea despite extensive suitable substrates and relatively 'clean' conditions.

In 2008 the largest population recorded was on rock groynes at Barton-on-Sea (total 307 specimens). Total *N. lapillus* counts in 2008 were generally slightly lower than those of 2006. (Figure 1; Table 1), however total counts from Highcliffe and Calshot increased in 2008.

Where *N. lapillus* were recorded, prey assemblages varied from site to site. Hayling Island had the highest percentage barnacle cover (49.7 ± 13.4%), but no *N. lapillus*. The sites with the lowest mean barnacle cover were Sandbanks with 1.0% (±0.6 SE); and Selsey (3.0 ± 0.4% barnacle cover) where *N. lapillus* were noted feeding upon the common periwinkle, *Littorina littorea* (see Crothers, 1985); the only other observed potential prey type present at Sandbanks was limpets on which *N. lapillus* will also forage (Crothers, 1985). An independent sample *t*-test comparison for percentage barnacle cover at Sowley and Selsey showed they were not significantly different, but whilst Selsey supported 276 *N. lapillus*, none were recorded at Sowley. Although Southsea did not support *N. lapillus*, mean percentage covers of each prey taxon were similar to Hengistbury Head (which supported a dogwhelk population); independent sample *t*-tests showed that the prey assemblages were not significantly different.

In 2006, all mainland sites (Figure 1) showed TBT impacts except Hurst Spit. For 2008, of the seven mainland sites supporting *N. lapillus* sufficient for imposexing, only Highcliffe was unaffected (RPSI, 0, VDS, 0), a reduction from the 2006 VDS range of 0–4 (Table 1).

In 2006 and 2008 the Sandbanks VDS range was 0–4. The 2008 Hengistbury Head, Barton-on-Sea and Hurst Spit populations showed little TBT impact. Only one female from each exhibited imposex (Figure 2; Table 1), with the one at Barton-on-Sea at VDS stage 3. Nevertheless, both Barton-on-Sea and Hurst Spit populations had an increased VDS range over 2006 results (Table 1). The remaining mainland locations with populations present (Table 1), Calshot and Selsey, had VDS ranges of 0–3, but, as with all sites, except Sandbanks in 2006 (Table 1), in both sample years the median VDS value was 0, highlighting the dominance of unaffected females. However, in 2008 the similar (>40%) percentage of affected females at the sites near commercial ports (Sandbanks and Calshot) highlights the on-going imposex impact at such locations (Table 1). In addition, despite suitable habitat, the other commercial traffic-affected location, Southsea, did not support any individuals, though this may equally be attributable to *N. lapillus* not yet having achieved successful colonization because of TBT impacts.

Mean male penis lengths varied from 1.7 mm (Calshot) to 3.1 mm (Barton-on-Sea) in 2008. Sandbanks had the greatest mean female penis length (0.34 mm) reaching 13.6% of the mean male penis length (2.52 mm). This is reflected in the RPSI of 0.25%; all other sites had RPSIs below 0.09% (Table 1).

Assessment on the Isle of Wight in 2007 showed population recovery on Solent shores (Bembridge, Ventnor and Hanover Point) and man-made structures at Cowes and at Yarmouth. At Bembridge and Hanover Point there were reduced imposex levels compared to 1997 values (Table 2). The other sites were not assessed for imposex in 1997 due to low abundance; Cowes was not assessed in either 1997 or 2007.

Shell lengths varied considerably, ranging from 12.2 mm (Hurst Spit 2008) to 45.4 mm (Highcliffe 2006). Hurst Spit (2006) had the highest proportion of small individuals (7.8% up to 14 mm). Lee-on-Solent's population (2008 only) consisted of only very large individuals ranging from 38.7 to 44.4 mm, although, only five specimens were found at this site. Two sample Kolmogorov–Smirnov Z-tests (KSz) (Siegel, 1956) were applied to the 2006 and 2008 data to determine whether neighbouring populations had similar size–frequencies, that might indicate the presence of metapopulations augmented by dispersers. Barton-on-Sea and Hurst Spit had similar populations in 2006 (6.3 km apart), and Hengistbury Head was similar to both Hurst Spit and Calshot in 2008; (12.1 km and 21.1 km apart respectively). All other neighbouring sites had significant differences (2006, KSz all others $P < 0.01$; 2008, all others $P < 0.05$). Analysis of 2006 and 2008 data demonstrated a significant negative logarithmic correlation between abundance and mean shell length ($r = 0.73$, $N = 14$, $df = 13$, $P < 0.05$; $y = -3.6678 \ln(x) + 48.124$) (Figure 3).

DISCUSSION

The results show an unexpectedly rapid spread of dogwhelks across the Solent into areas which have either never supported known populations, or where they have been extinct for around thirty years. This increase in distribution has taken place as restriction on the use of TBT has tightened, but appears to have been facilitated by the widening occurrence of man-made hard substrates. Where suitable natural habitat was present, such as at Bembridge on the Isle of Wight, engineered structures on the shore may have acted as stepping stones across less favourable habitats thus

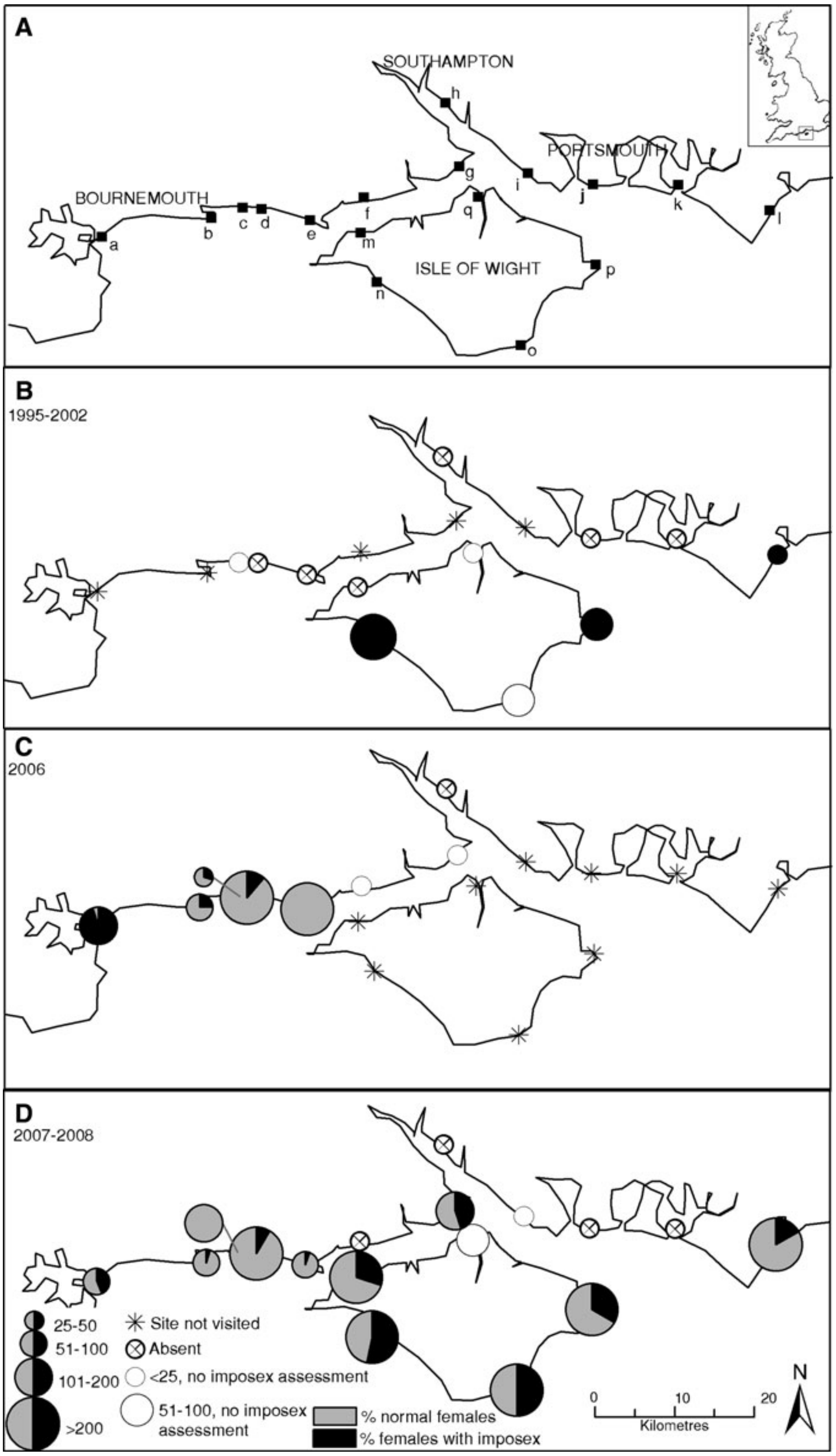

Fig. 1. Population of *Nucella lapillus* and imposex impact at sites in the Solent, Southern UK. (**A**) Site locations: a, Sandbanks; b, Hengistbury Head; c, Highcliffe; d, Barton-on-Sea; e, Hurst Spit; f, Sowley; g, Calshot; h, Netley; i, Lee-on-Solent; j, Southsea; k, Hayling Island; l, Selsey Bill; m, Yarmouth; n, Hanover Point; o, Ventnor; p, Bembridge; (**B**–**D**) status of populations at each site: (**B**) 1995–2002; (**C**) 2006; (**D**) 2007–2008 (with charts indicating the prevalence of imposex and population size).

accelerating re-colonization and regional recovery of populations. Distances between occupied sites varied from as little as 1.3 km (Highcliffe to Barton-on-Sea) to 35.6 km (Lee-on-Solent to Selsey Bill). This investigation confirmed that man-made rocky structures have potential to provide a valuable intertidal habitat for recovering *N. lapillus* populations. However, they are not essential for populations to survive, since *N. lapillus* were abundant at Selsey Bill, where there was little or no man-made or natural rocky substrate, but areas of gravel, large cobbles and concrete debris stabilized

Table 1. Site characteristics and dogwhelk population and imposex data for mainland coast Sandbanks (Dorset) to Selsey Bill (Sussex). Survey data for Lee-on Solent, Southsea, Hayling Island and Selsey Bill were only gathered in 2008. No individuals were found at Netley in either year. Abundance shows total number found in three 10 minute searches.

Site	Substrate	Abundance 2006	Abundance 2008	% females showing imposex 2006	% females showing imposex 2008	RPSI 2006 (%)	RPSI 2008 (%)	Median VDS 2006	VDS range 2006	Median VDS 2008	VDS Range 2008
Sandbanks	Rock groyne and sandy beach	123	87	95	43.8	3.1	0.3	4	0–4	0	0–4
Hengistbury Head	Breakwater and rock groyne on north-eastern (lee)	94	69	25	4.5	2.09×10^{-5}	3.42×10^{-6}	0	0–2	0	0–2
Highcliffe	Rock groyne and shingle/sandy beach	40	135	29.4	0	0.01	0	0	0–4	0	0
Barton-on-Sea	Boulder and rip-rap	319	307	11.1	8.3	0.0003	0.006	0	0–2	0	0–3
Hurst Spit	Rip-rap and rock groyne; gravel spit	245	92	0	5.6	0	0.0001	0	0	0	0–2
Sowley	Clay, pebbles, no structures	1	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Calshot	Outfall pipe; pebble spit	30	173	–	45	–	0.09	–	–	0	0–3
Netley	Sea wall; gravel and mud	N/A	N/A	–	N/A	–	–	–	–	–	N/A
Lee-on-Solent	Rock groyne; pebbles and fine sand	–	5	–	N/A	–	N/A	–	–	N/A	–
Southsea	Various: rip-rap, revetments sea wall	–	0	–	N/A	–	N/A	–	–	N/A	–
Hayling Island	Rock groyne; sand and shingle spit	–	0	–	N/A	–	N/A	–	–	N/A	
Selsey Bill	Shingle and boulder, plus concrete fragments stabilized by wooden groynes	–	276	–	16.7	–	0.0007	–	–	0	

RSPI, relative penis size index; VDS, vas deferens sequence; N/A, not applicable.

by timber groynes. *Nucella lapillus* aggregations were present on shingle surrounded single boulders and a highly TBT impacted population was recorded at Selsey as long ago as 1990 (Spence *et al.*, 1990) with evidence of high TBT levels experimentally recorded using imposex indices by Harding *et al.* (1992).

Whilst six recently established *N. lapillus* populations have been identified, with the mainland Solent dogwhelk distribution apparently having increased significantly, their persistence may be unstable because of the high proportion of juveniles (indicated by the smaller shells). The large population at Barton-on-Sea declined slightly from 2006 to 2008, while numbers increased at Highcliffe and Selsey; the notable abundance decline at Hurst Spit may be attributed to factors such as wave exposure and predation pressure influencing *N. lapillus* abundance (Miller *et al.*, 1999) as well as bad weather hindering searches, rather than TBT pollution. 'Abundance' in this study actually refers more to the rate of individuals found (animals per three 10 minute replicate searches), which reflects both the population density and the nature of the area being searched, so is subject to some degree of error; deep crevices take more time to investigate than flat surfaces. However, abundance as recorded appeared to have a significant relationship with shell size; smaller shells were found at sites newly colonized or recovering.

The continued use of TBT antifouling paint on large vessels and the restricted water and sediment movement within ports prevents complete recovery from TBT poisoning (Smith *et al.*, 2006). TBT has been observed to persist in sediments and could potentially provide a 'reservoir' of contamination for decades (Maguire, 2000). Benthic sediments are the primary means of TBT bioaccumulation in deposit feeders, particularly bivalves (Langston *et al.*, 1990). Contaminated sediments could continue to be a TBT pollution source well into this century (Langston & Pope, 1995). Desorption of TBT from sediments increases concentrations in overlying water to quantities which exceed the Environmental Quality Standard of 2 ng l^{-1} (Langston & Pope, 1995). Wave simulation experiments indicate that TBT paint particles move upwards to the sediment surface where it is most available (Eggleton & Thomas, 2004) and simulated removal of the top sediment layer releases TBT back into the water column, leading to a higher incidence of imposex (Svavarsson *et al.*, 2001). In addition, not only does the disturbance of contaminated sediment cause remobilization of TBT at dredge sites, levels at disposal sites have been implicated in imposex impacts in marine protected areas (Boersma & Parrish, 1999; Terlizzi *et al.*, 2004).

Ongoing dredging and disposal within the region may threaten complete recovery of *N. lapillus* populations. Measurements of TBT taken from East Brambles Buoy (2.5 km offshore of Calshot, at the entrance to Southampton Water) from February 2000 to February 2007, gave a mean water concentration of 2.465 ng l^{-1} (unpublished data, D. Lowthion, Environment Agency, 2007), enough to cause imposex in dogwhelks (Gibbs *et al.*, 1987) and Calshot had 45% of females with imposex in 2008 (Table 1). Thomas *et al.* (2000, 2001) indicated that TBT would be a factor in non-target organism impacts in the region for some time. This may continue to be reflected by the intensity of maritime activity around the Port of Southampton as well as sediment disturbance due to regular large scale dredging.

It is unclear why *N. lapillus* has not yet colonized Southsea, close to Portsmouth Harbour. Assessment of the potential

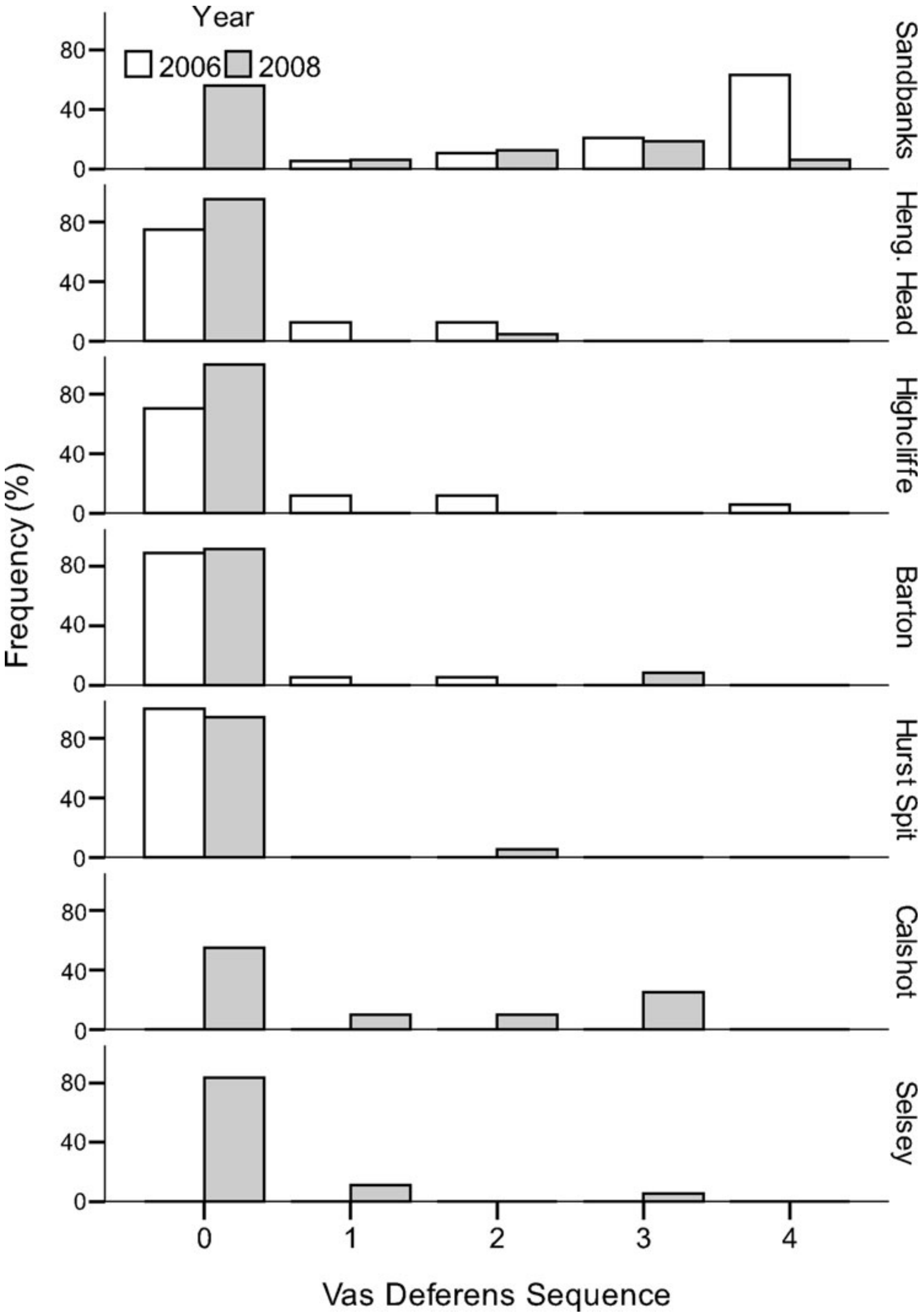

Fig. 2. The frequency of each vas deferens sequence stage for mainland Solent sites in 2006 and 2008. No imposex data were collected from Calshot and Selsey in 2006. No specimens exhibited stage 5 or stage 6 criteria.

food resources for dogwhelks indicate that the site is capable of supporting a population, yet the proximity of a port may be a key factor; its absence may be attributed to TBT levels as the site is within 1 km of Portsmouth Naval base and a commercial ferry route. Alternatively, it may be that recruitment is limited due to local hydrodynamics, and lack of nearby source populations; Lee-on Solent, itself with a small, isolated population, is 8.3 km away with extensive docks and dredged channels in between.

For mainland sites there was an overall decrease in RPSI between 2006 and 2008, except for at Barton-on-Sea and Hurst Spit, where although values increased (Table 1) they were still very low. The continued evidence of TBT impact in the Barton-on-Sea/Hengistbury Head/Hurst Spit area, which is distant from the larger regional harbours, may be due to persistent low level contamination or a local hotspot (perhaps TBT in sediments), or the irreversibility of imposex (Bryan *et al.*, 1986). The lifespan of *N. lapillus* is typically around six years (Feare, 1970; Crothers, 1985) meaning that individuals alive when TBT concentrations were higher may still be present. In 2008 all sites had low RPSI-negligible in comparison with other south coast sites in the 1990s (Spence *et al.*, 1990; Evans *et al.*, 1995, 1996; Huet *et al.*, 1996), though they were apparently not completely

Table 2. Site characteristics, dogwhelk population and imposex data for Isle of Wight for 1997 and 2007. Abundance data show number found in 30 minutes.

Site	Substrate	Abundance 1997	Abundance 2007	% females showing imposex 1997	% females showing imposex 2007	RPSI 1997 %	RPSI 2007 %	Median VDS 1997	VDS range 1997	Median VDS 2007	VDS range 2007
Bembridge	Rocky shore, reefs and boulders	117	338	100	80	11	0.420	3	1–4	0	0–4
Ventnor	Rocky shore, rocky boulders	69	242	N/A	86	N/A	0.070	N/A	N/A	0	0
Hanover Point	Rocky shore, reefs and boulders	208	372	100	81	18.2	0.096	3	2–4	0	0–4
Yarmouth	Pier piles	0	278	N/A	55	N/A	0.004	N/A	N/A	0	0–2
Cowes	Groyne	3	73	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

RSPI, relative penis size index; VDS, vas deferens sequence; N/A, not applicable.

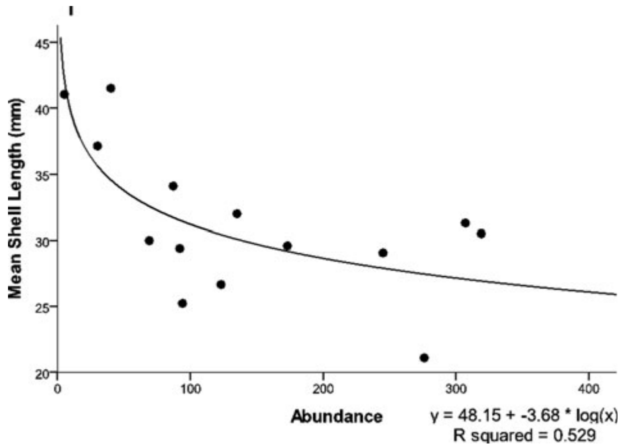

Fig. 3. Relationship between abundance and mean shell length at each, mainland Solent site in 2006 and 2008. Plot omits data (one individual) from Sowley in 2006.

TBT-free; with the exception of Highcliffe where the increased population has colonized man-made groynes.

Similarities in shell lengths between sites several kilometres apart could simply be attributed to wave exposure (comparable at these locations) rather than an indication of population connectivity, as it has been shown to influence phenotypic expression in *N. lapillus* (Staiger, 1957; Kitching *et al.*, 1966). However, medium distance movements of 10–100 km have proven fairly common for *N. lapillus*, assuming populations showing genetic similarity have been founded or augmented by one or another (Colson & Hughes, 2004), though the means of travel are poorly understood. Hydrodynamic forces may carry individuals for distances of up to 1 km during storms (Bray, 2005) and *N. lapillus* individuals were found rolling between rock groynes at both Hengistbury Head and Highcliffe. In addition birds may drop individuals (Crothers, 1985), but dislodgement and passive transport is more likely.

Shore macrofauna can travel hundreds of kilometres by rafting (as adults or eggs) on detached clumps of floating seaweed (Ingólfson, 1995). To determine whether this is the case for *N. lapillus*, placing surface drifters and performing genetic examination could highlight whether gene flow follows the direction of the currents (Muhlin *et al.*, 2008). The long-standing, relatively unaffected, intertidal populations on the south coast of the Isle of Wight (Herbert 1988; Bray & Herbert, 1998) may have been a source of founding individuals on the mainland. Populations on the north coast of the Isle of Wight had become extinct by the mid-1980s (Herbert, 1988; Bray & Herbert, 1998), yet have recovered since recolonizing individuals were observed in 1995 at East Cowes.

It is more likely that populations on the mainland are being replenished and/or augmented by dispersers from subtidal populations that have survived the worst of the contamination. Crothers (1998, 2003) postulated that a recolonized population of *N. lapillus* in Watermouth Cove in the Bristol Channel was repopulated by a subtidal population, taking 13 years to travel 30 miles. We noted a subtidal population on an outfall pipe at Hengistbury Head that extends into Christchurch Bay where there are shallow rocky ledges. Thus it may be that the Hurst Spit population was founded by subtidal colonizers, possibly explaining between-site similarity in cumulative shell lengths. Whether dispersers can form a viable population that persists in time depends on, amongst other things, demographic, environmental and genetic stochasticity (Shaffer, 1981), prey availability and also, more practically, engineering activity maintaining or changing sea defence structures. Some populations will not be successful because the habitat is unsuitable for them. This is most likely the case for Sowley where prevalence of prey was limited and substrates marginal, thus colonizers (as seen in 2006) cannot establish. The recovery of *N. lapillus* could be partly attributed to selection for individuals that have the ability to breed successfully, despite high concentrations of TBT (Birchenough *et al.*, 2002; Huet *et al.*, 1996, 2008). The recessive and uncommon male genital defect Dumpton Syndrome (DS) results in reduced penis size in males, and also in females affected by TBT (Gibbs, 1993). The condition was previously undetected, but TBT impacts highlighted it in some isolated populations (Gibbs, 2005). Populations exhibiting DS have survived in areas of high TBT contamination, as DS-affected females avert sterilization by imposex (Huet *et al.*, 1996). Males taken from Calshot had smaller penis sizes than other sites, a symptom of DS. However, as DS occurs in isolated populations and this work suggests possible connectivity between recolonizing groups, this may be because of general underdevelopment.

This study shows that following UK restrictions on the use of TBT, *N. lapillus* populations in the southern UK region have recovered and spread into locations where they may not have been previously present. The evidence presented here leads us to hypothesize that this recovery may have been accelerated through the construction of new sea defences, as the animals have been found on these structures at locations where they were previously unrecorded. These structures provide a new habitat, offering intertidal 'stepping stones' to sites where dogwhelks may not have been previously present or were eliminated by TBT pollution some 30–40 years ago. Some locations remain uncolonized, possibly due to residual TBT, or unsuitability and isolation; sites near to ports still show indications of TBT impact expressed as imposex, and no colonization has taken place within industrialized estuaries although extensive suitable substrate is present. The means of long-range dispersal of *N. lapillus* in the Solent remains unclear, but what has been demonstrated is that man-made substrates can provide useful habitat and facilitate more rapid recovery of *N. lapillus* as TBT pollution declines. For species with a short pelagic larval stage or with direct development, the population connectivity between patches of harder substrata may therefore be much greater than previously thought, even within a hydrodynamically complex region such as the Solent and central south coast of England.

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