Field Studies, **10**, (2003) 579 - 599

WEST ANGLE BAY: A CASE STUDY. THE FATE OF LIMPETS

ROBIN G. CRUMP*, ANDREW D. WILLIAMS$
FSC at Orielton Field Centre, Pembroke, Pembrokeshire SA71 5EZ
AND JOHN H. CROTHERS
Egypt Cottage, Fair Cross, Washford, Watchet, Somerset TA23 0LY

Abstract

The *Sea Empress* oil spill was an extremely traumatic event, both for limpets and their observers, but it provided the marine biologists at Orielton Field Centre with a quite remarkable natural experiment. The pollution dramatically reduced limpet densities and so facilitated colonisation of the shore by palatable red and green algae - which, in turn, enabled the surviving limpets to grow rapidly and reach a large size. Despite the major perturbation of limpet populations between 1995 and 2000, the situation in 2001 seemed to be very similar to that prior to the spill with high densities of small limpets.

Introduction

On the 15th February 1996, the 140,000 tonne oil tanker *Sea Empress* went aground on rocks at the entrance to Milford Haven. Over the next six days, an estimated 72,000 tonnes of Forties Blend crude oil and 360 tonnes of heavy fuel oil were spilled into the sea and contaminated over one hundred kilometres of the Pembrokeshire coast.

West Angle Bay, an SSSI and one of the most important teaching sites for Orielton Field Centre, was one of the most heavily impacted bays and was oiled on at least ten occasions by neat North Sea crude oil with an admixture of fuel oil. The immediate impacts of the oil on the animal and plant communities were described in a previous paper (Crump, Morley & Williams, 1999) based on the regular monitoring of a permanent transect on the northern side of the bay. Limpet mortality was high (over 50% in most places) and resulted in a release of grazing pressure, which produced a characteristic but nonetheless dramatic 'green phase' of *Enteromorpha* spp. within six weeks of the spill. This spring flush of green algae was followed by one of laver (*Porphyra* spp.) in the summer of 1996. By the late spring of 1997, the whole shore had become dominated by a 'brown phase' of *Fucus vesiculosus* var. *linearis* (Crump, *et al.*, 1999).

This paper describes the dramatic fluctuations in limpet populations during the first five years after the spill.

Methods

The population dynamics and growth rates of limpets (*Patella* spp.) on the south-facing 45° slopes on the north side of West Angle Bay were studied in four ways.

Site 1 Permanent quadrats

Six of the permanent quadrats established and photographed at West Angle Bay in February 1995 (see Crump *et al.*, 1999) still contained limpets after the spill. The diameter

present addresses
* Thrustle Mill Cottage, nr Stackpole, Pembroke SA71 5LT
$ FSC @ Kindrogan Field Centre, Enochdu, Blairgowrie, Perthshire PH10 7PG

of each surviving limpet was measured, with callipers, to the nearest millimetre at monthly intervals from March 1996 (immediately post spill) until March 1998 and then at three monthly intervals thereafter until 2001. The approximate position of each limpet was recorded on a gridded recording sheet. Various tagging methods were tried to individually mark limpets at other sites with little or no success but, since the surviving limpets remained on their home scars for most of the survey period, it was possible to obtain individual growth rates for some of the individuals. In addition, because the quadrats were relatively small and minutely examined for other tiny biota (barnacles, small periwinkles etc.) it was possible to determine the first appearance of juveniles.

No attempt in this study was made to separate the species of *Patella*, since certain identification requires the limpets to be removed from the rock and this, clearly, was not desirable. Subsequent examination of the populations of limpets at West Angle Bay by Dr. W. J. Ballantine confirmed that between 92-95% of the limpets on south-facing slopes were likely to be *Patella vulgata*.

Site 2 Horizontal belt transect.

A strip of south-facing limestone rock in the middle shore, immediately adjacent to the permanent quadrats, was selected for student sampling. This 25 m long strip was sampled systematically at half metre intervals using quarter metre squared quadrats in a horizontal belt transect. Random sampling within the strip, though theoretically preferable, was precluded by the extremely slippery nature of the slope when covered in the green alga *Enteromorpha* spp. In each quadrat, the diameters of limpets were measured to the nearest mm and the total number of limpets per quadrat was recorded. On most occasions at least 200 limpets were measured and counts were made in at least 20 quadrats.

In the early months post spill, counts and measurements were made by students attending field courses courses but, from October 1996, staff from Orielton Field Centre took over the sampling.

Site 3 Student Class Data.

A very large data set for limpet size and density had been collected, in the year prior to the spill, by students from Newcastle-under-Lyme School. During a class exercise in April 1995, quarter metre squared quadrats had been placed at random on a south-facing 45° slope in the middle shore region, approximately twenty metres inland of the permanent transect. As usual the limpets had been measured to the nearest millilitre and all limpets present in quadrats were counted. With the willing cooperation of their staff, Newcastle students sampled the same site in the same way in April 1996, shortly after the spill, and again during every Easter field course until April 1999.

Site 4 Vertical Cliff.

The vertical limestone cliff in front of the *Asterina* pools at West Angle Bay provided the opportunity to follow the progress of the juvenile year class without the complication of a large number of prespill animals. By April 1996, 98% of the *Patella* on this cliff had been narcotised by oil and were removed by the heavy wave action on this very exposed shore. The permanent quarter metre squared quadrat (located on a natural limestone peg) on this cliff had contained over 100 limpets in April 1995 (student project data). In April 1996 only three limpets survived.

The absence of limpets led to a particularly heavy settlement of *Enteromorpha* spp. on the cliff and the gully that led to it, which made access and sampling impossible over the next eighteen months. When the *Enteromorpha* and *Porphyra* spp. finally disappeared, in October 1997, and access was possible for the first time since the oil spill, the quadrat had been colonised by over 100 juvenile limpets. This cohort was measured and counted for the next five years.

TABLE 1 *Mean size and density of limpets in permanent quadrats at West Angle Bay pre- and post-spill 1995-2002. Shell size is inversely proportional to density (rs = -0.84, $p \leq 0.01$).*

	mean shell length (mm) ± standard deviation	range (mm)	n	density (m^{-2})
March 1995	19.50 ± 6.85	6 - 44	191	127.3
March 1996	19.69 ± 5.92	10 - 42	67	44.6
June 1996	25.00 ± 6.77	13 - 49	53	35.3
September 1996	28.92 ± 7.75	18 - 53	37	24.6
December 1996	29.02 ± 6.76	18 - 51	50	33.3
March 1997	30.12 ± 6.66	17 - 51	51	34.0
June 1997	25.88 ± 11.70	6 - 52	68	45.3
September 1997	22.19 ± 12.95	5 - 53	105	70.0
December 1997	19.94 ± 10.08	4 - 53	170	113.3
March 1998	20.47 ± 9.90	5 - 52	189	126.0
June 1998	19.39 ± 10.02	4 - 49	242	161.3
September 1998	16.64 ± 8.50	4 - 52	356	237.3
December 1998	16.87 ± 8.02	5 - 47	379	252.6
March 1999	17.22 ± 8.27	15 - 46	390	260.0
June 1999	18.23 ± 7.57	3 - 45	424	282.6
September 1999	19.74 ± 7.36	7 - 46	315	210.0
December 1999	17.97 ± 7.64	6 - 47	375	250.0
March 2000	16.46 ± 7.42	3 - 42	392	261.3
June 2000	16.47 ± 7.09	5 - 42	413	275.3
September 2000	17.12 ± 6.53	5 - 44	340	226.6
December 2000	17.48 ± 6.35	6 - 46	318	212.0
March 2001	16.96 ± 5.68	3 - 41	325	216.6
March 2002	15.72 ± 6.09	5 - 43	325	216.6

RESULTS

Site 1 Permanent Quadrats

Initial observations at West Angle Bay in the days following the spill indicated a very high mortality of limpets (50%) with large numbers of animals detached from the rocks, narcotised or moribund. There were large numbers of empty home scars and many limpets fell prey to oystercatchers and other sea birds, since they seemed incapable of sticking firmly to the rock. Initial counts in the six permanent quadrats, immediately post spill, showed a 65% decrease in the total number of limpets from 191 in March 1995 to 67 in March 1996 (Table 1).

The numbers of limpets in these six permanent quadrats are plotted at three monthly

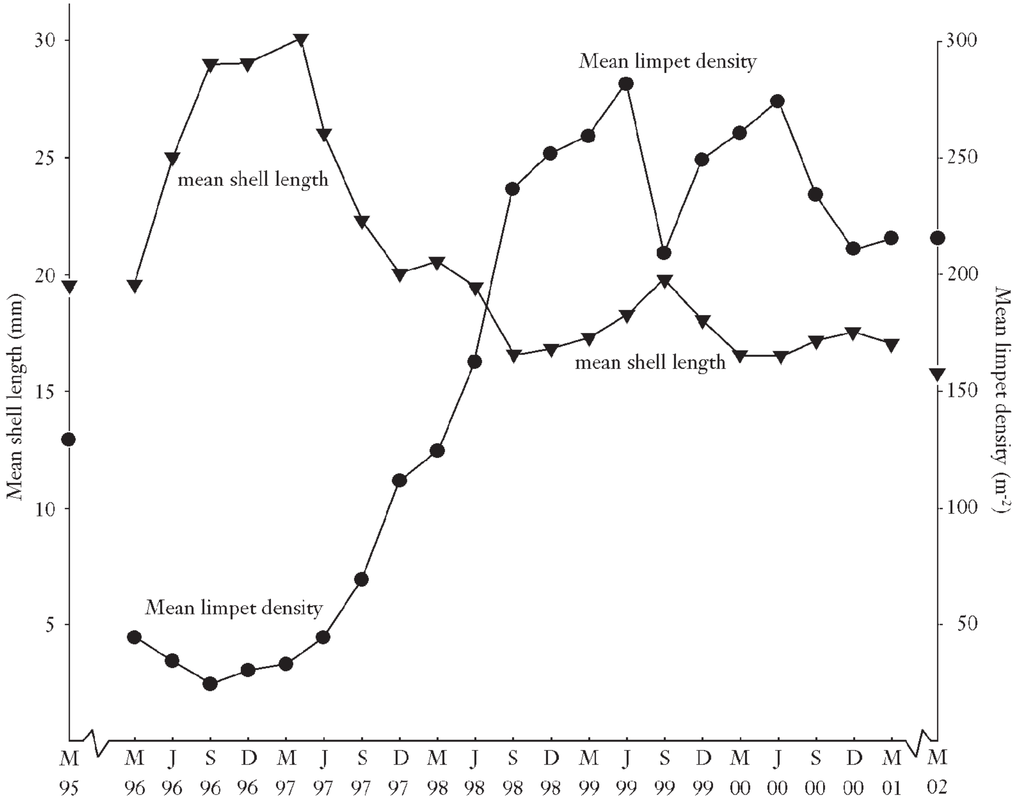


FIG. 1.

Changes in number of limpets, and their mean size, in the permanent quadrats on the north side of Angle Bay from March 1996 until March 2001. The March 1995 data show pre-spill values.

intervals against the mean size in Fig. 1. Numbers remained low throughout 1996 and in early 1997 until juvenile limpets began to appear in the quadrats in June 1997. As described by Crump *et al.* (1999), the dramatic decrease in limpet density led to a huge increase in *Enteromorpha* spp and a dramatic 'green phase'. This, in turn, provided the surviving limpets with an enormous potential food supply which, coupled with a marked decrease in competition for food, resulted in an equally dramatic increase in limpet size. Between March 1996 and March 1997, the mean size of limpets (Table 1, Fig. 1) increased from 19.69 ± 5.92 mm to 30.12 ± 6.66 mm. Growth increments in individual limpets of 10 mm in diameter were not uncommon and one animal grew from 21 to 33 mm in twelve months (Fig. 2). A 50% increase in length of limpets represents something like a four-fold increase on volume (Fig. 3) and wet weight (Ballantine, *pers. comm.*). Typical small flat 'exposed shore limpets' were converted into much larger, more pointed 'sheltered shore' type animals.

The dramatic increase in length of limpets from the permanent transect is well illustrated by size frequency distributions of limpets in March 1995 and March 1997 (Fig. 4). Further examination of these histograms show that a large cohort of juvenile limpets only became apparent in June 1997 (Fig. 4) even though they must have settled somewhere on the shore during the previous November or December. Large numbers of small limpets

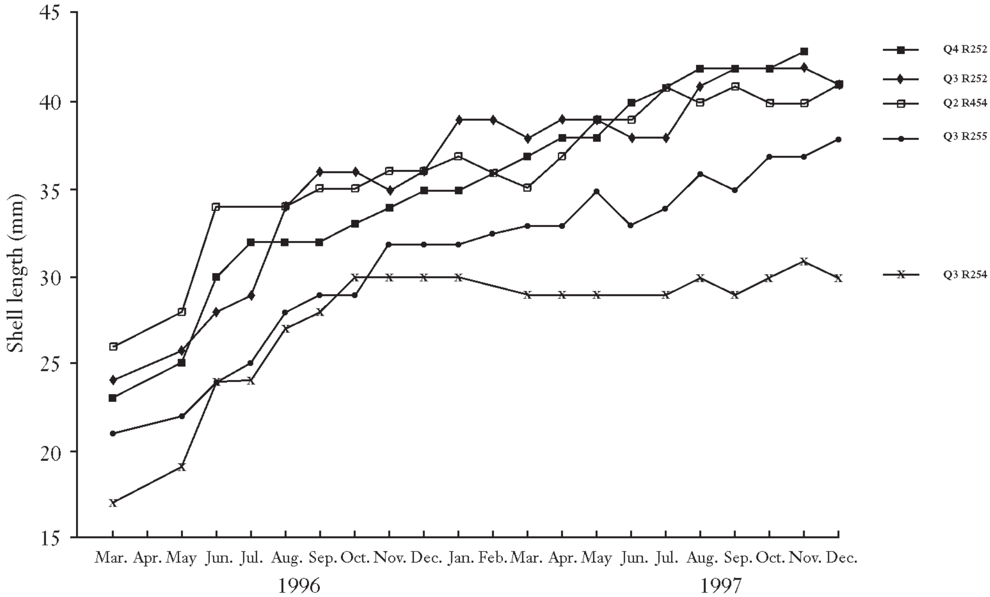


FIG. 2.
Individual growth curves for limpets living in the permanent quadrats on the north side of Angle Bay from March 1996 until December 1997.

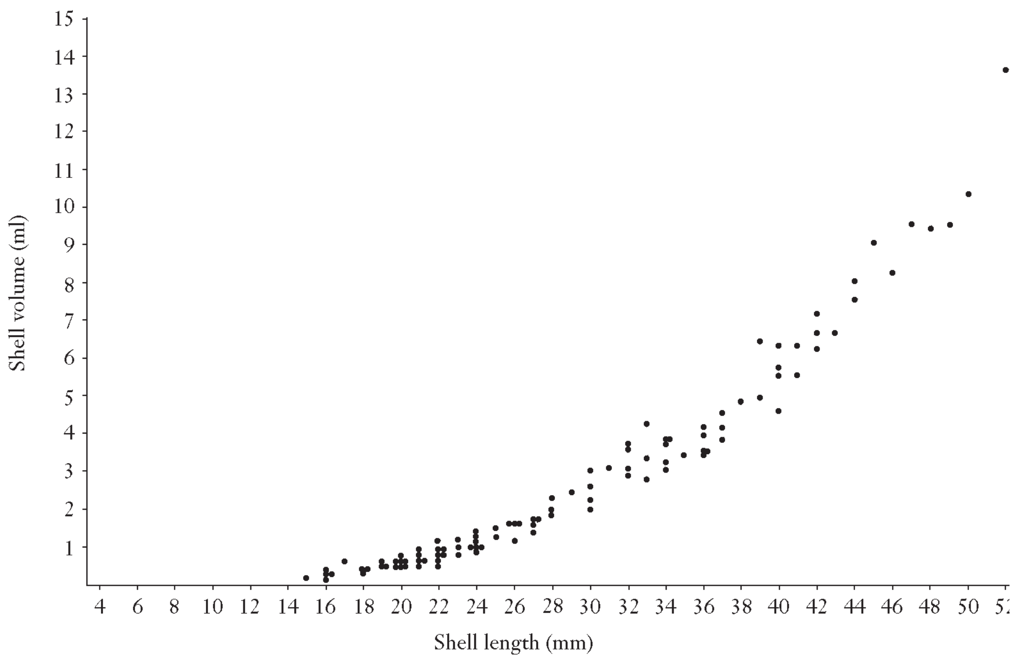
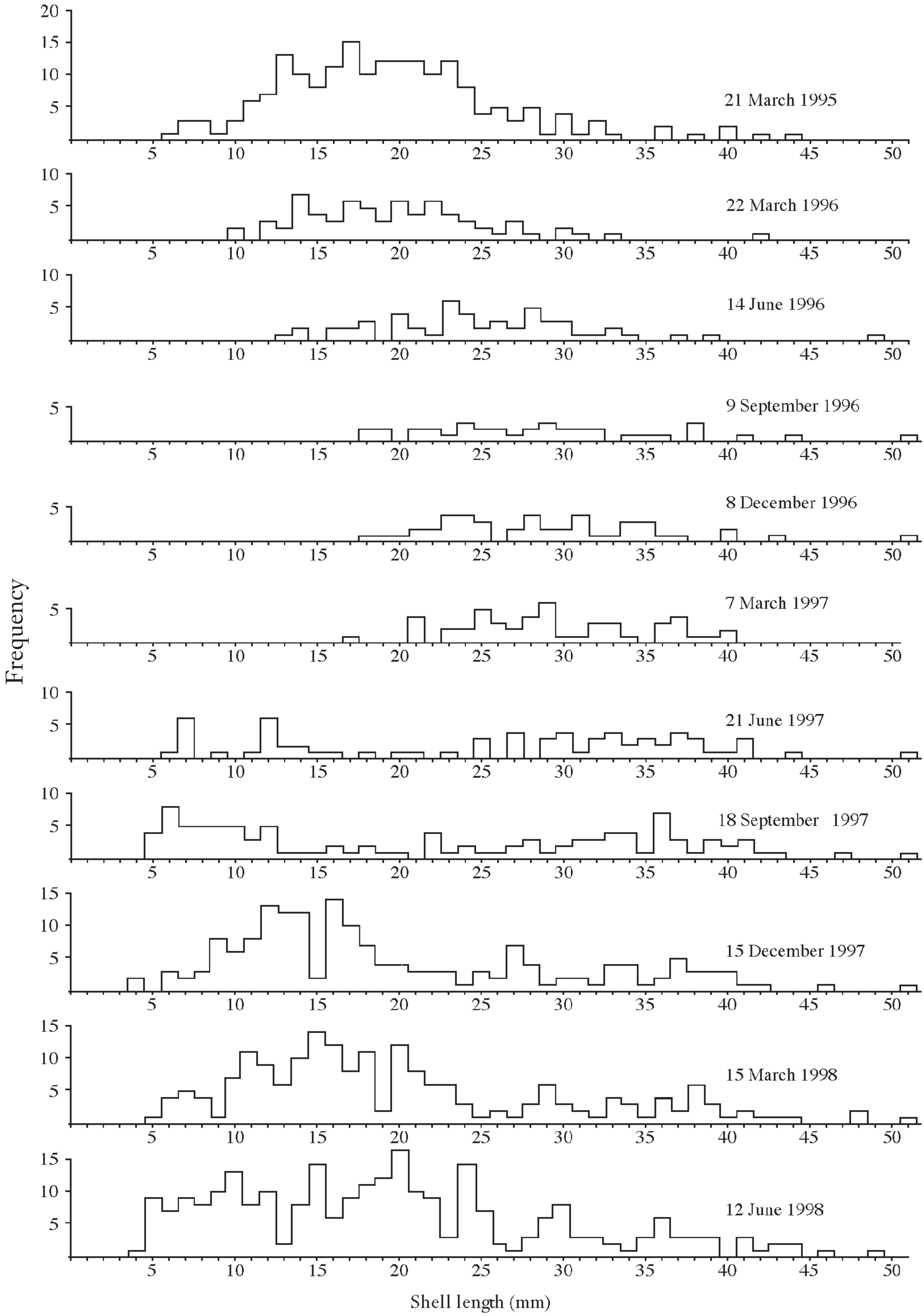


FIG. 3.
The relationship between length and volume of empty limpet shells collected from Angle Bay.



Frequency
21 March 1995
22 March 1996
14 June 1996
9 September 1996
8 December 1996
7 March 1997
21 June 1997
18 September 1997
15 December 1997
15 March 1998
12 June 1998
Shell length (mm)

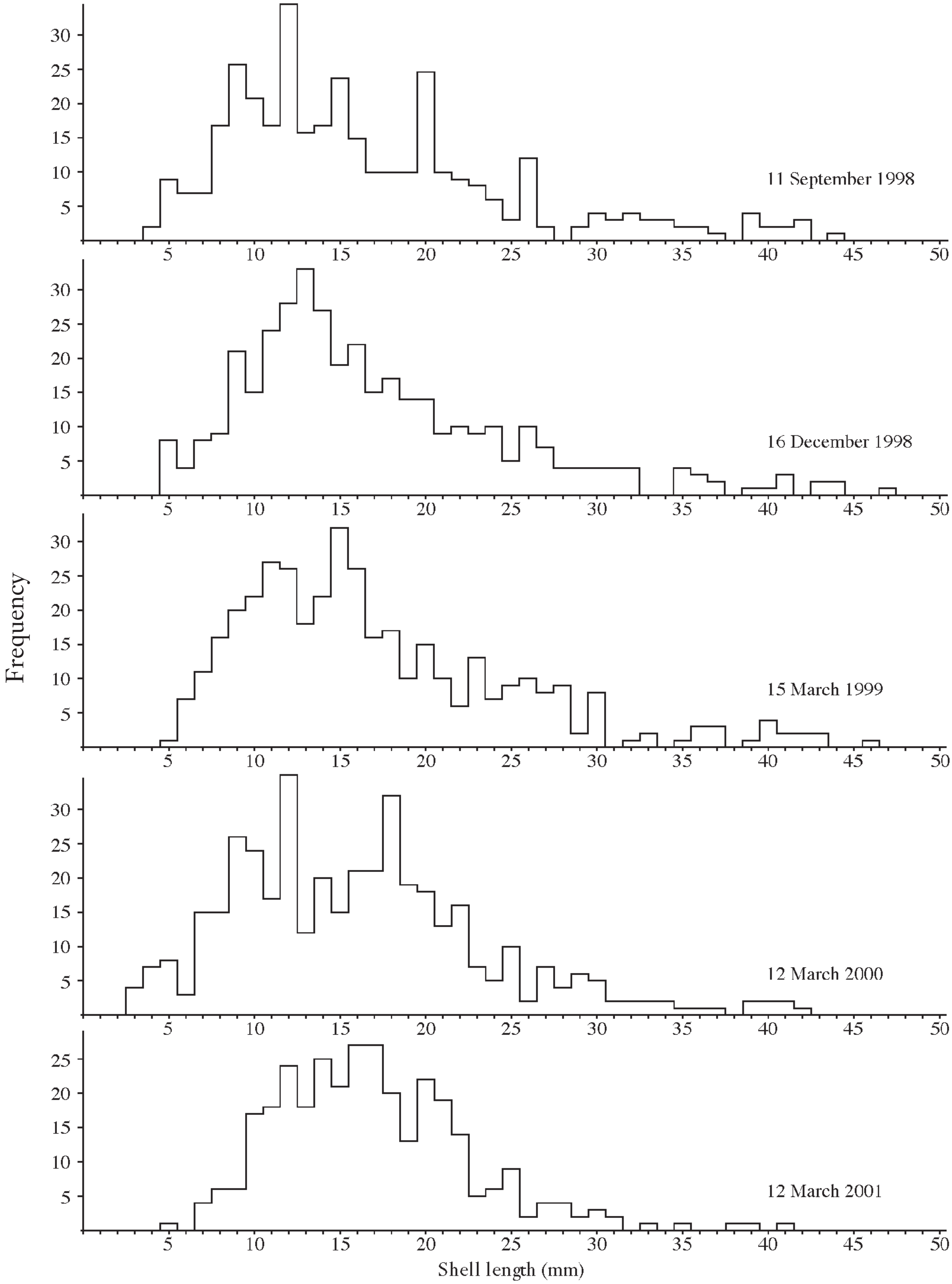


FIG. 4.
Size frequency histograms for limpets in the permanent quadrats on the north side of Angle Bay from March 1996 until March 2001.

Table 2 *Mean size and density of limpets from the horizontal belt transect at West Angle Bay, Site 2. Shell size appears to be inversely proportional to density but rs = -0.31, not signficant.*

	mean shell length (mm) ± standard deviation	n	mean density (0.25 m^{-2}) ± standard deviation	n
March 1996	18.47 ± 6.42	209	51.30 ± 15.99	25
June 1996				
September 1996	23.78 ± 3.94	100	5.30 ± 4.13	40
December 1996	25.78 ± 4.68	206	7.70 ± 3.79	30
March 1997	26.23 ± 4.86	200	7.96 ± 3.83	25
June 1997	16.85 ± 10.25	166	18.43 ± 16.97	30
October 1997	19.55 ± 9.14	214	18.16 ± 7.64	25
December 1997				
February 1998	19.19 ± 7.88	204	32.23 ± 7.84	22
June 1998	16.96 ± 7.99	224	54.85 ± 15.58	20
September 1998	18.50 ± 8.85	216	67.60 ± 17.72	20
December 1998	18.07 ± 7.87	230	67.00 ± 13.66	20
March 1999	18.23 ± 7.46	234	92.05 ± 20.89	20
June 1999	19.38 ± 6.20	204	89.20 ± 16.38	20
September 1999	19.48 ± 6.37	258	78.95 ± 17.61	20
December 1999	17.46 ± 6.32	190	85.95 ± 13.99	20
March 2000	17.85 ± 6.25	235	79.80 ± 11.56	20
June 2000	17.78 ± 6.07	223	77.45 ± 15.20	20
September 2000	17.73 ± 5.28	201	72.75 ± 9.67	20
December 2000	17.52 ± 5.30	194	57.80 ± 8.62	20
March 2001	16.85 ± 5.17	185	57.50 ± 5.84	20
March 2002	15.30 ± 5.63	201	62.30 ± 10.42	20

colonising the quadrats led to an overall decrease in mean size over the next year (see Fig. 1) and by March 1998 densities similar to those encountered pre-spill obtained. During the next twelve months, the numbers of limpets measured in the quadrats doubled, thanks to another large recruitment of juveniles, and the mean size declined further (Fig. 1). Between March 1999 and March 2001 these post spill limpets (< 30 mm) came to dominate the quadrats (Fig. 4) and the large (>30 mm) pre-spill limpets began to disappear from the population so that only one survivor of the spill (43 mm in diameter) remained in March 2002.

Site 2 Horizontal Belt Transect

The results from the small number of permanent quadrats were strongly reinforced by student data collected from a horizontal belt transect in the middle shore immediately adjacent to the transect (Table 2 and Fig. 5).

Densities here dropped from 51.3 per quarter metre squared quadrat (205 m^{-2} immediately post spill to 5.3 per quadrat (21.2 m^{-2}) in September 1996. Mean size over this period increased from 18.47 ± 6.42 mm to 23.78 ± 3.94 mm, presumably due to improved feeding conditions and decreased competition for that food. While mean size continued to increase to 26.23 ± 4.86 mm in March 1997 (Table 2) the most rapid growth was undoubtedly in the first six months post spill (March to September 1996) when the rocks

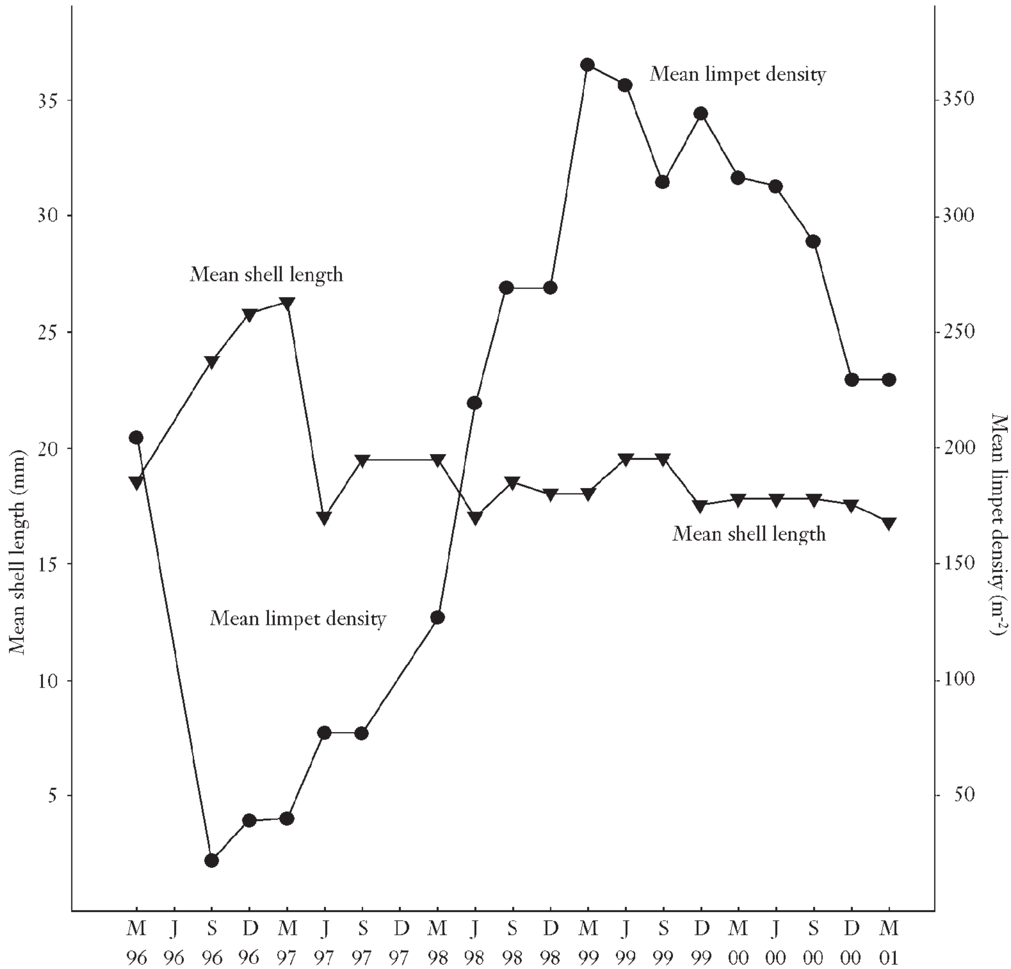


FIG. 5.

Changes in number of limpets, and their mean size, in the horizontal belt transect on the north side of Angle Bay from March 1996 until March 2001.

were covered in a dense film of *Enteromorpha* spp. [Unfortunately sampling at this site during this period was made impossible by the extremely slippery and dangerous nature of the slope and by the fact that many limpets were hidden under the *Enteromorpha*].

The size-frequency distributions for this site (Fig. 6) show the appearance of a 0+ juvenile cohort in July 1997 leading to bimodal distributions and a decrease in overall mean size. Densities, as a consequence, more than doubled in July 1997 and by July 1998 were back to 200+ m^{-2} (Fig. 5). The size frequencies (Fig. 6) show that in the next two years successive waves of young limpets entered the population and densities reached a maximum of 92 per quadrat (368 m^{-2}) in March 1999. Mortality was high in 2000 and many of the large pre-spill limpets disappeared so that, by March 2001, densities had once again returned to 200+ m^{-2} and mean size to 16.85 mm. Despite the major perturbation to limpet populations between 1995 and 2000, the situation in 2001 seemed to be very similar to that prior to the spill with high densities of small limpets.

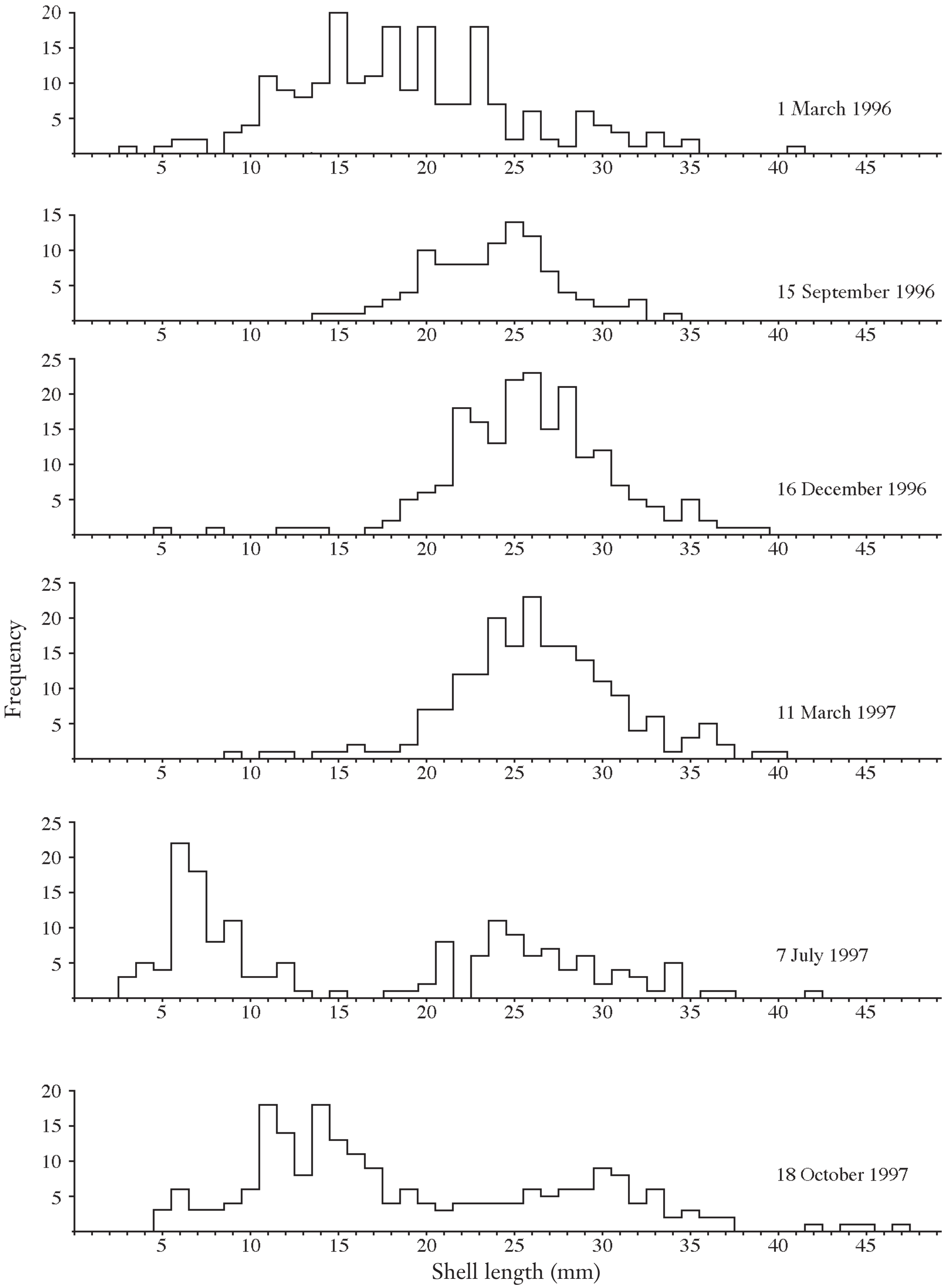
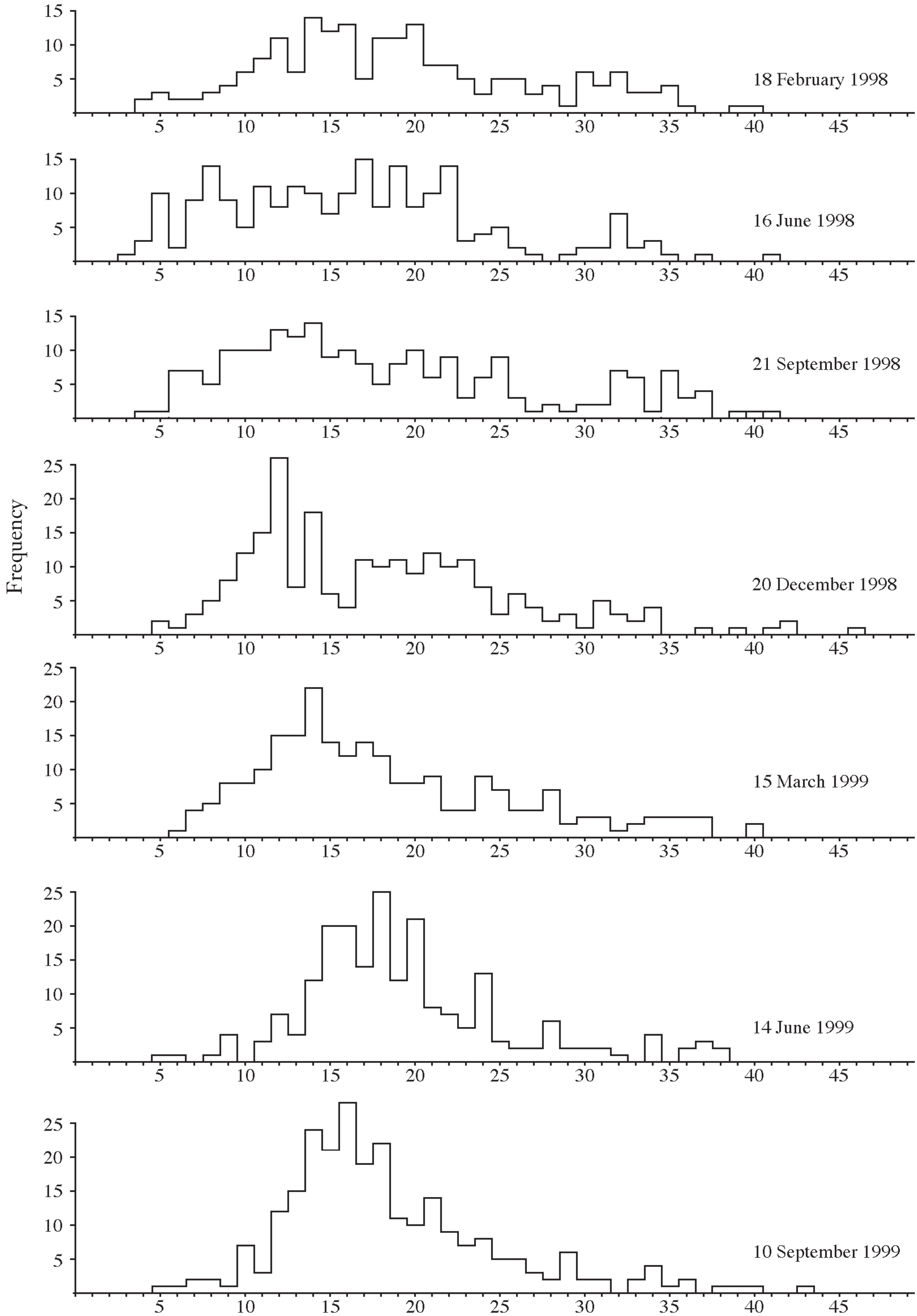


FIG. 6.
Size frequency histograms for limpets in the horizontal belt transect on the north side of Angle Bay from March 1996 until March 2001.


18 February 1998
16 June 1998
21 September 1998
20 December 1998
15 March 1999
14 June 1999
10 September 1999
Frequency
Shell length (mm)
5
10
15
20
25
30
35
40
45

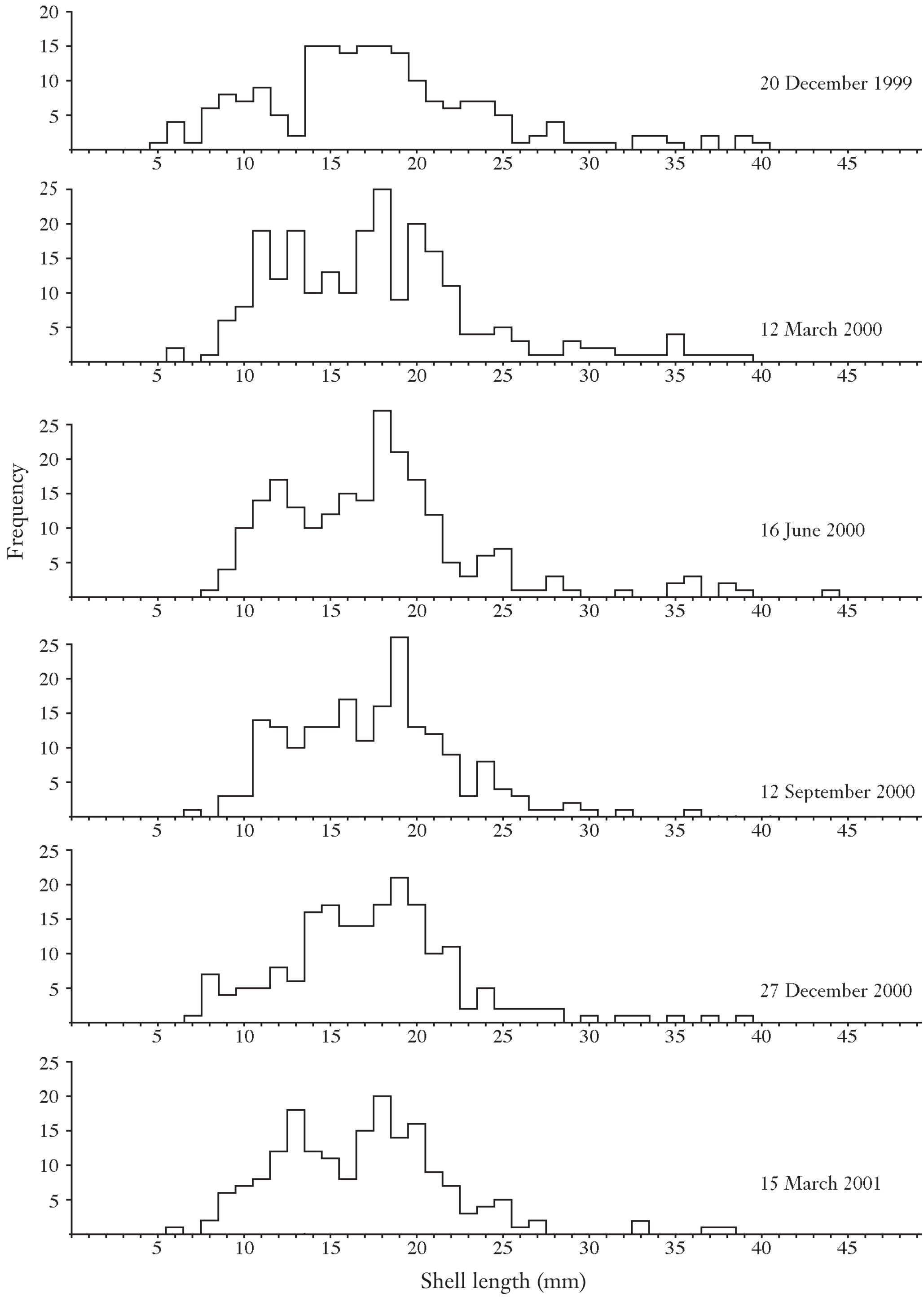


FIG. 6 concluded

TABLE 3 *Newcastle-under-Lyme School Data 1995-1999*

	Total number	Mean Size (mm) ± Standard deviation	Number Quadrat^{-1}	Mean density ± Standard deviation
April 1995	294	16.80 ± 5.07	36	43.83 ± 10.13
April 1996	401	16.01 ± 6.67	42	15.25 ± 11.59
April 1997	244	26.28 ± 5.80	30	8.20 ± 4.10
April 1998	267	18.12 ± 10.12	20	29.90 ± 8.20
April 1999	311	16.71 ± 8.65	30	47.96 ± 18.75

Site 3 Student Class Data

Further evidence of the main trends in the population changes at West Angle Bay was provided by the large data sets collected annually in April by students from Newcastle-under-Lyme School.

The original data were collected a year prior to the spill in April 1995 during a class exercise when students counted the numbers of limpets in 36 quarter metre squared quadrats and measured 294 of these in eight quadrats. The mean length was 16.80 ± 5.07 mm and the density 43.83 per quadrat (175 m^{-2}) see Table 3 and Fig. 7. With the willing cooperation of the staff, the Newcastle students sampled the same site six weeks after the spill (April 1996) when a high mortality of all sizes of limpets was observed. Thus, the mean size of the surviving limpets was similar to that before the spill (16.01 mm) but the density had dropped to 15.23 per quadrat (62 m^{-2}). One year later a similar student sample showed that density had dropped even further to 8.2 per quadrat (32.8 m^{-2}) and the surviving limpets had increased dramatically in size (mean 26.28 mm) and therefore volume.

As at the other sites the mean size had decreased significantly by April 1998 (18.12 mm) due to the presence of a large 1+ year class of juveniles and the density had risen to nearly 30 per quadrat (120 m^{-2}). The final visit and sampling by Newcastle-under-Lyme School showed that the limpets had recovered to pre-spill densities *i.e.* 48 per quadrat (192 m^{-2}) and had a mean size of 16.71 mm, similar to that found in April 1995. The size-frequency distributions (Fig. 7) show that a number of very large pre-spill limpets were still present at that time.

Sadly, Newcastle-under-Lyme School did not return to Orielton in 2000 and this run of data set terminated.

Site 4. Vertical Cliff

Prior to the oil spill, the permanent quadrat on the vertical cliff contained 103 limpets in April 1995 with a mean length of 17.06 ± 4.90 mm (data collected in a student project by Simon Bradbury). Almost all these limpets were killed during the spill; only three remained in April 1996.

Access to the site was prevented by the extremely dangerous nature of rocks covered in the green algae *Enteromorpha* spp. for the next 18 months. When the site finally became accessible again, in October 1997, the quarter metre squared quadrat had been colonised by 110 juvenile limpets, ranging from 4 to 20 mm in length, with a mean size of 10.74 ± 3.3 mm (Fig. 8). The majority of these limpets would have settled from the plankton in October/November 1996 and were therefore one year old. The size frequency histograms

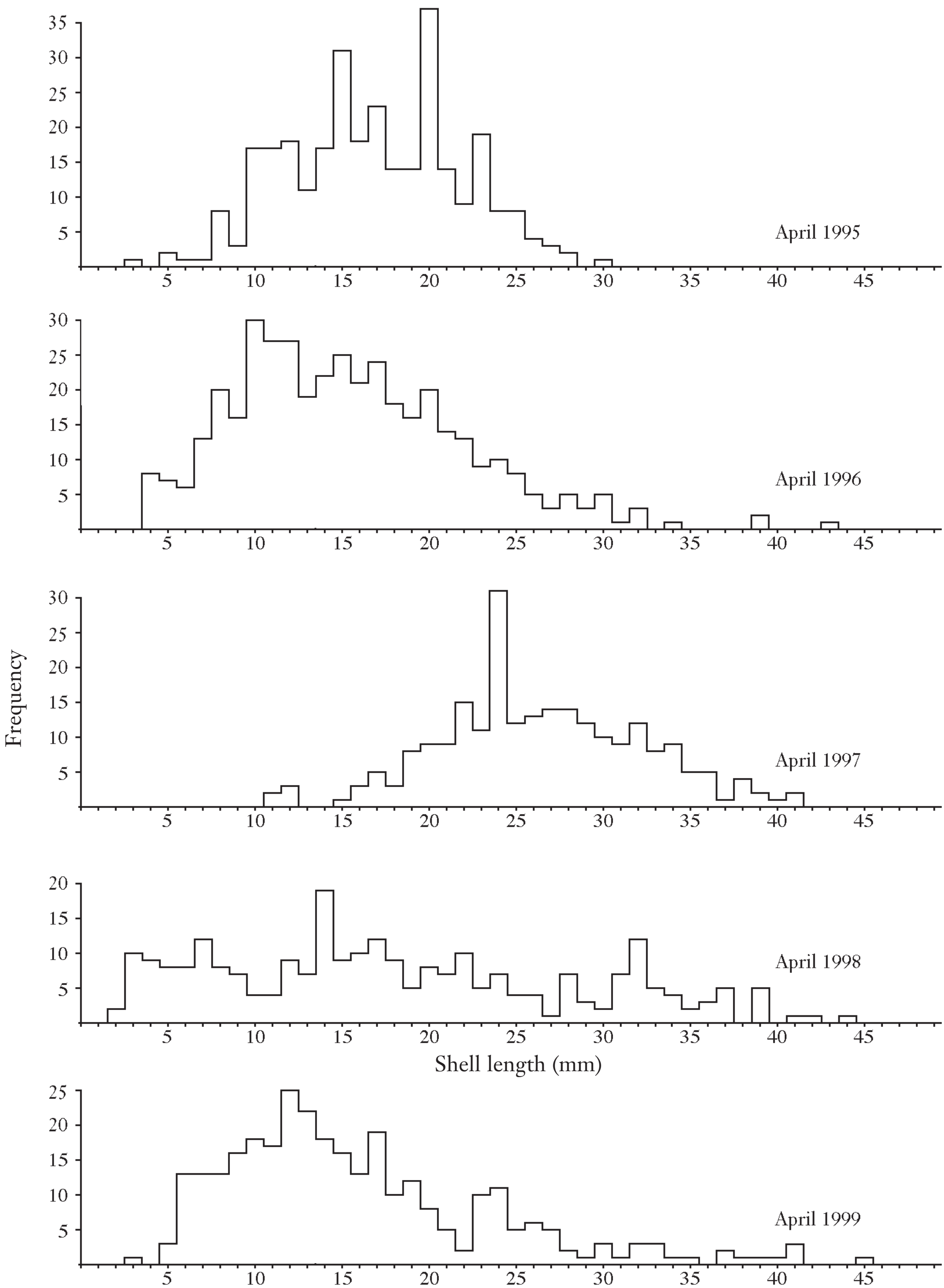


FIG. 7.
Size frequency histograms for the limpet data collected by students and staff of Newcastle-under-Lyme School in April from 1995 to 1999.

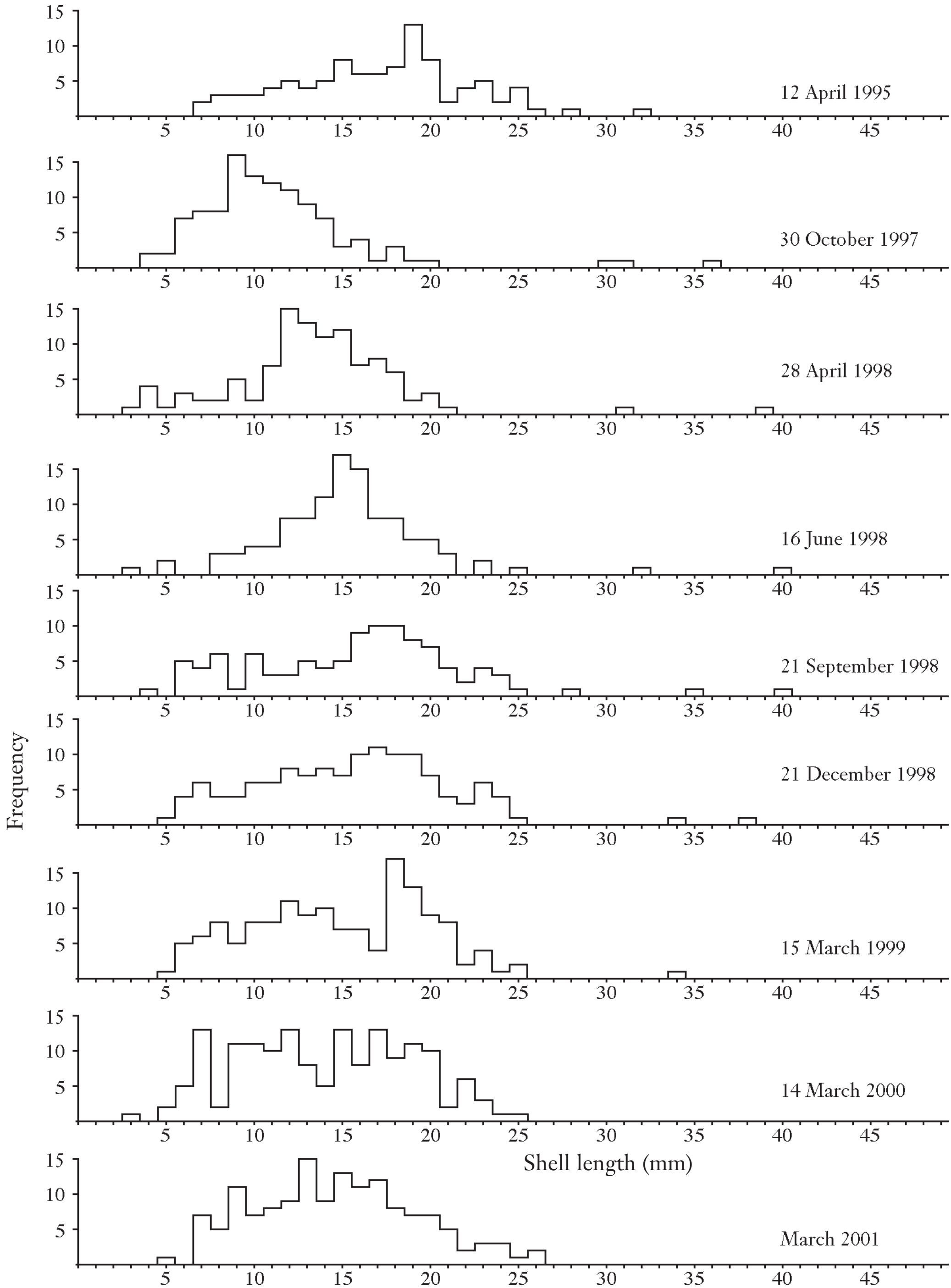


FIG. 8.
Size frequency histograms for limpets in the vertical cliff on the north side of Angle Bay from April 1995 until March 2001

for the vertical cliff limpets (Fig. 8) show the growth of this year class, which dominated the quadrat for the next five years. Small numbers of new juvenile limpets recruited to the site each year with maximum numbers (179) achieved in December 2000.

In the first two years of the new millennium, densities have settled down to approximately 150 per quadrat (600 m^{-2}), much higher than before the spill, and the mean size (14.16 ± 4.23 mm) is also significantly lower than before the spill ($x^2 = 8.43$; $p < 0.05$). It would appear that, at this extremely dynamic site with high wave action, it may be several more years before the natural equilibrium is restored. Small numbers of juveniles are recruited each year and, presumably, small numbers are knocked off by the waves.

DISCUSSION

Despite being so important, so abundant and so easy to study there are many unanswered questions about limpet populations. It is generally accepted (e.g. Fretter & Graham, 1962, 1976, 1994) that *Patella vulgata* is a protandrous hermaphrodite, maturing as a male and undergoing a subsequent sex change to become female. Spawning peaks between October and January, varying from place to place and year to year, apparently triggered by rough seas. The eggs are broadcast singly and fertilised in the seawater (males and females do not have to meet in order to breed together, only their gametes). The trochophore larva hatches after about 24 hours, and reaches the crawling stage at around 15 days. Metamorphosis into a snail is complete in 3 weeks and at a size of 200 µm. It is not likely that limpets end up living close to where their parents lived, and the breeding population in, say, Angle Bay may be drawn from many different genetic backgrounds. Growth rates, ultimate size and longevity have been shown to vary greatly from place to place and from time to time (Lewis & Bowman, 1975).

Limpets of the genus *Patella* are, arguably, the 'keystone' species (*sensu* Paine, 1966) on European Atlantic rocky shores because, by their grazing activity, they control the environment for everything else. For example, our sheltered shores are generally dominated by brown fucoid algae whilst, on more exposed sites, barnacles and limpets prevail. Early experimental work on the Isle of Man (Jones, 1948, Southward, 1964) clearly showed that *Fucus* spp. were prevented from covering more exposed shores by limpet grazing . The effect of grazing gastropods in general and limpets in particular in controlling the growth of green, brown and red algae has subsequently been well documented (Hawkins & Hartnoll, 1983, Hawkins *et al*., 1992 for reviews). Any environmental change (be it abnormal weather or pollution) that significantly affects limpet populations will, accordingly, have a knock-on effect on the whole rocky shore community over and above the direct effects of the pollutant itself. Ever since the *Torrey Canyon* incident (Smith, 1968) it has been known that limpets of the genus *Patella* are particularly susceptible to oil pollution. This is probably because a film of oil covering the air-water interface around the margin of the shell prevents the animal from breathing out of water at low tide. In their efforts to breathe, limpets leave their 'homes' and are at risk from predators, desiccation and dislodgment. Many die. The subsequent disruption to the rocky shore community after the removal of the 'keystone' species has been documented in detail for shores in Cornwall after the *Torrey Canyon* spill (Southward & Southward, 1978, Hawkins & Southward, 1992), in Pembrokeshire after the *Sea Empress* spill (Crump, Morley & Williams, 1999) and in many other parts of the world (see Clark, 1982, Moore & Guzman, 1995).

While it is true that the *Sea Empress* oil spill was an extremely traumatic event both for limpets and their observers, it did provide marine biologists at Orielton Field Centre with a quite remarkable 'natural experiment'. Many of the things we had taken for granted, but had never been able to prove, were demonstrated with great clarity. Four independent monitoring programmes tracked the recovery of limpet populations in different areas of West Angle Bay - and showed but minor variations on a single theme.

Some may query the use of student data in a published paper. It is, however, the experience of staff at several FSC Field Centres, that students are perfectly capable of collecting data accurately and may, indeed, be more objective than professionals because, not knowing the expected pattern of results, they have no temptation to 'massage' the data to fit it. A large class of students are also able to collect many more data on one sampling visit.

We wish to highlight five features of limpet biology that can be inferred from the data presented in this paper:

1. *There is no direct relationship between size and age in limpets of the genus* Patella; *size is principally controlled by food supply*.

Limpets grow throughout their lives which may exceed 16 years, so for any given individual, there *is* a relationship between its size and its age (e.g. Fig. 2). But because, as in so many invertebrate animals, growth rate depends more upon the quantity and quality of food (Bowman & Lewis, 1975) than on the period of time over which it was eaten, the size a limpet has attained is not a useful measure of age after its first few months. The death of so many limpets at West Angle Bay following the oil spill resulted in a greatly enhanced food supply in the form of a flush of green algae (eg. *Enteromorpha*). This abundant food enabled the limpets to grow extremely fast, doubling in length and quadrupling in volume in the space of twelve months. Such an increase in size might take ten years or more under normal conditions (Ballantine, *pers. comm.*). The accelerated growth rates in individual limpets were confined to the first twelve months after the spill (Fig. 3), after which growth almost ceased. Although this group of large limpets (35+ mm) remained visible, in ever decreasing numbers, until 2000, there was no sign of a comparable spurt of growth in the following years, perhaps because food supplies became limiting for the survivors.

2. *There is an inverse relationship between size and density in limpet populations.*

The often-observed fact that sheltered rocky shores support relatively few limpets which grow to a comparatively large size whilst exposed sites usually have high densities of small limpets, has formed the basis of many a student project, since the observation is easily quantified. The obvious assumption was that increased intraspecific competition for food at high densities on exposed shores results in the much smaller mean size. The current study demonstrates the effect of reducing the density (number m^{-2}) of limpets on exposed shores. Not only did the surviving limpets increase dramatically in size at the lower densities but also, as densities rose in subsequent years, the mean size decreased rapidly. The data presented in Figs 1 and 5 strongly suggest an inverse relationship between size and density. The increasing intraspecific competition for increasingly scarce food supply produced a situation where densities were higher and mean size lower in March 2002 than in 1995. We conclude that the small size of limpets normally seen on exposed shores is due principally to shortage of food - as a result of intraspecific competition.

For site A, a Spearman's rank correlation coefficient of -0.84 confirms that the inverse relationship between mean limpet size and limpet density was significant at the 1% level (data in Table 1). Although Fig. 5 suggests a similar inverse relationship in the horizontal belt transect, the data in Table 2 do not allow us to reject the null hypothesis at the 10% level (*rs* = -0.31).

Lewis & Bowman (1975) suggested that the idea of an inverse relationship between size and density was an oversimplification and that quality and quantity of food was more important. An increasing body of experimental work, including sophisticated caging experiments in the field (Boaventura *et al.*, 2003), has demonstrated the existence of intense intraspecific competition between size classes of limpets. The *Sea Empress* oil spill constituted a giant field experiment and the present study lends weight to the idea that size and density in limpet populations are indeed inversely related.

3. *Limpets settle in nursery areas and colonise the open rock surface some considerable time later.*
According to Fretter & Graham (1976) limpet larvae become snails at a shell length of 200 µm. The smallest limpet sampled in this survey was 2 mm long and it is obvious from Figs 4, 6, 7 and 8 that very small limpets were never a significant component of the sampled population. An element of observer error may be expected because very small snails are difficult to see - let alone measure - but, as mortality rates are high at this age, they must have been present at high densities somewhere on the shore in order to deliver the number of recruits the populations received later in the year. Lewis & Bowman (1975) suggest that newly settled spat settle in damp cracks and crevices and only venture out onto drier rocks at 4-5mm in length. In this study, colonisation of the permanent quadrats by the 1996-1997 cohort was first recorded in June 1997 (Fig. 4). No limpets smaller than 17 mm were recorded on 7 March 1997 but the young must have been on the shore by that date. Moreover, the members of this cohort increased in abundance during the following months indicating that more and more individuals were migrating into the quadrats as time passed. Table 1 records limpet density rising from 33.3 m^{-2} to 70 m^{-2} between March and September 1997, even though it is unlikely that any limpet spat settled during this period. These observations support a long-held assumption that the survivors of limpet settlement (in pools and tiny crevices, or on the lower shore) enjoy an active exploratory period before adopting a 'home' in which to live and from which to crop the available vegetation.

4. *Settlement is neither evenly nor randomly distributed across the shore but zoned.*
We do not wish to read too much into the data displayed in Table 4 (opposite) because these are counts from single quadrats; no replication of the data was possible. That being said, the tabulated data indicate some striking patterns.

Mean low water mark of spring tides in Milford Haven is at 0.7 m above Chart Datum (CD). Mean low water of neap tides is at 2.5 m and mean high water neaps is at 5.2 m. Quadrats 2, 3 and 4 are thus on the lower shore; quadrats 5, 6 and 7 are on the middle shore. At 0.6 m, in the sub-littoral fringe, quadrat 1 is rarely accessible; *Patella vulgata* is rare or absent at this site.

Survival of limpets in the presence of oil seems to have been best in quadrats 2 and 3, which accords with the hypothesis that suffocation is the primary cause of death since these quadrats only emerge from the sea for short periods of time.

The 1997 data suggest that settlement was also most successful in these quadrats; half of the limpets counted that year were in quadrats 2 and 3. In all subsequent years, most limpets were counted in quadrats 4 and 5. Grouping the quadrats in pairs allowed us to evaluate the patterns using *t* tests.

TABLE 4 *Numbers of limpets in the individual permanent quadrats at West Angle Bay pre- and post-* Sea Empress *Oil Spill 1995-2003; some of the raw data from which Table 1 was compiled.*

Height above CD Quadrat no	1.2 m 2	1.8 m 3	2.4 m 4	3.0 m 5	3.6 m 6	4.2 m 7	Total
March 1995	40	43	38	28	30	12	191
March 1996	24	15	6	9	8	5	67
June 1996	17	14	5	6	6	5	53
September 1996	11	7	5	4	5	5	37
December 1996	18	12	6	5	5	4	50
March 1997	18	12	7	4	5	5	51
June 1997	25	13	13	7	6	4	68
September 1997	30	28	17	20	5	5	105
December 1997	39	32	29	35	23	11	170
March 1998	46	40	28	35	30	10	189
June 1998	54	49	32	59	38	10	242
September 1998	56	70	57	109	56	8	356
December 1998	56	65	65	89	89	16	379
March 1999	58	61	66	85	94	26	390
June 1999	55	69	73	113	83	31	424
September 1999	44	52	57	62	76	24	315
December 1999	50	55	69	86	78	37	375
March 2000	59	64	70	83	72	44	392
June 2000	72	75	81	90	48	47	413
September 2000	50	57	78	60	51	44	340
December 2000	54	62	60	53	45	44	318
March 2001	40	62	70	59	59	35	325
March 2002	56	63	61	60	50	35	325
March 2003	56	68	77	65	50	34	350

In 1996, there were significantly more limpets in quadrats 2+3 than there were in either 4+5 or 6+7 (t = 4.46 and 4.69 respectively with seven degrees of freedom). In 1997 and 1998, there were significantly more in 2+3 than in 6+7 (t = 5.14 and 2.83 respectively) and more in quadrats 4+5 than 6+7 (t= 3.71 and 3.22). There were no significant differences thereafter.

These data suggest that the lower shore is the limpets' most successful settlement area at this site and post-juvenile individuals move to progressively higher levels when their density becomes too great for all to obtain an adequate supply of food. It is possible that the highest quadrat was colonised by older limpets in 2000 due to the lack of suitable cracks and crevices for juveniles. In pollution experiments on Somerset shores, Crothers (1983) recorded that the oiled quadrats were recolonised by sizeable limpets, not juveniles. There was no evidence, however, of the migrating 'fronts' of limpets observed by Hawkins & Southward (1992) after the 'Torrey Canyon' oil spill.

5. *The benign effect of bladderless bladder wrack on limpet populations*

In both Figs 1 and 5, the September 1999 figure for limpet density appears to be anomalously low. Examination of Table 3 shows that this was especially true in quadrat 5 where the number fell from 113 (June) to 62 before rising again to 86.

Reduction of grazing pressure, following the *Sea Empress* incident, enabled the bladderless bladder wrack, *Fucus vesiculosus* var. *linearis*, to colonise West Angle Bay (Crump *et. al.*, 1999). It appeared as short scattered plants in October/ November 1996 at the level of permanent quadrats 5, 6 and 7 and had expanded to blanket cover, notably in quadrat 5, by March 1997. Cover was maintained in June 1999 and the algae appeared healthy but, in September, the cover was greatly reduced and the remaining plants appeared brittle and old. In December 1999, there were no plants left in quadrats 5 and 6; the only *F. vesiculosus* var. *linearis* remaining were young plants in quadrat 7. They and all other plants of this species had been eliminated from the shore by March 2001.

Previous studies have suggested that juvenile limpets prefer *F. v*.var.*linearis* clumps and grow more quickly under this canopy (Hawkins & Hartnoll,1983, Hartnoll & Hawkins, 1985). We suggest that the 113 limpets present in quadrat 5 in June 1999 (the highest density recorded in Table 3) were predominantly young snails, protected from avian predation, insolation, desiccation and wave action by the algal cover. The storms at the beginning of August 1999 tore away most of the algae and by September 45% of the limpets had died, moved or been removed by waves from the quadrat.

There are many examples in the literature of the 'whiplash effect' of fucoids with long trailing fronds being swept back and forth across the rock surface and wiping the latter clean from young snails and barnacles. This is an example of the positive effect fucoid algae can have on limpet populations and the negative effects when that fucoid cover subsequently disappears.

ACKNOWLEDGEMENTS

We are grateful to Martin Corbet for technical assistance in establishing the permanent quadrats and to the many students and staff at Orielton Field Centre who assisted with the collection of data in the field. Outstanding contributions to the fieldwork were made by Fay Williams and the staff and students of Newcastle-under-Lyme School.

REFERENCES

BALLANTINE, W. J., (1963). *The biology of limpets*. unpublished PhD Thesis. Queen Mary College, London University.

BOAVENTURA, D., DA FONSECA, L. C. & HAWKINS, S. J., (2003). Size matters: competition within populations of the limpet *Patella depressa*. *Journal of Animal Ecology*, **72**, 435-446.

BOWMAN, R. S. & LEWIS, J. R., (1977). Annual fluctuations in the recruitment of *Patella vulgata*. *Journal of the Marine Biological Association of the UK*, **57**,793-815.

CLARK, R. B., (1982). *The long term effect of oil pollution on marine populations, communities and ecosystems*. Royal Society, London.

CROTHERS, J. H., (1983). Field experiments on the effects of crude oil and dispersant on common animals and plants of rocky sea shores. *Marine Environmental Research*, **8**, 215-239.

CRUMP, R. G., MORLEY, H. S. & WILLIAMS, A. D., (1999). West Angle Bay, a case study. littoral monitoring of permanent quadrats before and after the *Sea Empress* oil spill. *Field Studies*, **9**, 513-530.

FRETTER, V. & GRAHAM, A., (1962). *British Prosobranch Molluscs*. London, Ray Society. 755pp.

Fretter, V. & Graham, A., (1976). The Prosobranch molluscs of Britain and Denmark. Part 1. Pleurotomariacea, Fissurellacea and Patellacea. *Journal of Molluscan Studies*, Supplement 1.

Fretter, V. & Graham, A., (1994). *British Prosobranch Molluscs*, Second edition. London, Ray Society. 820pp.

Hartnoll, R. G. & Hawkins, S. J., (1985). Patchiness and fluctuations on moderately exposed rocky shores.*Ophelia*, **24**, 53-63.

Hawkins, S. J.& Hartnoll, R. G., (1983). Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology Annual Review*, **21**, 195-282.

Hawkins, S. J. & Southward, A. J., (1992). Lessons from the Torrey Canyon Oil Spill: Recovery of Rocky Shore Communities. In *Restoring the Nation's Marine Environment*, 583-631.

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.

Lewis, J. R. & Bowman, R. S., (1975). Local habitat-induced variations in the population dynamics of Patella vulgata. *Journal of experimental marine Biology and Ecology*, **17**, 165-203.

Moore, J. & Guzman, L., (1995). Biological impacts of Oil Pollution: Rocky Shores, *IPIECA Reports*, Series 7.

Paine, R. T., (1966). Food web diversity and species diversity. *American Naturalist*, **100**, 65-75.

Smith, J. E., (1968). *Torrey Canyon pollution and marine life*. Cambridge University Press.

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., (1964). Limpet grazing and the control of vegetation on rocky shores. In Crisp, D. J. (ed.). *Grazing in marine and terrestrial and marine environments*. pp. 165-273. Blackwell Scientific Publications, Oxford.

Southward, A. J., & Southward, E. C., (1978). Recolonisation of rocky shores in Cornwall after the use of toxic dispersants to clean up the *Torrey Canyon* oil spill. *Journal of the Fisheries Research Board of Canada*, **35**, 682-786.