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Phil. Trans. R. Soc. Lond. B 1983 **300**, 513-552
doi: 10.1098/rstb.1983.0019

Phil. Trans. R. Soc. Lond. B **300**, 513–552 (1983) [513]
Printed in Great Britain

THE ECOLOGICAL IMPACT OF THE SEA URCHIN *PARACENTROTUS LIVIDUS* (LAMARCK) IN LOUGH INE, IRELAND†

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(*Received* 16 *February* 1982)

CONTENTS

† This paper is no. 22 in the series 'The ecology of Lough Ine'. No. 21 was published in *Phil. Trans. R. Soc. Lond.* B **287**, 1–44 (1979). Earlier papers in the series were published in other journals.

An ecological account is given of the rocky shallow sublittoral of Lough Ine, County Cork, Republic of Ireland, from low water level to about 1 m below this level. With increasing distance from the Rapids mouth a forest of laminarian algae gives way to low algal bush, and still further into the lough the sea urchin *Paracentrotus lividus* destroys all soft upstanding algae. Much of the grazed area becomes overgrown by crustose coralline algae. Patches of the green algae *Codium fragile* ssp. *tomentosoides* and *Enteromorpha clathrata* fringe the *Paracentrotus* graze patches.

An account is given of the effects of *Paracentrotus* on the shallow sublittoral community. Algae in the ungrazed areas accommodate large numbers of individuals and many species of invertebrates, especially amphipods, small gastropods and small polychaetes. In grazing, *Paracentrotus* destroys this population and its habitat. However, the removal of these algae, and of the sediment that they trap, provides a new habitat, suitable for plant and animal species that can resist *Paracentrotus*. Crustose coralline algae cover much of the rock, and are burrowed into or enclose the tubes of a characteristic and entirely different polychaete fauna. On the surface of the rocks are found saddle oysters (*Anomia ephippium*), limpets (*Patella aspera*) and other hard-shelled animal species.

The relations between *Codium* and *Paracentrotus* have been investigated by transfer experiments in the 'field' and by observations with an aquarium tank. *Paracentrotus* readily eats *Codium*, especially when the urchins are at a high population density; but *Codium* benefits from the clearance of other algae, and is a quick recolonist, so that on balance it benefits from the presence of the urchin.

Paracentrotus feeds mainly by day, and on a steep shore some wander up into the littoral region as the tide rises and destroy *Fucus serratus*. This accounts for the almost complete absence of *F. serratus* from the North Basin. *Paracentrotus* does not move upwards by night.

The hard-shelled animal species *Anomia*, *Patella*, *Chlamys varia*, adult *Gibbula cineraria* and *Pomatoceros*, found plentifully on graze patches in the North Basin, diminish in abundance southwards even within grazed areas, while the numbers of the starfish *Marthasterias glacialis* under the rocks increase. Experiments show that *Marthasterias* readily eats *Anomia*. These *Marthasterias* are quite small. As they grow bigger they move away onto muddy areas and extend their diet to include large buried lamellibranchs.

Small *Paracentrotus* are usually found in larger numbers underneath boulders than above, while larger ones tend to come up by day onto the tops, where they form graze patches. From a study of growth lines in the interambulacral plates and from growth in cages we conclude that a horizontal diameter of 30–40 mm (with considerable variation) is reached in 3–4 years from settlement. The peak in numbers of *Paracentrotus* visible in the South Basin in 1979 might perhaps be ascribed to a good settlement in the warm summers of 1975 and 1976. Temperature of the shallow marginal water of the lough is subject to diurnal fluctuation, as in a tide pool, and can reach high levels in summer. This might favour *Paracentrotus*. However, numbers of *Paracentrotus* are probably severely reduced by predators in the South Basin. Crabs have already been implicated. It is possible that the small or half grown *Marthasterias* under shallow sublittoral rocks might destroy newly settled *Paracentrotus*, although this still has to be demonstrated.

1. Introduction

Lough Ine is almost completely enclosed, its catchment area is small, and its tidal exchange is considerable, so that, apart from in a few restricted areas, its salinity is close to that of the sea outside. It provides a range of current strength, sedimentation, and water temperature from the Rapids entrance at its southeast corner (figure 1) to the North Wall, which bounds its northern margin. Although the extreme richness of its flora and fauna greatly complicates the work involved, Lough Ine is ideally suited for the ecological investigation of its community structure. We hope also that an investigation of its present ecology will prove useful for comparisons in the future. Changes will certainly occur as a result of climatic drift, if for no other reason. Changes in the distribution of species are likely to be more sensitive to environmental change than presence or absence of species. It is therefore important to know about the distribution of plants and animals within the lough, about the factors controlling this distribution, and about variations in distribution from year to year. The importance of providing detailed information as to the sites within the lough where different species have been found, rather than simply reporting their occurrence, has led us to record these in our Appendix.

In this paper we explore the interrelations of organisms living on shallow sublittoral rock surfaces. Our study concerns a depth range from the low littoral to about 1 m below the lowest tide. We are concerned with the striking changes in the community of plants and animals that accompany the changes in physical conditions: the series of dominant algae from the Rapids westwards and northwards around the South Basin, with their associated flora and fauna; the destruction of these in graze patches in the South Basin and continuously around much of the North Basin by the sea urchin *Paracentrotus lividus*; and the establishment of a flora and fauna, resistant to sea urchin grazing, in the urchin-dominated areas. We shall follow the part played by starfish in this gradient of dominants, and the susceptibility of urchin-resistant hard-shelled animals to destruction by starfish. We have little information

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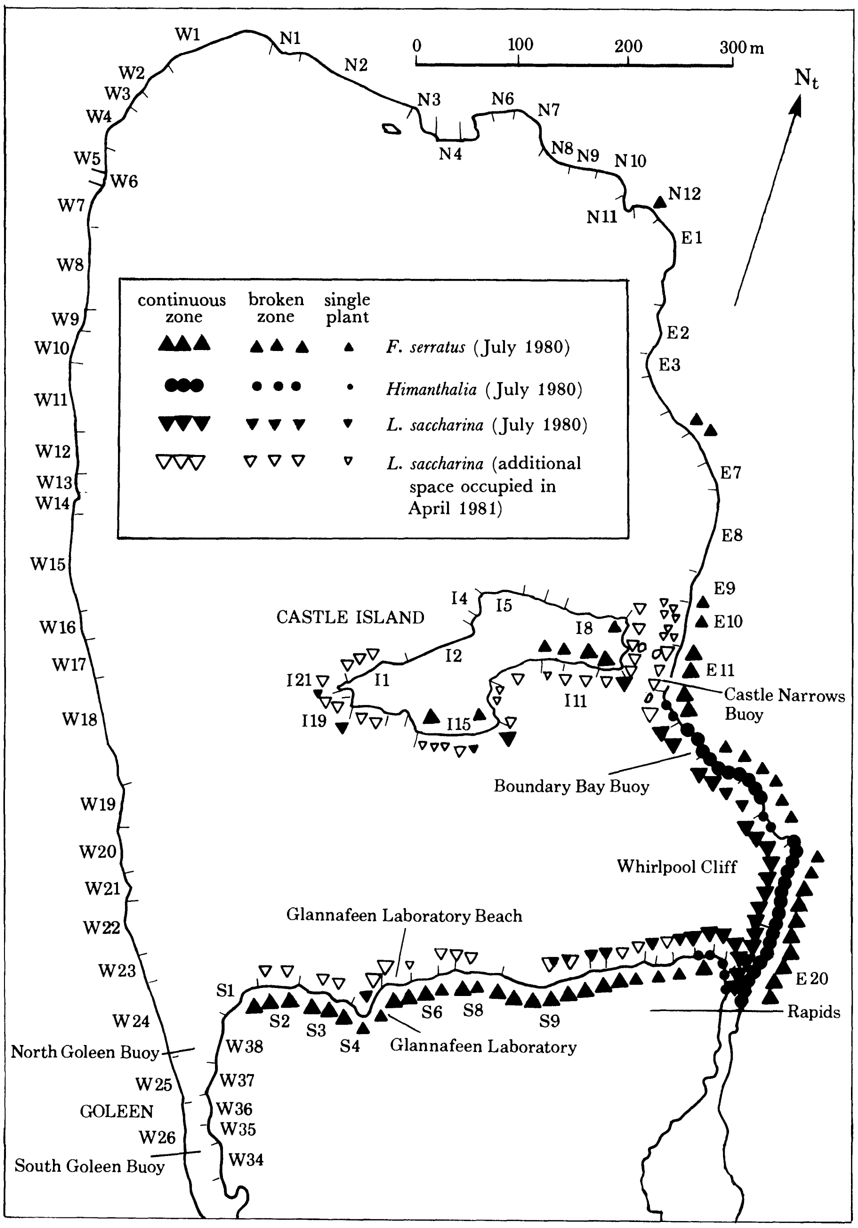

FIGURE 1. Distribution in Lough Ine of *Fucus serratus* (on landward side of low water line) and *Himanthalia elongata* (on low water line) and *Laminaria saccharina* (on seaward side of low water line). No mapping was carried out south of the line across the Rapids. The positions are also marked of four stations used for temperature profiles (see § 3 *a*).

as yet as to the part played by other predators, such as the numerous gobies and other small fish, and some of the crabs.

Although the common plants and animals of our study area have shown the same patterns of distribution throughout the period of our visits, in some cases boundaries have fluctuated. These fluctuations will be shown to provide opportunities for fast-growing species that would not persist in a climax state.

Our investigation owes much to the pioneer work of Renouf (1931) and Rees (1935) in Lough Ine. Records of the occurrence of many common species at sites in the Lough Ine–Barloge area, by which comparisons can be made between the lough and the open coast, are given by Ebling *et al.* (1960), but no continuous maps of distribution are yet available of any of the principal shallow sublittoral species. Detailed study of the rocky shallow sublittoral has been confined to the Rapids and their immediately surrounding area (Renouf 1931; Ebling *et al.* 1948; Lilly *et al.* 1953). *Paracentrotus* has been shown to control the growth of *Enteromorpha* on the unstable shell gravel bottom of Curlew Bay (I 2 in figure 1), and in so doing to reduce drastically the numbers of four invertebrate species that inhabit the *Enteromorpha* turf (Kitching & Ebling 1961). The present investigation is concerned with the stable rocky shallow sublittoral all around the lough. In areas not grazed by *Paracentrotus* this supports a dense growth of larger seaweeds, which in turn accommodates a large and complex fauna. Similarly, for grazed areas we shall be concerned with the whole community of which *Paracentrotus* is the dominant feature, including the extensive fauna inhabiting the crustose coralline algae that spread over the rock surface.

The larger predators are highly mobile and do not observe the same boundaries as *Paracentrotus*. The part played by the larger crabs has already been investigated by Muntz *et al.* (1965), and the role of diurnal migrations in the structure of the community is described by Ebling *et al.* (1966) and Thain (1971). The abundance of *Anomia* at a grazed site at the north end of the lough was associated by Muntz *et al.* (1965) with a lack of the starfish *Marthasterias glacialis*; we shall extend information about the part played by this important predator and its consequences for *Paracentrotus* and its community.

Finally, we shall present information about the growth of *Paracentrotus*, about the formation of graze patches, and about fluctuations from year to year of the population of *Paracentrotus* in Lough Ine.

The distribution of *Paracentrotus* in tide pools on the west coast of Ireland has been described by Southward & Crisp (1954). In some respects the shallow sublittoral of Lough Ine approaches the conditions of a mid-littoral tide pool.

2. Methods

(*a*) *Shore sectors*

Renouf (1931) subdivided the north, east, south and west shores of the lough, and the shore of Castle Island, into numbered sectors, as shown in figure 1. These sectors were designed in such a way that the littoral region of each is reasonably uniform within itself in the characteristics of its substrate. These sectors are also convenient for designating shallow sublittoral sites. The boundaries between sectors have frequently been used for sampling because they are precisely located; they are designated with a stroke, e.g. S2/3. In sector E10 there is a *Paracentrotus* graze patch at the north end, and samples from that patch are recorded as from E10 north.

(*b*) *Depths*

All depths are referred to 'standard level' (s.l. on graphs) (Bassindale *et al.* 1948), a negative sign indicating 'below'. Standard level was originally defined as 157 cm below the top of the Rapids Quay at mark 3. The iron ring in the quay at mark 3 has disintegrated, but the spot can be identified by the slot into which it fitted. A number of convenient marks at sites around Lough Ine have been correlated by means of the level of the water during the turn of the tide in the Rapids. Thus standard level = Rapids Quay − 1.57 m = Glannafeen

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Laboratory Quay − 1.29 m = Curlew Rock (I3) − 1.49 m = North Quay (N4) (southwest corner) − 1.88 m = Barloge Quay (see figure 1 in Goss-Custard *et al.* 1979) − 1.96 m = Pinnacle (figure 2 in Goss-Custard *et al.* 1979) − 3.19 m. Standard level is at about the level of low water of a neap tide in the lough, which is lower than low water of a spring tide.

(*c*) *Continuous mapping*

Continuous mapping all around the lough has been done for certain algae, for areas grazed clean by *Paracentrotus*, and for *Anomia* and *Patella* on grazed areas. Assessments of the average abundance of sublittoral *Anomia* and *Patella* visible on the upper surfaces of rocks within 1 m of lines running out from the low water mark were made at 5 or 10 m intervals where the graze patches were continuous or extensive. For small individual patches the estimates covered the whole grazed area. Areas of rock with a visible covering of sediment and areas above standard level (where *Anomia* and *Patella* form a line in some parts of the lough) were excluded. Although neither species was removed from the rock surface, experience has shown that almost all the anomiids on graze patches are *Anomia ephippium*, and most but not quite all the *Patella* are *Patella aspera*.

(*d*) *Samples*

The size of quantitative samples had to be sufficient to include a reasonable number of specimens of the species under consideration but not so large as to involve an overwhelming labour in sorting and counting. Thus different sizes of sample were used for different species, and with the smallest animals, such as amphipods and minute prosobranchs, there was the likelihood of patchiness of distribution.

Quadrats were of 1 m × 1 m unless it is stated otherwise, and were collected in July, August or September. Normally all rocks were lifted within a quadrat down to soft sediment or solid rock. The choice of quadrat sites could not be determined by chance; all rocks within a quadrat had to be capable of being lifted, and all or nearly all the quadrat surface had to consist of rock and little or none of soft sediment.

Rocks for sampling were chosen for convenience of size, without conscious biological selection. They were always from the top layer of rocks, from sites where they rested on other rocks rather than on mud, and from 0.25–0.4 m below standard level. Rock samples of series 1 were collected in mid April for sediment and small sessile fauna. Each rock was raised carefully through the water surface, upstanding soft algae (only present at an ungrazed site) were picked off, and the sediment from the top of the rock was brushed off with a tooth brush into a basin containing a little sea water. The sediment was then washed, dried, and weighed. Surface areas of the rock were measured with a grid, and numbers of sessile organisms were counted. Rock samples of series 2 were collected in July or August. No sediment was separated from them. Upstanding soft algae were removed from those rocks collected from ungrazed areas, but the layer of filamentous algae and young shoots, with embedded sediment, was retained. After some preliminary examination and measurement of surface areas the rocks were placed in 6% formaldehyde solution. After not less than 3 days in this solution they were transferred to 10% acetic acid for several days, until any crustose coralline algae had been decalcified. The residual spongy matrix was separated off and returned to formaldehyde solution. It was subsequently teased apart to release the excellently preserved polychaetes from their tubes within it.

Samples of algae, for survey of their associated fauna, were collected from −0.25 to −0.4 m

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into muslin bags (mesh 0.5 mm) held under water, and the wet mass of alga was determined. The complete samples were preserved in formaldehyde. The samples cover four important bushy algae over seasons ranging from April to September; most were taken from the south shore of the lough, but a few from the Castle Narrows (E10, E11), and (for *Enteromorpha clathrata*) from the North Basin (I8) and west shore (W18/19).

(*e*) *Systematic records*

The full systematic names of all species recorded in this paper are given in the Appendix, which also gives information as to the sectors of the lough where specimens were found. It is likely that in most cases species are much more widely distributed than our records assert.

(*f*) *Census of visible Paracentrotus in the South Basin*

After some initial practice and comparison of results, two or three rowing boats were rowed very slowly over the shallow sublittoral of the South Basin, each boat covering a separate stretch of the shore. Numbers of *Paracentrotus* visible in each shore sector were recorded separately by two observers in the stern of the boat, and were normally averaged. This census was always carried out in July in fine weather, near midday so that diurnally migrating urchins would be on the tops of the rocks.

(*g*) *Census of Codium in the South Basin*

The *Codium* census was also made in July, at a time when the tide was at an intermediate level, so that visibility was good but the *Codium* floated upwards. Two or three boats were used, and there was initial practice over the same shore sector. The procedure for each sector was as follows. (1) The boat was rowed along the length of the sector with a graduated pole held horizontally across the stern. The two observers looking over the stern determined the width of a band that would enclose all the visible *Codium* except perhaps for a few aberrant specimens inclusion of which would greatly diminish the accuracy of estimates. (2) The boat returned to the start of the sector and was rowed very slowly and steadily along the sector. Every 10 s, as called out by the recorder, the two observers estimated the percentage coverage by visible *Codium* of a rectangle of width equal to the 'effective width' of *Codium* in the sector (as already described), read off on the marked pole still in position, and length 1 m (astern from the boat). (3) The average percentage coverage for the sector was calculated. Then the area fully occupied by *Codium* in the sector = percentage coverage × effective width × length of sector/100.

3. Physical conditions

(*a*) *Water temperature: observations*

Water temperature in the Castle Narrows is of special interest because this is an area of sharp change in the flora and fauna (see §4*d*). Temperatures at seven sites (A–G in figure 6) were recorded automatically and continuously over the period 19–30 August 1979. Site C is in the gentle tidal current that flows through the Narrows. The probes were mounted on rocks that were submerged in such a way as to hold them at 0.25 m below standard level in places free from seaweed.

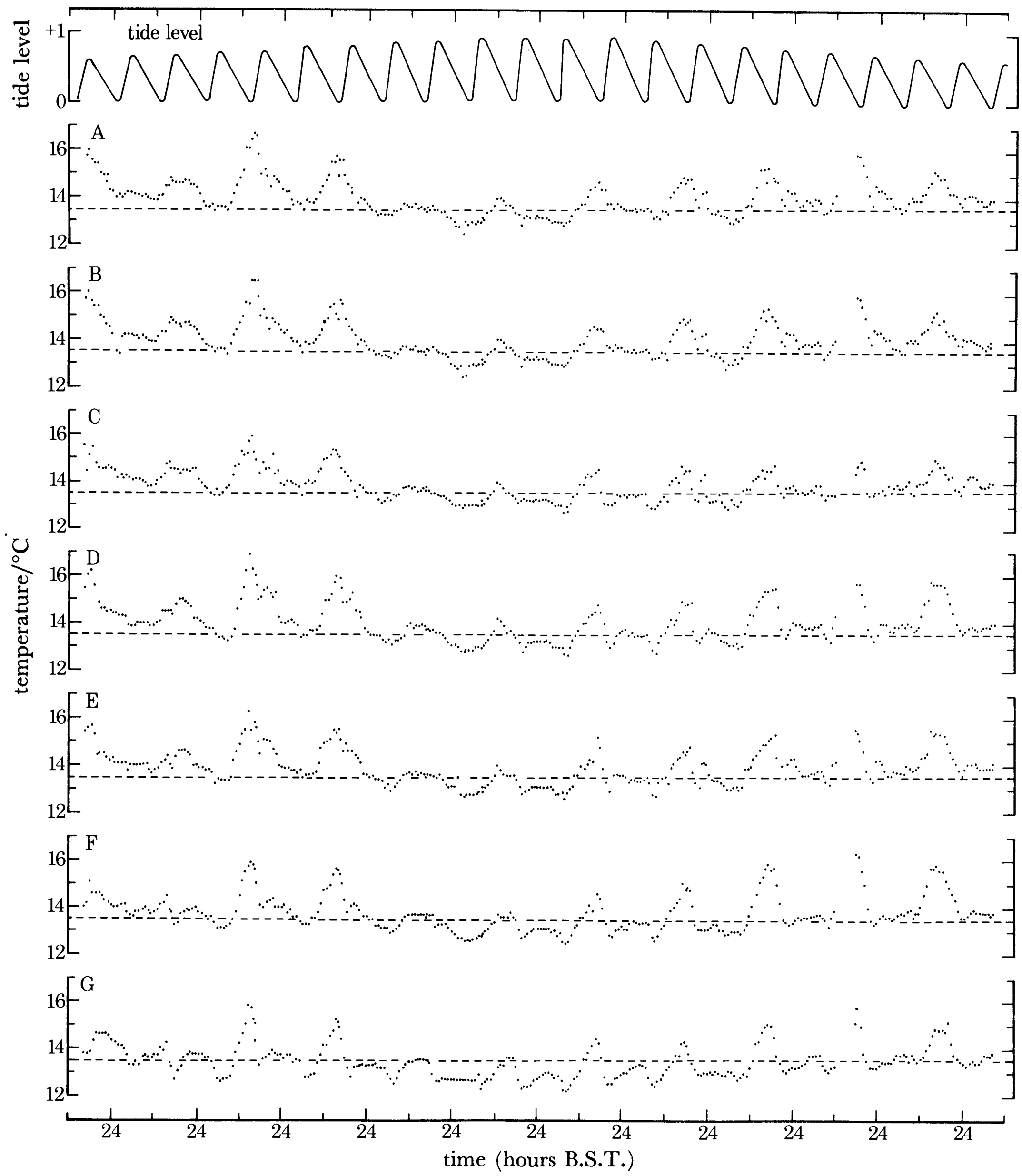


FIGURE 2. Temperatures at seven sites (marked in figure 6) in the Castle Narrows, at −0.25 m, on 19–30 August 1979. To facilitate comparison, a broken line is shown at 13.5 °C for each site. The calculated height of the tide, with respect to standard level, is shown in the top panel.

The lowest temperatures (figure 2) were attained at the southernmost site (G), where there was a minimum during each inflow period. Site F also showed traces of a semidiurnal cycle. Further north maxima and minima coincided with day and night, and both were slightly but distinctly higher than at F and G. The time spent at low temperatures was longer at F and G than further north.

Temperatures were measured on 19 April 1981 at a series of depths at two stations in the Castle Narrows area (Castle Narrows Buoy off E11 and Boundary Bay Buoy off E14) and at two stations in the midline of the Goleen (North Goleen Buoy off W38 and South Goleen

Buoy off W34/35). The sites are shown in figure 1. A preliminary set of readings was taken at the North Goleen Buoy in the morning during early outflow. Readings were taken at all four stations in the early afternoon during late outflow, and in the late afternoon during mid inflow. Low slack water was at about 16h00 and high slack water at about 20h00. Salinity samples were also taken by suction up a tube with a plastic pump, to reveal any stratification that might have become established. It was fine and sunny all day.

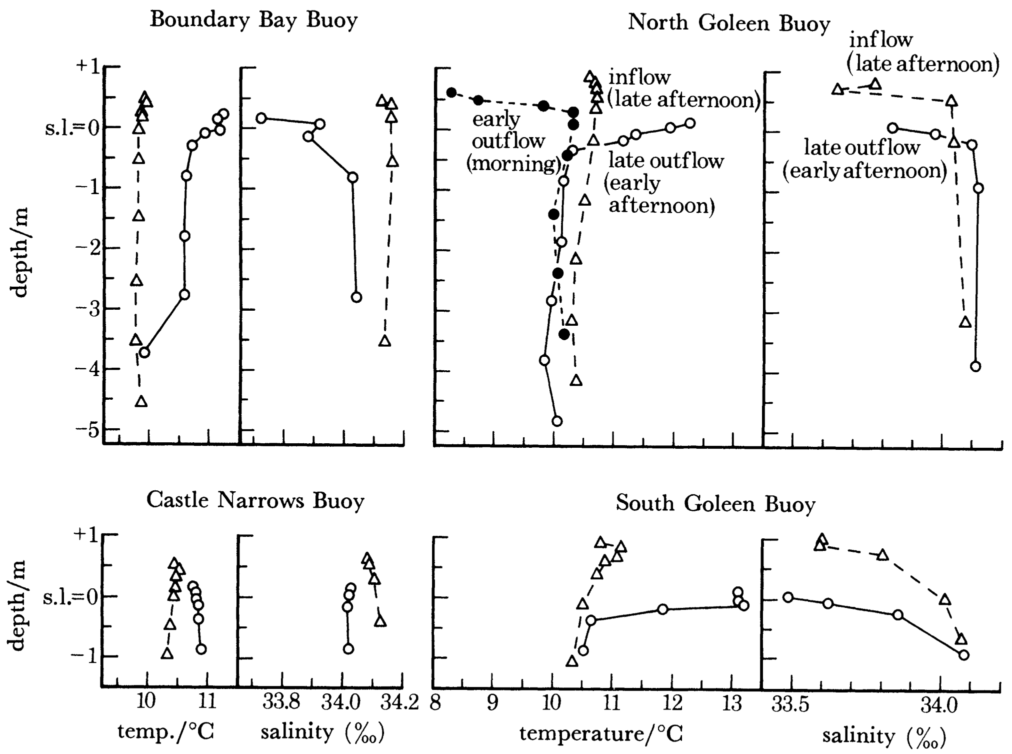


FIGURE 3. Profiles of temperature and salinity at two stations in the Goleen and at two stations in the Castle Narrows area on 19 April 1981. For sites see figure 1. In each profile the highest point is at 0.01 m below the water surface. Black circles denote temperature only, and at North Goleen only, at about 10h15, during early outflow. Empty circles are for early afternoon (14h00–15h45) during late outflow. Empty triangles are for late afternoon (17h30–19h20) during mid to late inflow.

Results are shown in figure 3, in which allowance is made for the rise and fall of the tide. During inflow the temperature in the Rapids was 9.25 °C and the salinity 34.26‰. At all the stations the water temperature was higher near the surface during outflow in the early afternoon than during inflow in the later afternoon, but the maxima attained at the two Goleen buoys were much higher than at the other two buoys. A slightly reduced salinity persisted at the surface in the Goleen, and it is likely that this stabilized the very cold surface layer that was observed in the morning, after a cold night.

(*b*) *Water temperature: conclusions*

From April to October (Kitching *et al.* 1976) the water entering the lough through the Rapids is colder than that running out. The cold inflow water undergoes vigorous mixing in the inflow area, between the Rapids and the Whirlpool Cliff (figure 1) (Bassindale *et al.* 1957), so that the fall in temperature at the south end of the Castle Narrows, although still semi-diurnal, is much less than at the Rapids mouth. Further up the Castle Narrows, and at stations remote from the inflow area, the oscillations of temperature are diurnal, with a maximum during the day or evening and a minimum at night or in the early morning. The maximum also tends to coincide with outflow and the minimum with inflow. Presumably these effects result from a warming up by day and a cooling down by night, and on occasion from the rise and fall of a temperature-graded water column with the tide. At stations remote from the inflow area the minima in summer are less extreme than at stations near the inflow area, and the maxima observed in rather cool summer weather were slightly higher. In a warm summer the differences are likely to be greater. The most extreme shallow water stratification was observed in the Goleen. After a cold night in April the temperature was lower by 2 °C at the surface than below. Although it rose during the day by 4 °C at the surface, there was very little change below -0.5 m. Between these two levels lies the *Paracentrotus* zone.

The pattern of changing water temperature at sites around the lough must depend in part on the direction and velocity of the wind, which will affect the distribution of surface water and the extent of vertical mixing. A full comparison between sites could only be made on the basis of long-term automatic recording. However, it is to be expected that in still hot weather sites in relatively shallow areas of the lough will reach higher temperatures.

(*c*) *Sediment*

The low algal bush around the South Basin traps sediment from the slowly moving water, and sediment forms a film over the surface of the rock under the bush. Areas grazed by *Paracentrotus* are much cleaner. The dry masses of sediment from the tops of three rocks from each of three sites are summarized in table 1. There was much more sediment at an ungrazed site (S5) on the south shore than at grazed sites at the north end of the Castle Narrows (E10 north) and in the northeast corner of the lough (N9).

TABLE 1. SEDIMENT AND PRINCIPAL SESSILE ORGANISMS ON THE TOPS OF ROCKS AT SITES IN THE SHALLOW SUBLITTORAL, COLLECTED 13–17 APRIL 1981

(Three rocks at each site.)

	S5 (ungrazed)		E10 north (grazed)		N9 (grazed)		significance (*P* by *t* test) of difference between sites S5:E10 north	S5:N9
surface area of tops of rocks/cm² . . .	356, 178, 245		257, 128, 266		416, 504, 245			
quantity per 100 cm²	mean	s.e.	mean	s.e.	mean	s.e.		
dry mass of sediment/g	4.51	0.52	0.35	0.24	0.05	0.01	0.01	0.002
area of *Lithophyllum incrustans*/cm²	0		26.7	13	11.2	2.4	—	0.002
area of algal holdfasts/cm²	15.3	4.85	0		0		0.05	0.05
number of *Pomatoceros* tubes	0.1	0.31	12.4	2.2	22.3	3.7	0.01	0.002

4. DISTRIBUTION OF ALGAL COVER AND GRAZE PATCHES

(*a*) *Algal cover in the shallow sublittoral*

Most of the bottom of the Rapids is occupied by a forest of the laminarian alga *Saccorhiza polyschides*, but around the Rapids mouth this gives way to *Laminaria saccharina* (figure 9 of Bassindale *et al.* 1948). *L. saccharina* extends up the east shore of the South Basin to the Castle Narrows, and intermittently along the south shore, as shown in figure 1. Its distribution was more extensive in 1981 than in 1980. The extended distribution mapped originally in April 1981 was unchanged in July, but all the plants in question were then decayed both at the tips and along the margins.

Around those parts of the South Basin not scoured by *Paracentrotus* (as described below), both among *Laminaria saccharina* and outside the area dominated by that alga, there is a dense cover of many low-growing algae: *Corallina officinalis* and *Gelidium* sp. as an undergrowth to the *L. saccharina*, *Laurencia* sp. increasingly abundant further away from the Rapids mouth, *Stilophora* overgrowing much of this mixed cover in summer, and many other epiphytes, including especially *Sphacelaria cirrosa*. Low-growing algal cover extends around the ends of Castle Island, but soon gives way to *Paracentrotus*.

Relatively pure patches of *Codium fragile* spp. *tomentosoides* are scattered around the lough, and *Enteromorpha clathrata* locally forms a blanket-like cover.

The standing crop of algae in two 1 m × 1 m quadrats in E20 (July 1981) amounted to 7070 and 4851 g (fresh mass), with *Laminaria saccharina* contributing 96%. At S6 the corresponding figures were 2565 and 2254 g, of which *Laurencia platycephala* and *Stilophora rhizodes* each contributed about 40%. These last two quadrats represent the crop that is prevented from developing by the grazing of *Paracentrotus*. We have marked (*) in the Appendix the 16 species of alga found at three or more ungrazed sites but not at any grazed sites except in a grazed or immature condition. We conclude that these species are discouraged by *Paracentrotus*. No doubt the list could be greatly extended.

(*b*) *Algal cover in the low littoral*

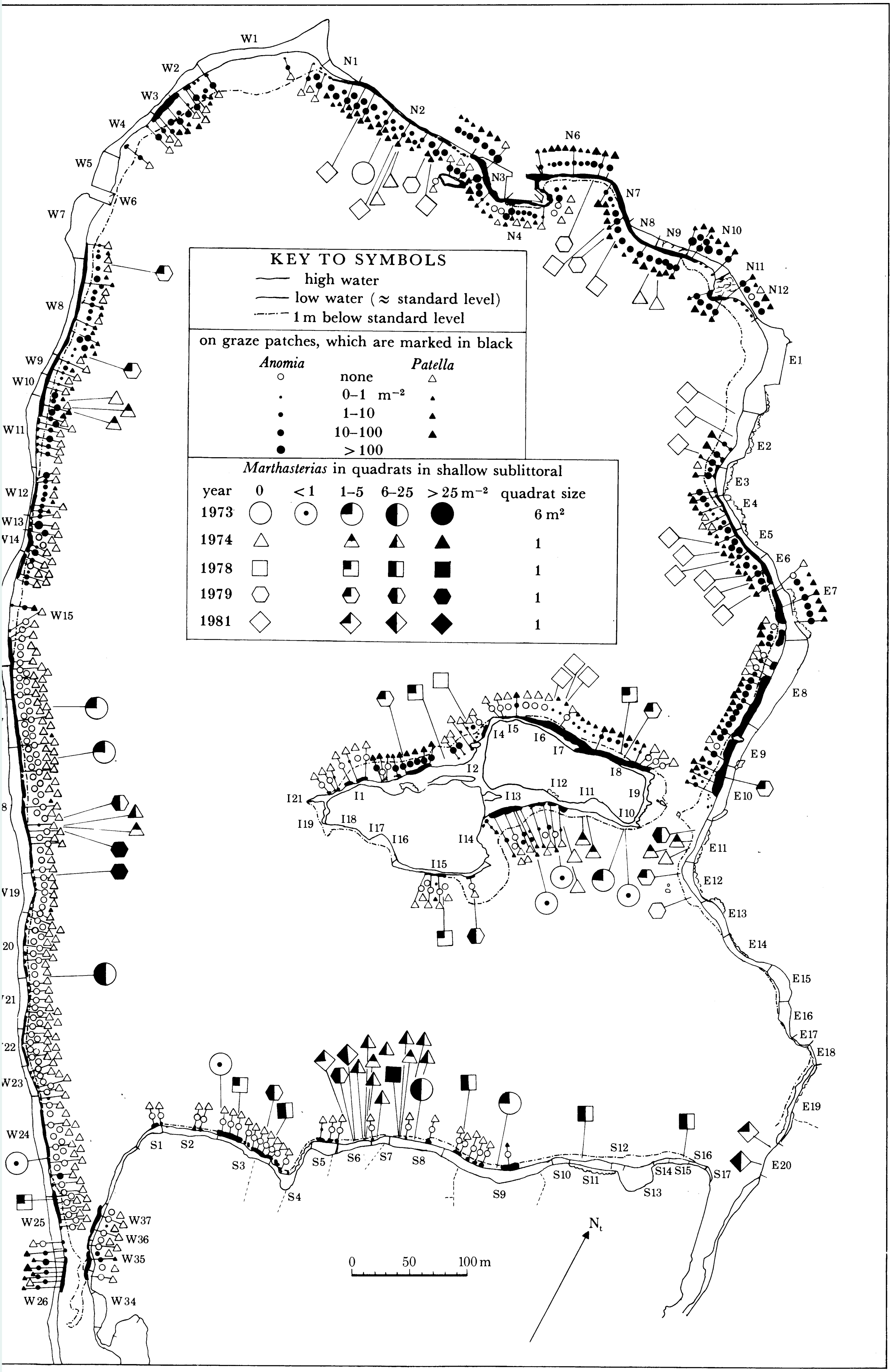
Himanthalia elongata is limited to stretches of the shore disturbed by the inflow current (figure 1).

Fucus serratus extends (figure 1) along the east and south shores of the South Basin and along parts of the south shore of Castle Island. It is missing from the Goleen, from the whole west shore of the lough, and from all the North Basin except for small patches in N12 (just below the lodge gates) and in E5 and E10. It is confined to nearly horizontal boulders. Its distribution could be explained on the supposition that it is prevented from occupying sites overhung by *Ascophyllum nodosum* or adjacent to high concentrations of *Paracentrotus* (see §8). The plants in N12 (observed there over a number of years) are separated from the adjacent grazed area by a very narrow strip of mud.

(*c*) *Paracentrotus graze patches around the lough*

Paracentrotus graze patches have occupied the rocky shallow sublittoral of the North Basin as an almost continuous band, except where the bottom is soft (W1, W5–7, E1), for as long as we can remember (back to 1946). In the South Basin they vary considerably from year to year; they reached a peak in 1979. The distribution of graze patches in July 1979 is shown in figure 4. They extended in depth between standard level and −0.5 to −1 m. No graze patches approached the Rapids mouth, either from E11 southwards or from S10 eastwards.

Lithophyllum incrustans and other crustose coralline algae spread over the rock on graze patches. Although the surface of the rock appears free from upstanding algae, close examination of samples from N2, N9 and E10 north revealed scattered microscopic tufts, some evidently cropped. Dr E. M. Burrows found 14 species of algae present in this material, including *Cladophora* spp., *Enteromorpha clathrata*, *Ectocarpus* spp., *Sphacelaria cirrosa*, and *Polysiphonia*



KEY TO SYMBOLS
high water
low water (≈ standard level)
1 m below standard level
on graze patches, which are marked in black
Anomia
Patella
none
0–1 m⁻²
1–10
10–100
> 100
Marthasterias in quadrats in shallow sublittoral
year
0
< 1
1–5
6–25
> 25 m⁻²
quadrat size
1973
6 m²
1974
1
1978
1
1979
1
1981
1
0
50
100 m
N
W1
W2
W3
W4
W5
W6
W7
W8
W9
W10
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urceolata. There were unorganized *Codium* filaments with occasional utricles characteristic of *Codium fragile* ssp. *tomentosoides*. Records of these species are marked ‡ in the Appendix. *Paracentrotus* evidently grazes down these algae as fast as they grow.

(*d*) *Transitional areas*

There is a well defined transition between bushy algal cover and grazed area in the Castle Narrows, where physical conditions no doubt also change substantially within a short distance. Along the south shore of the lough the transition is more gradual; graze patches are scattered and the area that they occupy varies from year to year. Even so, they occupy the same sites, diminishing eastwards.

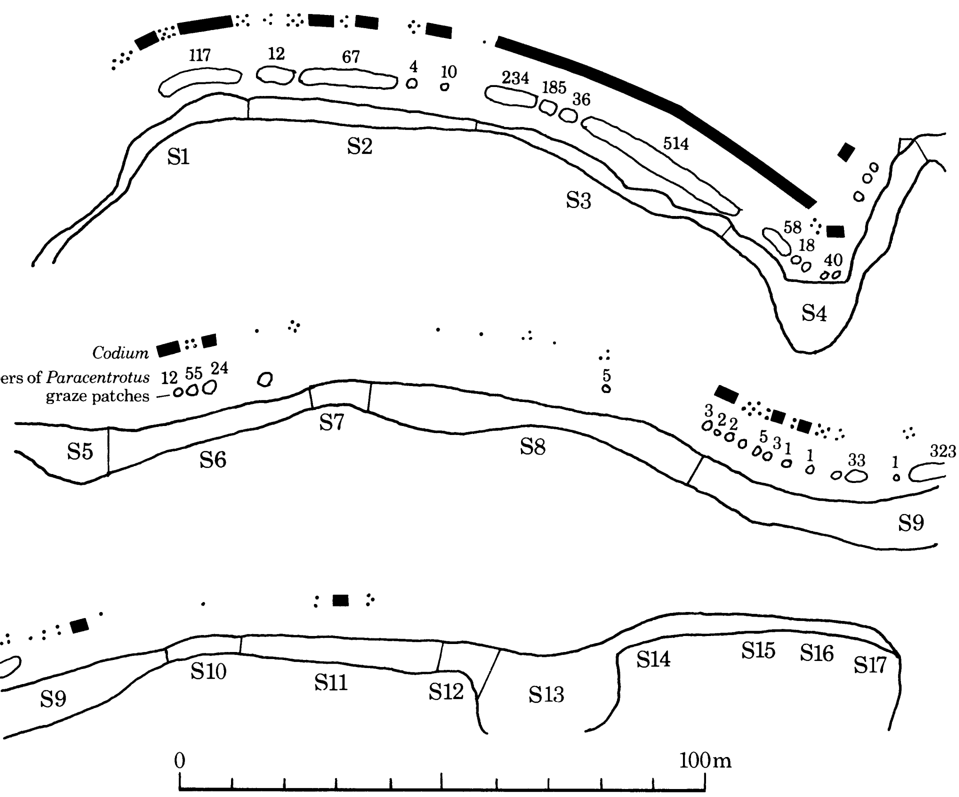

Figure 5. Distribution of *Codium*, numbers of visible *Paracentrotus*, and graze patches along the south shore of Lough Ine in July 1977. This map indicates distribution parallel with the shore; the distance of symbols out from the low water line has no significance. Dots indicate single plants of *Codium*, and a solid black band indicates more than five *Codium* plants per metre of shore.

A map of the south shore, showing diagrammatically the distribution of graze patches, numbers of *Paracentrotus* visible from above, and abundance of *Codium* in July 1977 is given in figure 5. It is evident from this map that *Codium* occurred near where there was *Paracentrotus*. As seen from a boat, the *Codium* fringed the graze patches. All the remaining area except for graze patches was covered by a blanket of algae, of which (in July) *Stilophora rhizodes* was the most conspicuous.

Figure 4. Distribution of *Paracentrotus* graze patches (in black), of sublittoral *Patella* spp., and of sublittoral *Anomia ephippium*, all in July 1979, and of *Marthasterias glacialis* on various occasions.

Mapping of graze patches and of algae in the rocky shallow sublittoral of the Castle Narrows was done in the period 8–14 September 1979, down to the outer limit of rock but no further (figure 6). The effective northern limits of *Fucus serratus*, *Himanthalia* and *Laminaria saccharina* in the Castle Narrows approach the southern limit of graze patches (though not of all *Paracentrotus*), both on the east shore and on the shore of Castle Island flanking the Narrows. The 'Pobbles' are not grazed, and these three algae are all present on them all. *Codium* again fringes the graze patches and is missing from the ungrazed southern region. The relation of *Codium* with *Paracentrotus* is described further in § 9.

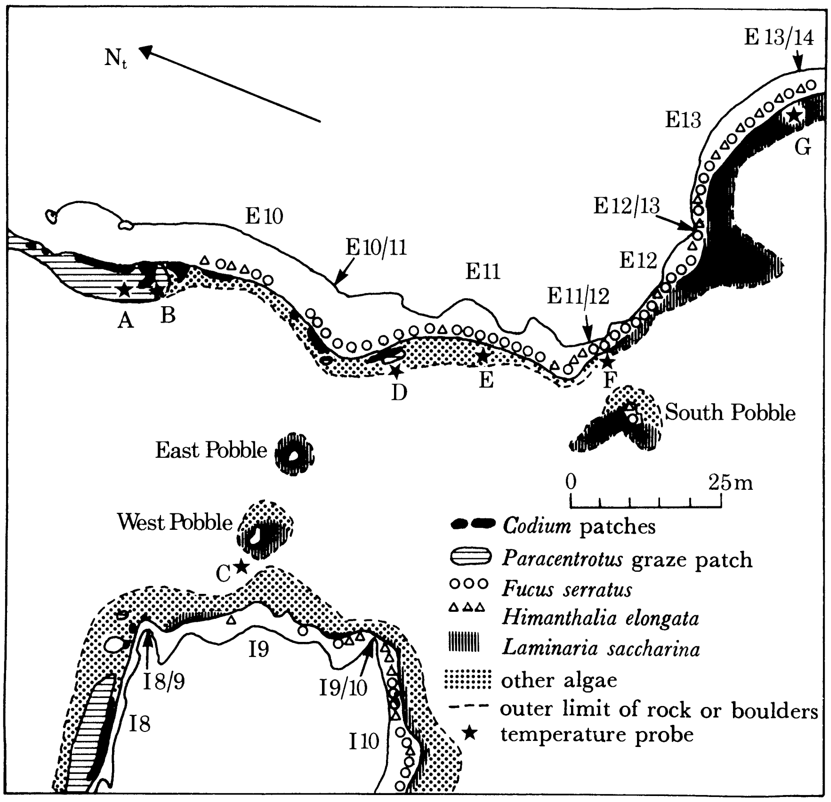

FIGURE 6. Distribution of *Fucus serratus*, *Himanthalia elongata*, *Laminaria saccharina*, *Codium*, *Paracentrotus* graze patches, and other algae in the Castle Narrows in September 1979. No mapping has been done in areas covered by soft bottom, outside the broken line. The positions of temperature probes for the work described in § 3*a* are also shown.

Paracentrotus occurs in smaller numbers in areas not visibly grazed, mainly under rocks and mainly small. In quadrats (figure 7) taken along the south shore in July 1977 and July 1978, it was clear that numbers of *Paracentrotus* under rocks were only substantial at sites where there were *Paracentrotus* on the tops also, forming graze patches. Numbers under rocks were negligible towards the Rapids mouth. The factor that controls distribution acts at an early stage in their life history.

Numbers of *Paracentrotus* were examined in a 2 m × 2 m quadrat taken in the *Laminaria saccharina* forest on the east side of the Rapids mouth, near the border of *L. saccharina* with *Saccorhiza polyschides*, on 15 July 1980. A total of eight *Paracentrotus*, measuring 10–37 mm in horizontal diameter, were uncovered, all several boulders deep within the boulder pile. It seemed unlikely that they would ever have come up to the surface. Two 1 m × 1 m quadrats were taken in the *Laminaria saccharina* forest in E20, on the outside of the Harbour wall, on 15 July 1981, primarily for determining the standing crop of algae. They yielded altogether nine small *Paracentrotus* (range 5–20 mm in horizontal diameter), five of them under the boulders. It seems unlikely that they would have exerted any serious influence on the composition of the algal flora.

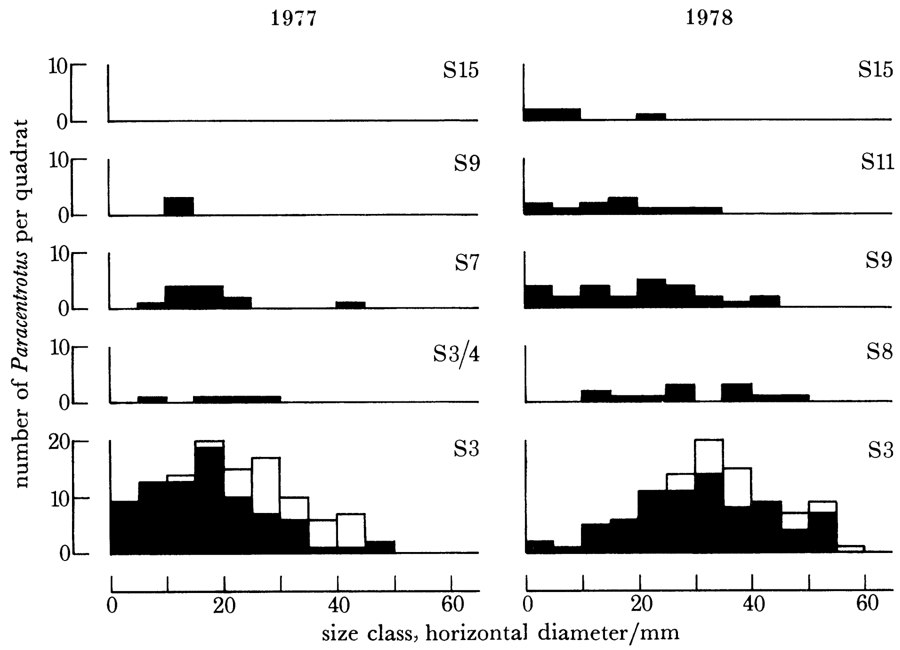

FIGURE 7. Size-frequency histograms for *Paracentrotus lividus* in 1 m² quadrats on the south shore of Lough Ine in July 1977 and July 1978. White, above rocks; black, below rocks.

5. Fauna of ungrazed areas

The algal bush that covers ungrazed areas, and the rock surface that carries it, provide accommodation (and in some cases food) for many small invertebrates: small polychaetes, amphipods, small gastropods, and the larvae of Diptera. Sediment is trapped by the algae and lightly covers the rock surface (§3*c*). Some of the invertebrates were common in the algal bush and on the rock beneath it, but were scarce or absent on grazed rock, as shown in table 2. Others were found both on grazed and on ungrazed surfaces, and any preference is not yet established. Numbers of individuals of a species varied greatly from sample to sample, even of the same alga. However, a few species showed preference for a particular alga. *Cladonema* was found mainly on *Stilophora*; *Elysia viridis* was found mainly on *Codium*, with which it has a special relation (Trench *et al.* 1973; Gallop *et al.* 1980); *Scrupocellaria reptans* covered the older main shoots of *Codium* in September. The amphipod *Corophium bonnellii* reached its maximum density of population on ungrazed boulders, where it found sediment in which to burrow. Other species, which inhabit grazed areas, were either scarce or absent on ungrazed rock: *Anomia*, *Pomatoceros*, *Verruca*, *Polydora* spp. and the crustose coralline alga *Lithophyllum incrustans* (table 2). Sediment and the overgrowth of algae were no doubt responsible.

We have recorded a total of 149 animal species from ungrazed areas of the shallow rocky sublittoral of the lough. Of these 28 (marked * in the Appendix) are regarded as preferring

TABLE 2. NUMBERS OF SOME COMMON ORGANISMS IN SAMPLES OF ALGAE FROM UNGRAZED AREAS, COLLECTED APRIL–SEPTEMBER, AND ON ROCKS FROM UNGRAZED AND GRAZED AREAS, COLLECTED IN JULY–AUGUST AND DECALCIFIED

(C, *Codium*; L, *Laurencia*; S, *Stilophora*; E, *Enteromorpha clathrata*.)

ALGAL SAMPLES: total fresh mass of each algal species/number of samples of that species: C, 3630 g/10; L, 304 g/4; S, 1267 g/6; E, 328 g/3; total mass for all algal species, 5529 g; total number of samples, 23

ROCK SAMPLES (SERIES 2)

species	number of algal samples in which species was present	total number of specimens	algae on which present	site... S5 (ungrazed but soft upstanding algae removed)		E10 north (grazed)		N9 (grazed)		N2 (grazed)
			area of surfaces/cm²: top...	69	158	42	56	68	105	38
			other surfaces...	89	305	110	143	170	162	109
Species found preferentially in areas not grazed by Paracentrotus				numbers of specimens in samples						
Hydrozoa										
Cladonema radiatum	6	67	S	0	0	0	0	0	0	0
	1	1	C							
Polychaeta										
Pionosyllis serrata	15	103	C, L, S, E	23	90	0	0	0	0	0
Janua pagenstecheri	6	*ca.* 20 000	S	present in small numbers but not counted owing to decalcification						
	1	1	C							
Amphipoda										
Stenothoe monoculoides	10	73	C, L, S, E	31	177	0	1	1	1	1
Dexamine thea	19	249	C, L, S, E	20	155	0	0	0	3	0
Amphithoe neglecta	18	484	C, L, S, E	8	150	0	1	0	0	0
Corophium bonnellii	7	23	C, L, S, E	124	255	27	14	0	1	0
Gastropoda: Prosobranchia										
Rissoa parva	22	6254	C, L, S, E	190	973	0	4	1	10	0
Cingulopsis fulgida	11	323	C, L, S, E	37	139	0	0	0	0	0
Bittium reticulatum	21	5566	C, L, S, E	9	22	0	1	0	1	0
Gastropoda: Opisthobranchia										
Elysia viridis	9	55	C	0	0	0	0	0	0	0
	2	2	L, E							
Species found preferentially in areas grazed by Paracentrotus										
Algae: Rhodophyta (area/cm² covered by species, rather than number of specimens is given)										
Lithophyllum incrustans	0	0	—	0	0	54	58	0	20	0
unidentified crustose coralline	0	0	—	0	0	10	83	65	124	121
Polychaeta										
Syllis gracilis	1	1	L	1	0	15	51	2	29	0
Polydora giardi	0	0	—	0	0	622	417	3	22	7
Dodecaceria concharum	0	0	—	0	0	24	65	1	12	2
Fabricia sabella	2	53	C, L	8	28	297	540	35	247	31
Pomatoceros spp.	5	5	C, S	0	0	25	88	44	44	31
Crustacea: Cirripedia										
Verruca stroemia	0	0	—	0	0	0	0	0	102	26
Species found both in grazed and in ungrazed areas; preference has not yet been demonstrated										
Polychaeta										
Brania clavata	16	859	C, L, S, E	22	76	2	11	13	26	18
Exogone gemmifera	6	149	C, L, E	8	30	8	20	5	12	2
Crustacea: Tanaidacea										
Leptochelia savignyi	0	0	0	50	91	110	47	17	98	6
Insecta: Diptera (larvae)										
Halocladius fucicola	12	185	C, L, S, E	2	2	0	0	3	0	1
Clunio marinus	11	221	C, L, E	2	36	5	15	1	8	1

ungrazed areas, 11 of them on the basis of the numbers taken in samples, as shown in table 2, and a further 17 because they were found at very substantially more ungrazed than grazed sites, even though the numbers of individuals were small. The very mobile Crustacea Decapoda, Asteroidea and Pisces have not been classified with respect to preferences, although they are included in the total present.

6. Fauna of graze patches

(*a*) *On the surface of the rock*

The rock surface of graze patches is clean of sediment (§3*c*), and is devoid of upstanding algae except for occasional minute tufts. Crustose coralline algae are widespread but irregularly distributed, especially the thick knobbly coralline *Lithophyllum incrustans*. *Anomia ephippium* and *Patella aspera* were abundant on graze patches all along the north shore, and along the east shore of the North Basin (figure 4). *Anomia* was well distributed between upper and lower surfaces of the rocks, but *Patella* was mainly on the tops. Both were found to diminish in numbers southwards along the west shore, and were almost absent from the South Basin except in the Goleen and on Castle Island. They were also almost absent from four quadrats in ungrazed areas in E11, E12 and S6.

Muntz *et al.* (1965) reported substantial numbers of *Chlamys varia* and of fully grown *Gibbula cineraria* at N2. Our observations from quadrats taken in July 1979 extend these observations to other grazed sites. *Chlamys varia* was found mainly underneath rocks. *Gibbula cineraria* reached high numbers at N6–N7, with frequency peaks at shell heights of 2–3 mm and 7–9 mm, whereas those from soft upstanding algae in the Castle Narrows were all small, with a peak at about 2 mm.

Pomatoceros was plentiful on the tops of rocks in grazed areas (tables 1–3). It was scarce on tops at ungrazed sites (table 1), although patches were sometimes seen on bottoms that were relatively free from sediment. *Verruca* (table 2) was only found at grazed sites and then only on the bottoms of rocks (mean 169 (standard error 23) per 100 cm^2 of rock surface, for the bottoms of three rocks (series 1) at N9).

The stalked colonial tunicate *Morchellium argus* differs from all those invertebrate species so far detailed in this section: it has no protective shell. An experiment in an aquarium with running sea water showed that *Paracentrotus* would destroy it if it walked over it, although it did not seem to be attracted to it. *Morchellium* was found in substantial numbers on upper

Table 3. Upper surface 1m × 1 m quadrats on graze patches, three quadrats per site, taken on 13 and 14 July 1981

(Quantities have been estimated per square metre of rock surface and then averaged for each site separately.)

site ...	N7	E6	N2	E2	I6	E7
percentage rock	92	78	93	82	62	87
Paracentrotus (number)	33	61	27	15	34	24
total crustose coralline (percentage coverage)	10	15	15	30	38	80
Lithophyllum incrustans (percentage coverage)	0.33	3.8	7.6	21	25	59
Morchellium (number of colonies)	0	2.5	0	15	17	20
Anomia (number)	12	12	2.9	8.6	19	21
Chlamys varia (number)	0.7	0.7	1.5	2.0	2.0	2.5
Patella spp. (number)	3.7	2.7	6.8	23	14	16
Pomatoceros (percentage coverage)	9.4	6.7	7.9	26	21	29

and lower surfaces of rocks in quadrats taken in July 1979 and July 1981 at grazed sites on the east shore of the North Basin and on the north shore of Castle Island. It was scarce or absent (table 3) from quadrats taken on the north shore.

Distribution on rock surfaces within the grazed areas is not uniform. Eighteen upper surface quadrats (three at each of six sites) taken in July 1981 were used to calculate correlation coefficients between various invertebrate species and the percentage cover with *Lithophyllum incrustans*. Allowance was made for minor areas of mud bottom in the quadrats, so that all quantities were expressed per square metre of rock. Correlation coefficients with areas of *Lithophyllum incrustans* per square metre of rock were: *Anomia*, +0.53 ($P < 0.05$); *Patella*, +0.70 ($P < 0.01$); *Pomatoceros*, +0.69 ($P < 0.01$), *Morchellium*, +0.76 ($P < 0.001$). There was also a significant correlation with total crustose coralline per square metre of rock for all except *Patella*. Although the data for each quadrat were used separately for these calculations, they are averaged for each site in table 3. It is possible that the wrinkly surface of *Lithophyllum incrustans* provides some protection to young individuals of these species. It is also possible that frequency of visits by *Paracentrotus*, which will be related to the pattern of rock on mud as well as with urchin abundance, may control both settlement by hard-shelled invertebrates and growth of *Lithophyllum*. The tubes of grown *Pomatoceros* showed no sign of damage in the aquarium in spite of repeated grazing over them by *Paracentrotus*, but *Lithophyllum incrustans* suffered some superficial scouring. Damage to crustose corallines by sea urchins is summarized by Lawrence (1975).

(*b*) *Embedded in crustose coralline algae*

Examination of *Lithophyllum incrustans* alive showed very many paired tentacles of *Polydora giardi* and crowns of *Fabricia sabella* protruding from the general surface. *P. giardi* was especially associated with *L. incrustans*; *Fabricia* was also found in small numbers in ungrazed areas both on soft upstanding algae and on rocks (table 2). *Dodecaceria concharum* (table 2) was only found embedded in or under *Lithophyllum*. Other polychaetes found in the crustose corallines (capitellids and other species of *Polydora*) are recorded in the Appendix. Crustose corallines, and especially *Lithophyllum incrustans*, provide a safe habitat for all these worms.

(*c*) *Numbers of animal species*

We have recorded a total of 114 animal species from grazed areas. Of these, 14 are held to prefer grazed to ungrazed areas: six of them on account of their numbers in samples (table 2) and the others from mapping (figure 4) or numbers of sites of occurrence (Appendix). Sixty-five species were found both at grazed and at ungrazed sites; these are included in the totals given in this section and in §5.

Many fewer species prefer grazed than prefer ungrazed sites, and the total species list from grazed sites is also shorter.

7. General predators

(*a*) *Marthasterias with Anomia*

The starfish *Marthasterias glacialis* was found in the rocky shallow sublittoral, up to standard level, along the south shore and (diminishing in numbers northwards) along the west shore. It was not found in any of the numerous quadrats taken (down to −0.5 m) in the shallow sublittoral of the north shore or of the east shore of the North Basin southwards to the Castle Narrows (figure 4). Its abundance and size at two contrasting sites were investigated in August 1981 by members of the Bristol University Underwater Club. *Marthasterias* was found on the steep rock slope of the west shore (at W23–W24) at all depths explored (0 to −7 m), and sizes ranged from 14 cm (in radius) downwards. By far the largest number were in the 2–3 cm size range and at depths little below standard level. In contrast, on the northeast shore (E2–E3) *Marthasterias* was absent from standard level down to −1 m, but was numerous on a bottom of soft sediment and scattered stones from −2 to −4 m, where it ranged from 10 to 25 cm in radius. The small and medium-sized specimens at W23–W24 were feeding mainly on small *Ascidiella* and *Pomatoceros*. The large specimens found at E2–E3 were eating mainly *Anomia ephippium* (on scattered stones), *Venerupis rhomboides* and *Venus verrucosa*; a few were found over holes or depressions in the mud as though digging for bivalves.

Large *Marthasterias* were found by Ebling *et al.* (1966) to eat *Anomia* placed with them in cages. We have since found that small *Marthasterias* (2–5 cm in radius) eat many *Anomia* in cages. To test the extent to which this interaction may control the distribution of *Anomia* in the 'field', groups of rocks with *Anomia* on them were set up on 11 July 1966 at three sites (S11, E18, W19) in the shallow sublittoral of the South Basin, each group being flanked at each end by a cage containing additional rocks with *Anomia*. On 28 August, 37 of the 39 *Anomia* in cages were alive, while 95 of the 120 *Anomia* in the open were empty, with their shells intact. The starfish *Marthasterias*, *Asterias*, *Asterina*, *Henricia* and *Luidia ciliaris* were seen among the experimental rocks at one or more of the sites. The inverse relation in distribution of *Anomia* and *Patella* with *Marthasterias* is shown in figure 4.

(*b*) *Marthasterias with Paracentrotus*

Cages were set up in July 1968 containing four small (radius 3–4 cm) or three medium-sized (5–7 cm) or one large (15–20 cm) *Marthasterias* in company with 12 small (diameter 3–13 mm) or nine medium (15–20 mm) or four large (35–50 mm) *Paracentrotus*, with every possible combination of sizes of starfish and sea urchins. Additional cages held groups of *Paracentrotus* without starfish, and of starfish together with mussels to make sure that they were ready to feed.

After 9 days the small and medium *Marthasterias* had left three and one *Paracentrotus* empty, all of them small. All 'control' *Paracentrotus* were intact. The small and medium *Marthasterias* supplied with mussels had eaten many; the large *Marthasterias* had destroyed only one mussel.

In a further experiment in July 1978, two cages each contained a single *Marthasterias* (11 or 8 cm) together with a mixture (in each) of five small and three medium-sized *Paracentrotus*. After 3 days two small (9 and 12 mm) and four small (7–12 mm) *Paracentrotus* had been reduced to empty shells. All medium-sized *Paracentrotus* were intact.

It appears likely that small *Paracentrotus* are vulnerable in the wild.

8. Relations of *Paracentrotus* with intertidal algae

(*a*) *Excursions into the low littoral*

A preliminary series of observations was made on 18 July 1980 on the western half of the southward-facing outer end of North Quay (N4), chosen because its steep slope (about 70–75° from the horizontal) seemed particularly favourable for vertical migrations. During the midday high water the highest *Paracentrotus* were well up into the *Fucus vesiculosus* and *Ascophyllum* zone, and these algae were in fact very sparse and tattered on the quay face. The urchins retreated downwards in the afternoon with the falling tide as the water lapped them. They failed to come up with the night high water. During the day we saw *Paracentrotus* eating pieces of *Codium*, *Enteromorpha*, *Ascophyllum* and *Fucus vesiculosus*. *Ascophyllum* and *Fucus vesiculosus* were plentiful and healthy-looking on the eastern half of the quay face, where the urchins remained spread out on a shallow sublittoral shelf of fallen blocks.

A further series of observations was made on 10–11 April 1981, at N7. Here the north wall of the lough stands at about 75° from the horizontal and extends from far above high water down to 5–10 cm above standard level. Below this the boulder-strewn bottom of the lough extends southwards at a low angle of slope and is densely populated with *Paracentrotus*. Observations were made over a 15 m length of wall, marked in 5 m sections, and over the bottom immediately adjoining. On each occasion of observations the heights of all the *Paracentrotus* on the wall (within the 15 m length), and of the uppermost *Paracentrotus* on the adjoining bottom in so far as was necessary, were recorded; and the tide level was noted before, during and after these observations. Twelve sets of observations were made within a 28 h period which included a midday, a midnight, and a second midday high water. Conditions were calm at the site until the second morning, when the wind strengthened and veered to the south, causing a continuous lapping of the water surface.

The records of vertical height of *Parcentrotus* were arranged in rank order for each set of observations. The levels of the top 5, 10 and 25 urchins are shown for each occasion as those of the lowest member of each of these groups (figure 8). Some *Paracentrotus* moved up

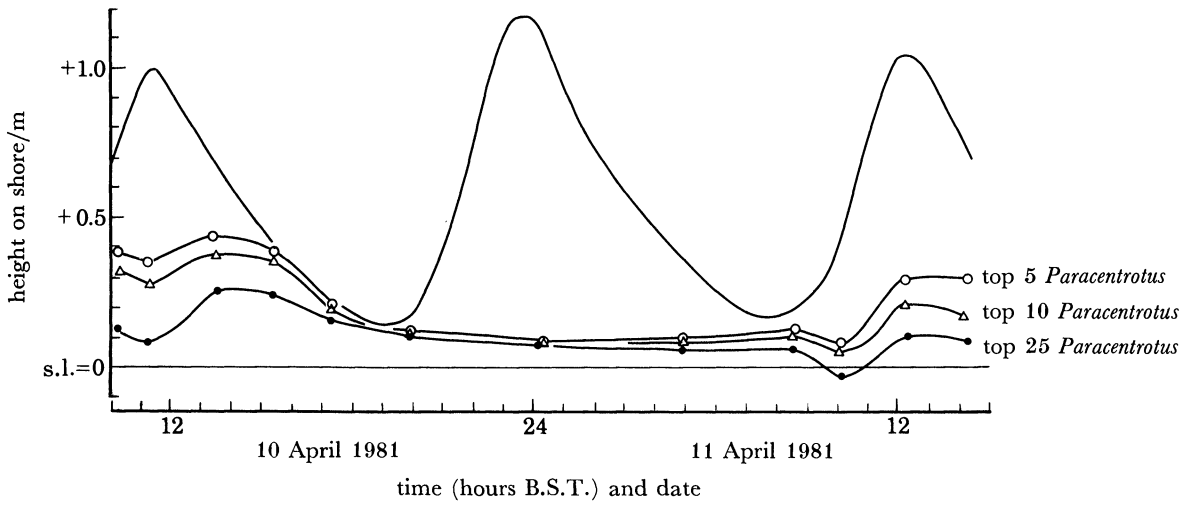

FIGURE 8. Vertical migrations of *Paracentrotus* on the North Wall of Lough Ine at N7 on 10–11 April 1981.

the wall at midday while the water was high, but down again as the falling water lapped them. There was no upward movement by night. On the first day the highest *Paracentrotus* were well up into the zone normally occupied by *Ascophyllum*. The rise of *Paracentrotus* was much less striking on the second day, perhaps as a result of the onshore wind and the lapping of the water.

At the end of the sector, and still more so further east, boulders and rocks projected from the base of the wall. *Ascophyllum* and *Fucus spiralis* were plentiful on the wall above the boulders, but over most of the section used for observation lacking these projecting boulders at the base, there were almost no fucoids except for *Pelvetia*.

(*b*) *Transfer of Fucus serratus to the North Basin*

In a preliminary test 15 *Paracentrotus* and a rock carrying *Fucus serratus* were placed in each of two cages and then set up in the shallow sublittoral at the Glannafeen Laboratory Beach. The *Paracentrotus* detached pieces of *F. serratus*, used them as hats, and ate them. The *F. serratus* was reduced to a bunch of stalks.

Accordingly, six rocks bearing *Fucus serratus* were transferred from E19 to the same level in the low littoral at E5 on 15 August 1980. The site was examined on six subsequent occasions, for the last time on 7 September. Urchins were found in contact with all the plants, usually underneath the fronds hanging down at the lower side of the plants. Loose pieces of *F. serratus* were found in close association with four of the plants, ends of fronds were missing from five of the plants, especially on the lower side, and two of the plants were very tattered over the last 3 days of the experiment.

Five rocks bearing *Fucus serratus* were transferred on 31 August 1980 from S9 to N6/7, and were installed at the same level at the foot of the wall bordering the north end of the lough. Many *Paracentrotus* collected under or in contact with all the plants, and separated pieces of the *Fucus* were being held over the urchins. By 7 September all the plants were very tattered, with most or all of their fronds missing. One main stalk was completely bitten through, and another nearly so. One *Paracentrotus* was found with a stalk of *F. serratus* in its mouth.

9. Relations of *Paracentrotus* with *Codium* and *Enteromorpha*

(*a*) *Transfer of Codium to graze patches*

Experiments were done to investigate the relation between *Paracentrotus* and the clusters of *Codium fragile* ssp. *tomentosoides* that fringe many graze patches.

Eight rocks with *Codium* growing upon them were collected from the edge of a graze patch at E3 on 15 August 1980 and transferred to the same depth (about -0.2 m) in the middle of a graze patch at E5. Small weights (steel nuts) were tied to some of the outer branches to hold them down on five of the plants. The plants were examined on 11 separate occasions, finishing on 7 September. *Paracentrotus* clustered around and over the weighted branches, and pulled other outer branches down over their backs. During the period of the experiment all weighted branches and some originally erect outer branches disappeared. Four plants disappeared completely, and the remaining four had the appearance of narrow inverted cones, with only the central branches remaining Other *Codium* plants bordering graze patches had the same shape.

In a second experiment eight rocks bearing *Codium* were collected at I1 and placed in a continuous densely populated graze patch at E7 (50–90 *Paracentrotus* per square metre, and dense concentrations at the foot of the north wall of the lough, close by) on 20 August 1980. Four of the *Codium* plants were held down flat with heavy iron door hinges placed across their tops, and four remained upright. On 21 August all the prostrate *Codium* was covered and completely hidden by *Paracentrotus*. Urchins were also concentrated around the bases of the erect *Codium*, and two of these urchins that were lifted were found to have *Codium* in their mouths. During the following days the outer branches of the erect plants were successively pulled down over the tops of the urchins, and pieces were detached and used as hats or eaten. By 29 August the prostrate plants had been completely destroyed, and only a few detached pieces remained. The erect plants gradually disappeared, and by 3 September nothing remained of them except for one broken-off piece.

(*b*) *Removal of Paracentrotus from a graze patch*

All *Paracentrotus* were removed from an isolated graze patch in I1 on 24 August 1980. These comprised 98 urchins from the upper surface of boulders and 165 from lower surfaces, together ranging from 8 to 58 mm. The rocks were replaced each as before, and mapped. The grazed area measured 3–4 m^2.

The site was revisited on 3 July and 20 August 1981, and collections were made of algae growing upon it. There were a number of plants of *Codium fragile* ssp. *tomentosoides*, much *Enteromorpha clathrata*, and small quantities of other algae, including *Sphacelaria cirrosa*.

The persistence of traces of *Codium* and *Enteromorpha* after grazing is described in §4*c*. The interaction of *Codium* with *Paracentrotus* is discussed in §12*a*.

10. Growth of *Paracentrotus*

(*a*) *Mass and horizontal diameter*

Body mass was used as a measure of growth in §(*b*). It was related to horizontal diameter by measurements made on urchins in two 1 m × 1 m quadrats collected at the west end of Castle Island (I19–I20) on 20 and 24 August 1966. The two quadrats yielded 132 and 165 specimens. All were weighed fresh, and then spines were scraped off on opposite sides for measurement of horizontal diameter. There were frequency maxima at 6–15 mm and 26–35 mm for each collection. The plot of $\log_{10}$ (mass, M/g) against $\log_{10}$ (diameter, D/mm) gave a closely fitting straight line with no significant difference between the two collections. For the combined collection $M = 0.71\, D^{2.91} \times 10^{-3}$.

(*b*) *Growth of Paracentrotus in cages*

Cages containing rocks from the shallow sublittoral and *Paracentrotus* of known size range (by mass) were set up in the shallow sublittoral on the Glannafeen Laboratory Beach, at S5, on 29 August 1966. Twelve *Paracentrotus* of restricted mass range were placed in each of ten cages. Starting masses were such as to correspond with the diameter classes 10–15, 15–20, 20–25, 25–30 and 30–35 mm, there being two cages for each class. Rocks from the ungrazed shallow sublittoral, with their associated algae, were placed so as to cover the bottoms of the cages. The *Paracentrotus* were reweighed on 12–14 August 1967. The rocks were replaced with new ones, and a few *Paracentrotus* were removed from two of the cages to avoid overcrowding. Seven deaths had occurred. The *Paracentrotus* were reweighed on 22 August 1968. A further 12 deaths had occurred.

The mean masses of groups of *Paracentrotus* in August of 1966, 1967 and 1968 are shown in figure 9, and the mass changes are fitted together to form a growth curve in the same figure.

(*c*) *Growth of Paracentrotus from rings in plates*

Dark bands in the interambulacral plates were recorded by Jensen's (1969) method. An interambulacral row of plates is cut out, slightly scorched in a gentle flame, and examined

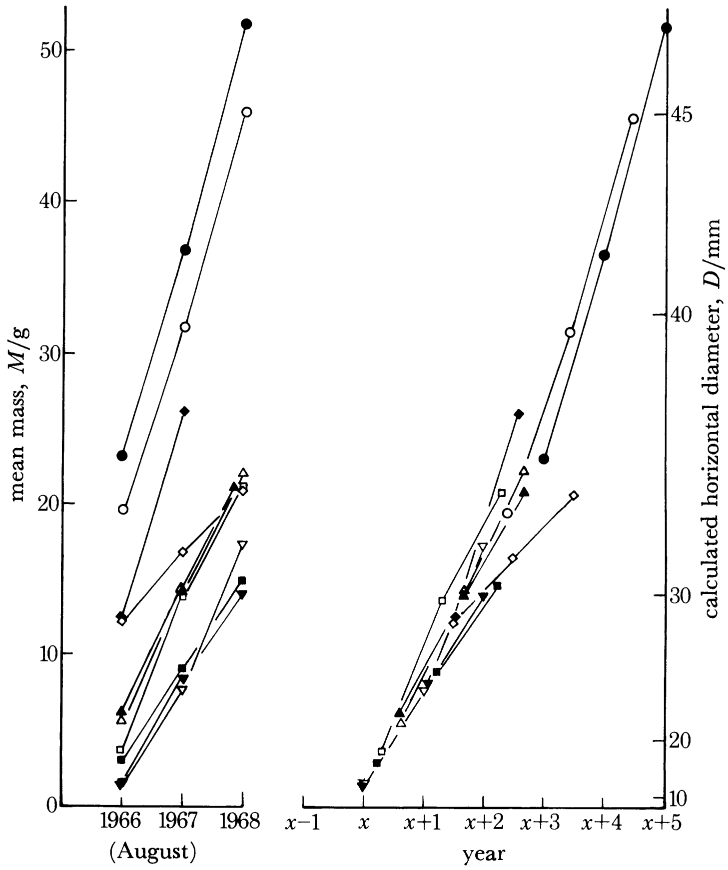

FIGURE 9. Growth of *Paracentrotus* in cages in the shallow sublittoral of the Glannafeen Laboratory Beach (S5–S6). Left: mean mass of *Paracentrotus* in each size group over a period of 2 years. Right: curves fitted together to form a composite growth curve. Diameters are calculated from wet masses in accordance with the formula given in § 10*a*.

in methyl benzoate. As plates are added at the aboral end of the row during growth it is necessary to use plates not too far from the oral end for assessment. The centre of the plate may show either a fully dark patch or a light patch surrounded by a dark band. This dark patch or band is thought to be laid down during the first summer, immediately after settlement of the larva. Additional dark bands on either side of the central area are thought to represent subsequent periods of fast (summer) growth, separated by white (winter) bands. The edges of the plate are normally dark in July. The number of dark zones reported here includes any dark central area and the dark surface zone.

The results for *Paracentrotus* collected in July 1973 from several sites in Lough Ine are shown graphically in figure 10. Although there is considerable overlap in horizontal diameters for successive years and an error of one band (or year) is easily possible in the assessment, the urchins appear to grow steadily until they reach a diameter of about 50–60 mm in 4–5 years from settlement. Allain (1978) has reported a very wide range of sizes in any one ring class in *Paracentrotus* collected on the coast of Brittany.

(*d*) *Early growth from settlement on collectors*

Paracentrotus were found by Mr D. A. Minchin of the Irish Department of Fisheries to have settled on collectors that he had set out in various parts of Lough Ine to obtain information

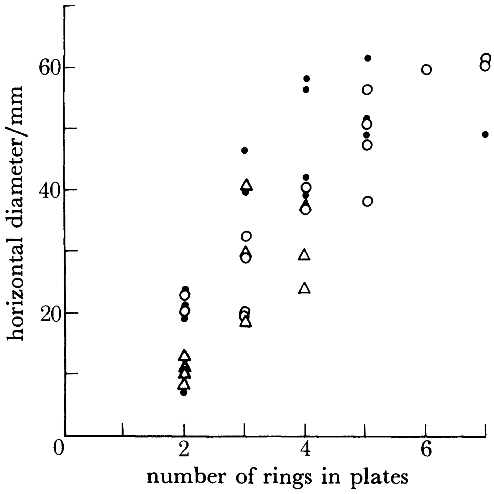

FIGURE 10. Horizontal diameter of *Paracentrotus* in relation to the number of dark bands in interambulacral plates, revealed by Jensen's (1969) method. The central and marginal dark zones are included in the number of bands: July 1973. Empty circles, collected on 10 July from I1; empty triangles, collected on 11 July from W17–W20; dots, collected on 21 July from I1 and I10.

about the settlement of larval scallops. Collectors set out on 31 July 1975 were found on 3 October to be carrying *Paracentrotus* of 1.5–3 mm in horizontal diameter, and others set out on 30 May 1977 yielded *Paracentrotus* 2–5 mm in horizontal diameter by 30 October of that year.

11. Fluctuations in visible population density of *Paracentrotus* and *Codium* in the South Basin

(a) *Annual census of Paracentrotus*

On returning to Lough Ine in July 1971 we immediately observed that there had been a drastic fall in the number of *Paracentrotus* visible in the South Basin, and that *Codium* had extensively occupied the areas vacated by the sea urchins. Accordingly we restarted an annual census of *Paracentrotus* (and started one of *Codium*) in the South Basin (sectors S1–S17, E11–E20, I10–I18, W18–W26 and W34–W38).

The results are summarized in table 4. It is to be noted that the number of *Paracentrotus* visible is only an indirect indication of the number present. There are probably two to three

TABLE 4. ANNUAL CENSUS, TAKEN IN THE SOUTH BASIN IN JULY, OF NUMBERS OF *PARACENTROTUS* VISIBLE FROM ABOVE AND OF QUANTITIES OF *CODIUM*, 1971–1981

year	number of visible *Paracentrotus*	quantity of *Codium* as area fully covered/m²
1971	3230	587
1972	1405	515
1973	1378	781
1974	1203	277
1975	797	160
1976	6292	5
1977	5031	92
1978	10562	240
1979	15530	230
1980	4933	126
1981	2230	200

times as many under the rocks, although from quadrats it is likely that those not seen were mainly smaller.

In the early years of this census (1971–5), when numbers were low, visible *Paracentrotus* were still plentiful in W26 (north end), W35–W37, E11, and I11–I13, and these continued to be sites of abundance (with the exception of E11) during the 1980–1 decline. These areas are relatively remote from deep water. In the years of increasing numbers (1976–9) new graze patch areas developed all along the west shore of the South Basin (W18–W25), on the south shore of Castle Island (I14–I15) and along much of the south shore of the lough (S1–S9, but excluding S5 and S7). No *Paracentrotus* were seen on any occasion on the shores of the lough adjacent to the Rapids entrance (S10–S17 and E12–E20), although occasional specimens, too few to form graze patches, would not have been observed. The upper Goleen (W27–W32) is largely mud, and the Whirlpool Cliff (E16–E17) is vertical or nearly vertical and composed of hard sandstone, so that the absence of *Paracentrotus* from these areas is not surprising.

(*b*) *Annual census of Codium*

Casual specimens of *Codium* from the shallow sublittoral have always proved to be *Codium fragile* ssp. *tomentosoides*, and we may assume that our observations refer to this taxon in spite of occasional records of other species from deeper water.

The total estimated area for *Codium* coverage in the South Basin for each year is given in table 4. *Codium* declined to a low minimum in 1976, the year after the minimum for *Paracentrotus*, and it then increased again along with the increase in the numbers of *Paracentrotus* visible.

These observations support the view (developed in §12*a*) that *Codium* grows on areas cleared by *Paracentrotus* but infrequently revisited, and that it cannot ultimately compete with other more slowly growing algae.

12. Discussion

(*a*) *The role of Paracentrotus within the community*

The complicated interactions of physical factors and living organisms in the rocky shallow sublittoral of Lough Ine are illustrated schematically and somewhat speculatively in figure 11. Physical conditions such as water temperature and sedimentation must ultimately determine the series of changes in the biological community that take place from the Rapids mouth to the north end of the lough. They will act directly on some plants and animals, but in other cases indirectly, through effects on prey, on predators, on competitors, or on organisms that act as substrate or provide living accommodation.

Paracentrotus is likely to exert most influence where its population density is high. The change from *Saccorhiza* forest in the Rapids to *Laminaria saccharina* at their northern end is on a steep gradient of current strength. We ascribe this change to a direct effect of water current on competition between these two algae. Without sufficient water movement *Saccorhiza* becomes stunted and deformed (Ebling & Kitching 1950; Norton 1969) and will be at an increased disadvantage. *Paracentrotus* is not sufficiently numerous in this area to limit the *Saccorhiza*, as claimed by Norton (1970); and further into the South Basin other unfavourable influences supervene (Norton 1978).

Laminaria saccharina dominates in those parts of the South Basin stirred by the inflow current, where the temperature in summer is likely to be slightly lower. It also flourishes best where

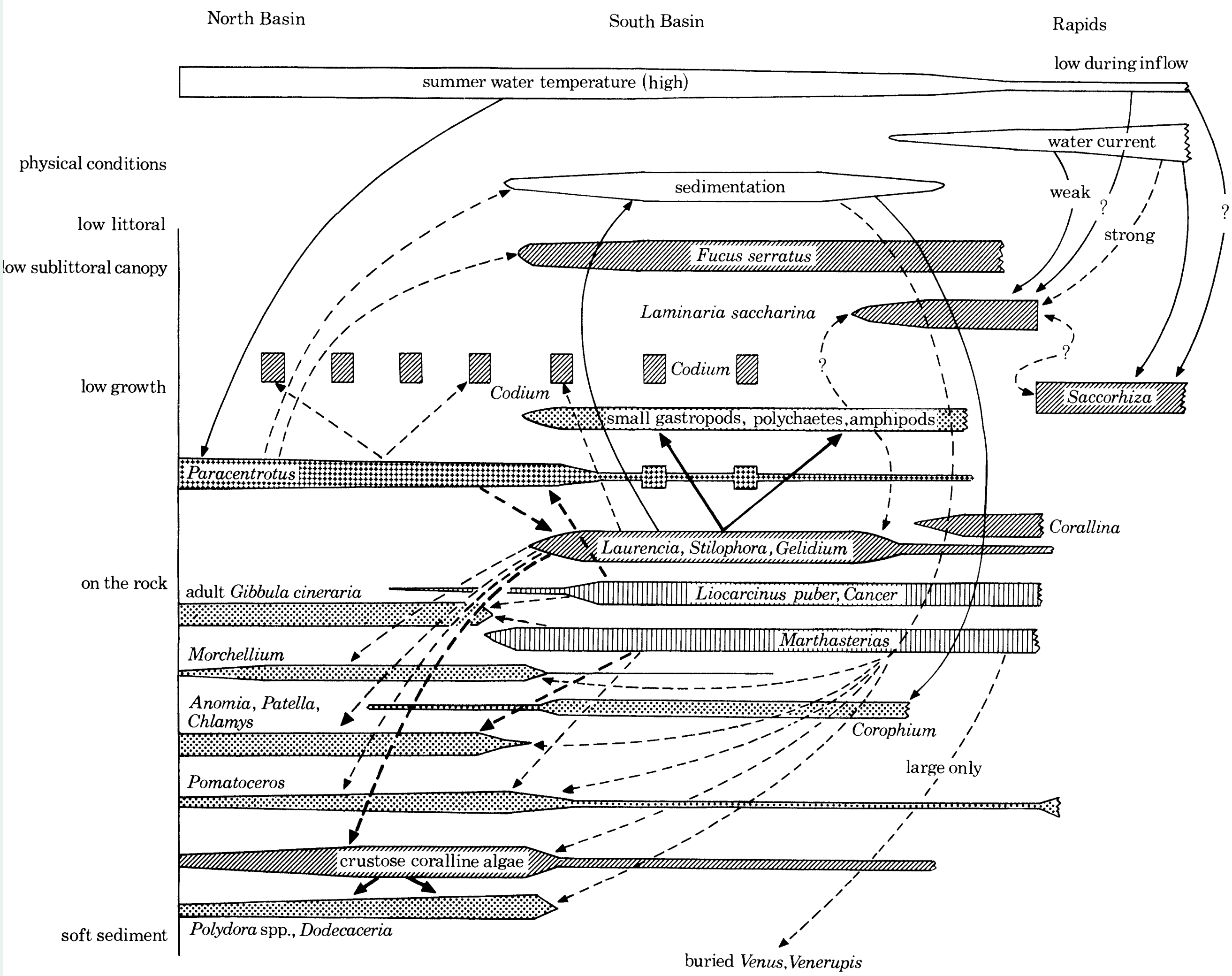

FIGURE 11. Diagrammatic representation of some important interactions of physical factors, plants and animals in the shallow sublittoral of Lough Ine. An arrow with continuous line indicates 'encourages'; an arrow with broken line indicates 'discourages'.

the rock surface is steep, perhaps because the blades hang down into cooler water. The sporophytes of *L. saccharina* live for up to 2–3 years (Parke 1948). They were unhealthy in culture at 18 °C (Kain 1969). Outflow temperatures can reach 17 °C in summer (Kitching *et al.* 1976). The wider distribution of *L. saccharina* in 1981 (figure 1) could be a result of the exceptionally cloudy summer of 1980. This wider distribution may have brought *L. saccharina* into contact with substantial numbers of *Paracentrotus* in the Castle Narrows (figure 6); these will graze upon it if given the opportunity.

Low bushy algae (*Laurencia*, *Stilophora*, *Gelidium* and many less conspicuous species) are bounded by grazing, and *Paracentrotus* clearly limits their distribution. In so doing it destroys the whole community associated with them (summarized in table 2 and in the records of the Appendix). Thus a richly diverse miniature forest is replaced by a habitat that is little more than two-dimensional and therefore less rich in number of species. Large-scale destruction of algal cover by sea urchins is well known elsewhere (Leighton *et al.* 1966; Jones & Kain 1967; Paine & Vadas 1969; Lowrie & Pearse 1973; Breen & Mann 1976).

In Lough Ine *Codium fragile* ssp. *tomentosoides* and *Enteromorpha clathrata* are found on the edge of graze patches. They were also the chief recolonists 1 year after a graze patch had been completely cleared of *Paracentrotus*. They quickly reoccupy empty surfaces. *Codium* probably survives around the edges of graze patches because it is not visited too frequently, because when visited it probably loses only the outer branches, and because it grows again quickly between attacks. Growth form can give protection even though an alga is readily eaten when accessible (Himmelman & Steele 1971). Thus although *Paracentrotus* will eat *Codium* it clears away other algae and (as illustrated in figure 5) its net effect on *Codium* is beneficial. *Codium* in turn accommodates many invertebrate species that would be more severely reduced if the urchins grazed intensely over the whole of their territory, and one invertebrate species (*Elysia viridis*) greatly benefits. Enrichment of the fauna in a non-climax state has been much discussed (see, for example: Menge & Sutherland 1976; Paine 1977).

Paracentrotus clears the rock surface both of soft upstanding algae and of any sediment that may settle, and makes that surface available to those organisms that can resist its grazing: crustose coralline algae and hard-shelled invertebrates. The crustose corallines, and especially the thick knobbly *Lithophyllum incrustans*, accommodate various tubicolous polychaetes (table 2). Of the six species of *Polydora* (see Appendix) that we have found in the corallines, five were recorded by Mesnil (1896; see also Blake & Evans 1973) from crustose corallines on the coast of France, and *Polydora giardi*, reported by Mesnil as specially abundant in crustose corallines, is by far the commonest in *Lithophyllum incrustans* in Lough Ine. *Lithophyllum incrustans*, absent from ungrazed areas in the South Basin, reappears in shallow tide pools on Urchin Reef and on the open coast at Carrigathorna (both outside Lough Ine), at sites where conditions other than the presence of *Paracentrotus* prevent the establishment of algal bush or the settlement of any sediment, and there also it is heavily infested with *Polydora giardi*. Similarly *Patella aspera*, normally intertidal but subtidal on graze patches, is found permanently submerged in tide pools on the open coast where the bottom is not overgrown, and occupies tide pools from which the seaweeds have been removed (Goss-Custard *et al.* 1979); and *Pomatoceros*, numerous on clean boulders in grazed areas but scarce in ungrazed areas of the South Basin, is plentiful in the Rapids, where the bottom is kept clean by the current.

The hard-shelled invertebrates that adhere to the open rock surface (*Anomia*, *Patella*, *Chlamys*), while resistant to crabs, are an easy prey for starfish, of which *Marthasterias* is the commonest. Only small *Marthasterias* are found in the very shallow sublittoral at Lough Ine. They are missing along the North Wall and east shore of the North Basin (figure 4), but are responsible for almost eliminating *Anomia* and *Patella* from graze patches around much of the South Basin. *Marthasterias* appears to be missing from the shallow sublittoral where the slope is gentle. Large *Marthasterias* leave the very shallow sublittoral to feed largely over soft sediment on buried bivalves. They are abundant around the north and northeast shores of the lough at depths below the general range of *Paracentrotus*.

Most small *Paracentrotus* remain underneath the rocks (Muntz *et al.* 1965). Many at or over 30 mm come out onto the tops and make graze patches, and from our growth curves (figures 9, 10) it appears that they are about 3 years old or over. Grazing is by day at Lough Ine (Ebling *et al.* 1966) but by night near Marseille (Kempf 1962), and is probably timed to avoid predators. Emergence from under the rocks is probably in response to hunger. (See also Thain (1971) for the diurnal migration of *Gibbula cineraria*.)

Paracentrotus was observed by Renouf (1931) to move up into the littoral during high water.

Our observations indicate that this movement is not a general and directed upward movement, but only a random dispersion during their daytime activity into a region that has temporarily become accessible. While there, *Paracentrotus* browses on the available fucoids, notably *Fucus serratus* but also *Ascophyllum*. This destruction of fucoids is most noticeable where the rock is steep so that only a short upward excursion is needed to bring the urchins to quite a high level on the shore. There is no upward movement at night.

(*b*) *The population of Paracentrotus*

The abundance of *Paracentrotus* visible in July in the South Basin varies from year to year, and our comments on these variations are purely speculative. (No census has been attempted in the North Basin; there are always very many *Paracentrotus* there.) A poor year group might result from low spawn production or from losses during larval life, during settlement, or during subsequent growth. In the Mediterranean spawning is reported to occur twice during the summer, first as the temperature rises to a critical level and later as it falls to that level again (Fenaux 1968). Crapp & Willis (1975) have concluded that there are similarly two peaks of spawning in the tide pools of Bantry Bay. Although water temperature in Lough Ine follows a pattern somewhat resembling that of tide pools (§3), it does not reach the extremes found by Goss-Custard *et al.* (1979) in mid-tidal pools at Carrigathorna. A critical temperature might not be reached until later in the year than in a tide pool, and a temperature high enough for spawning or early development might not be reached at all in some years. Moore & Lopez (1972) reported a failure to settle for *Lytechnius variegatus* at Miami during a succession of cool years. It is possible that the peak population of *Paracentrotus* in Lough Ine reached in 1979 resulted from an unusually successful spawning or settlement in the warm summers of 1975 and 1976. Many *Paracentrotus* larvae were seen in the plankton in 1976 (D. A. Minchin, personal communication), and many 5–10 mm *Paracentrotus*, which had presumably settled in 1975, were observed under rocks on the south shore in July 1976. Much more information is needed about the spawning and larval development of *Paracentrotus* in Lough Ine.

Variation in the production of larvae of *Paracentrotus* will not account completely for variation in the visible population of the South Basin. Where *Paracentrotus* occurs along the south shore, it is always centred in the same places, which tend to be in slight recesses (S9, S6 and the innermost part of S4) and not at sites where the land projects slightly into the lough (S10, S7, S4/5). Pressoir (1959) has reported that in culture (at 19 °C) the larvae of *Paracentrotus* (from the Mediterranean) settle 1 month after fertilization. Larvae, when produced, must be widely distributed throughout the lough and must reach the unoccupied sites. Either they fail to settle at these sites, or (more probably) they perish at an early stage in their further development.

Graze patches come and go from year to year in that part of the lough where small *Marthasterias* are found under the rocks of the shallow sublittoral. A few small *Paracentrotus* have been eaten by *Marthasterias* experimentally, in cages. Newly settled *Paracentrotus*, with much shorter spines, might be much more vulnerable. We have no evidence as to the importance of this possible interaction, and for this reason it is not shown in figure 11. *Paracentrotus* of substantial size transferred to sites not normally occupied by it was attacked by crabs (Muntz *et al.* 1965), so that it seemed likely that *Cancer pagurus* and *Liocarcinus puber* would destroy *Paracentrotus* in an area infested by them. The occurrence of occasional *Paracentrotus* under but not on the top of boulders along the east shore of the Rapids implies that predation is important there. The sudden rise in numbers of *Paracentrotus* in the South Basin in 1964 was provisionally attributed by Ebling *et al.* (1966) to an adverse effect of the cold winter of 1962 on predators such as crabs. More investigation is needed of the action of predators on newly settled and very small urchins.

This work has been made possible by the generous help of the Royal Society and the provision of excellent laboratory facilities by the University of East Anglia. We are indebted to many students of this University for their help in the 'field' work. Members of the Bristol University Underwater Club surveyed the distribution and food of the starfish *Marthasterias glacialis* at two sites in the lough. Professor F. J. Ebling and Dr T. A. Norton took part in some of the earlier visits to Lough Ine, including occasions of the annual census of sea urchins and *Codium*. The work at Lough Ine was based on the Glannafeen Laboratory. Mr S. R. Jones of the M.A.F.F. Fisheries Laboratory, Lowestoft, made the determinations of salinity. Mr D. A. Minchin of the Irish Department of Fisheries has given us useful information about newly settled *Paracentrotus*. We are indebted to all the authorities listed in the Appendix for their systematic help, and in particular to Dr E. M. Burrows who determined for us a very large number of algae. We have received much local help from Mr John Bohane of Dromadoon, Skibbereen. We are indebted to the Irish Minister for Fisheries and Forestry for permission to work in the Lough Hyne Nature Reserve since its declaration in June 1981.

Appendix. Records of flora and fauna

Undated records are from the years 1977–81 inclusive. Sites are designated in accordance with Renouf's (1931) sectors of the lough, shown in figures 1 and 4. Inevitably our records are mainly drawn from those sectors where we have mainly worked. Nomenclature for algae follows Parke & Dixon (1976), and that for animals follows various recent authors, with attention drawn to any differences from that of the Plymouth Marine Fauna (Marine Biological Association 1957). Numbers in parentheses, placed after the specific names, refer to specialists who have identified or confirmed the identification of some of the material. These specialists are listed at the end of the Appendix.

Material recorded from sectors E10–E20, S2–S15, I8 Ent. and W18/19 was from ungrazed sites in these sectors, the last two being from *Enteromorpha* samples. Material recorded from sectors N2–N9, E1–E10 north, 12, 18, I15 and W18 was from grazed sites. Material from I1 was from a graze patch cleared of all *Paracentrotus* 1 year previously and overgrown with algae.

Those species for which we have sufficient evidence, either from table 2 or from records in this Appendix, have been classified in relation to the effect upon them of grazing by *Paracentrotus*.

* discouraged by grazing;
† encouraged by grazing;
‡ algae present as very small tufts or filaments on grazed areas (see §4*c*).

Cyanophyceae

Schizothrix sp. (1) N2
* *Calothrix crustacea* Thur. ex Born. et Flah. (1) I8 Ent., E11, S5, I1

Florideophyceae

Audouinella corymbifera (Thur. in Le Jol.) Dix (1, 2) S3 epiphytic on *Codium fragile* ssp. *tomentosoides*
Audouinella daviesii (Dillw.) Woelkerling (1) E11 in blanket weed
Audouinella floridula (Dillw.) Woelkerling (1) S5
Audouinella sparsa (Harv.) Dixon (1) S5
* *Gelidium* spp. N2, I8 Ent., E11, E20, S5, S6; we have not distinguished between *Gelidium pusillum* (Stackh.) Le Jol. (1, 2) material from E11, and *Gelidium latifolium* (Grev.) Born. et Thur. (3)
*‡ *Asparagopsis armata* Harv., sporophyte (1) N2, N9, E20, S5, S6, S7
‡ *Bonnemaisonia hamifera* Hariot, sporophyte (1) E10 north, S5
Plocamium cartilagineum (L.) Dixon (1) S5
Corallina officinalis L. (1) E20, S6
* *Jania rubens* (L.) Lamour. (1) S5, S6, S7
† *Lithophyllum incrustans* Phil. (19) N2, N7, N9, E2, E6, E7, E10 north; tables 1–3
Schmitziella endophloea Born et Batt. in Batt. (1) E11
Chylocladia squarrosa (Kütz.) Le Jol. (1) E11
Lomentaria clavellosa (Turn.) Gaill. (1) E11
Ceramium ciliatum (Ellis) Ducluz. (1) S6
‡ *Ceramium diaphanum* (Lightf.) Roth/*strictum* Harv. (1) N2, N9, I8 Ent., E10 north, E11
Ceramium echionotum J. Ag. (1) E11, S6
Ceramium pedicellatum DC (1) E20 (probably), S7
*‡ *Ceramium rubrum* (Huds.) C. Ag. (1) N9, I8 Ent., E10, E11, S5
Corynospora pedicellata (Sm.) J. Ag. (1) (probably) S6
Griffithsia flosculosa (Ellis) Batt. (1) E11 in blanket weed
Plumaria elegans (Bonnem.) Schmitz (1) S7
* *Laurencia platycephala* Kützing (see Magne 1980) (first found in Lough Ine by Dr M. D. Guiry) (3) E11, E20, S6, S9; probably all our shallow sublittoral material from the lough belongs to this species
* *Polysiphonia fruticulosa* (Wulf.) Spreng. (Newton (1931) as *Pterosiphonia*) (1) E10 in blanket weed, S5, S6; I1
‡ *Polysiphonia urceolata* (Lightf. ex Dillw.) Grev. (1) N2, N9; E10 north, E11

Bangiophyceae

Goniotrichum alsidii (Zanard.) Howe (1) E11

Phaeophyceae

‡ *Ectocarpus siliculosus* (Dillw.) Lyngb. (1) I8 Ent., E10 north
‡ *Feldmannia globifera* (Kütz.) Hamel (Newton (1931) as *Ectocarpus*) (1) E10 north
Feldmannia irregularis (Kütz.) Hamel (Newton (1931) as *Ectocarpus*) (1) I8
Feldmannia simplex (Crouan frat.) Hamel (Newton (1931) as *Ectocarpus* (1) S3
Leathesia difformis (L.) Aresch. (1) S5; forms zone at about standard level
Myriactula rivulariae (Suhr in Aresch.) J. Feldm. (1) S5
Isthmoplea sphaerophora (Carm. ex Harv. in Hook.) Kjellm. (1) E20

* *Stilophora rhizodes* (Turn.) J. Ag. (1) I8 Ent., E11, E20, S2, S3, S4, S5, S6; an annual little developed in April
Asperococcus fistulosus (Huds.) Hook. (1) S6
Dictyosiphon chordaria Aresch. (1) I8 Ent.
Colpomenia peregrina Sauv. (1) S7, at about standard level
Laminaria digitata (Huds.) Lamour. in Rapids
Laminaria saccharina (L.) Lamour. (see figures 1 and 6)
Saccorhiza polyschides (Lightf.) Batt. in Rapids
*‡ *Sphacelaria cirrosa* (Roth) C. Ag. (1) N2 sporelings and fragmentary propagules, N9, I1, I8 Ent., E10 north, E10, E11, S5, S6
Halopteris filicina (Grat.) Kütz. (1) S6
* *Dictyota dichotoma* (Huds.) Lamour. (1) E10, S5, S6, S7
Ascophyllum nodosum (L.) Le Jol. widespread in lough
* *Fucus serratus* L. (see figures 1 and 6)
Himanthalia elongata (L.) S. F. Gray (see figures 1 and 6)
Bifurcaria bifurcata Ross (1) S7
Cystoseira nodicaulis (With.) Roberts (1) S6
Cystoseira tamariscifolia (Huds.) Papenf. (1) (probably) S2

Chlorophyceae

Chlorochytrium cohnii Wright (1) E11 in *Schizonema* tube
Chlorochytrium facciolae (Borzi) Bristol and var. *minor* (Borzi) Bristol (1) S5 July 1980
Monostroma grevillei (Thur.) Wittr. (1) S5
‡ *Enteromorpha clathrata* (Roth) Grev. (1) widely distributed around lough; N2, N9, I8 Ent., E10 north, E10, E11, S5, S6, W18/19; I1
* *Enteromorpha intestinalis* (L.) Link (1) E11, S5, W18/19
Enteromorpha prolifera (O. F. Müll.) J. Ag. (1) (probably) E20, S6
* *Ulva lactuca* L. (1) E11, E20, S6
Ulva rigida C. Ag. (1) I8 Ent., E20
‡ *Phaeophila leptochaete* (Huber) Nielson (1) on *Cladophora* sp. E10 north, in graze patch
Chaetomorpha capillaris (Kütz.) Børg. (1) E11
*‡ *Chaetomorpha linum* (O. F. Müll.) Kütz. (1) I8 Ent., E10 north, E11, S5, S6
‡ *Cladophora albida* (Huds.) Kütz. (1) I8 Ent., E10 north
* *Cladophora dalmatica* Kütz. (1) E10, E11; I1, I8 Ent.
Cladophora hutchinsiae (Dillw.) Kütz. (1) E11
Cladophora laetivirens (Dillw.) Kütz. (1) S5
* *Cladophora rupestris* (L.) Kütz. (1) E11, S5, S6
‡ *Cladophora sericea* (Huds.) Kütz. (1) I8, E10 north
‡ *Codium fragile* ssp. *tomentosoides* (Goor) Silva (1) widespread around lough (see figures 5 and 6 and table 4); I1

Porifera

Terpios fugax Duchassaing & Michelotti N6/7, E12, S6
Hymeniacidon perleve (Montagu) E10 north, S6
other Porifera not identified

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Coelenterata: Hydrozoa

* *Cladonema radiatum* Dujardin S2/3, S4, table 2; S15

Coelenterata: Anthozoa

Parerythropodium coralloides (Pallas) (= *P. hibernicum* Renouf 1931) I15 September 1979

Anthopleura ballii (Cocks) N6/7, N9, E2, E12, I2, I8, I12, I15, S3, S4, S5, S6; common and widely distributed in lough

Caryophyllia smithii Stokes E12, I15, S3

Platyhelminthes: Turbellaria: Polycladida

Prostheraeus vittatus (Montagu) S2

Annelida: Polychaeta

Lepidonotus squamatus (L.) E8

Harmothoe extenuata (Grube) (*Lagisca* in Plymouth Marine Fauna) E10 north, I8, S2/3, S15

Pholoe minuta Fabricius S15

Euphrosyne foliosa Audouin & Milne Edwards I8; I15 with two specimens having long setae as described for *E. intermedia* Saint-Joseph (Fauvel 1923), which is probably only a variety (4)

Eulalia spp. N2, N9, E10 north, S5

Notophyllum foliosum (Sars) I8, in cleavage plane of rock

Eteone sp., probably *E. picta* Quatrefages from markings, I18, S5

Kefersteinia cirrata (Keferstein) (4) N9, E10, S5

Magalia perarmata Marion & Bobretzky (4) E10 north, S5

† *Syllis gracilis* Grube N9, E10 north, E11, I2, S5, table 2

Typosyllis prolifera Krohn or *Trypanosyllis*? E10 north, E10, E11, S2/3, W18/19

Eurysyllis tuberculata Ehlers S5, S15

* *Odontosyllis gibba* Claparède E10, I8 Ent., S2/3, S5

* *Pionosyllis serrata* Southern E10, E11, S2, S3, S4, S5/6, S9, S15, table 2

Autolytus sp. I8

Brania clavata (Claparède) (*Grubea* in *Plymouth marine fauna* (Marine Biological Association 1957)) N2, N9, E10 north, E10, E11, I8 Ent., S2, S3, S4, S5/6, table 2; S15

Brania pusilla (Dujardin) N2, N9, E10 north, S5

Sphaerosyllis pirifera Claparède (4) S5, one specimen, July 1980

Sphaerosyllis sp. resembling *S. bulbosa* Southern but has some papillae on the body; N9, E10 north, E10, E11, I8 Ent., S5

Exogone gemmifera Pagenstecher N2, N9, E10 north, E11, I8 Ent., S3, S5, table 2

* *Micronereis variegata* Claparède E11, S2/3, S5

Nereis pelagica L. N6/7, E10 north

Perinereis cultrifera (Grube) one specimen, I8, September 1978

* *Platynereis dumerilii* (Audouin & Milne Edwards) S3; S4, several in 'Heteronereis' stage, April 1978; S5. Small Nereidae found in large numbers on the south shore of Lough Ine probably belong to this species.

Nephtys sp. S3
Ephesia gracilis Rathke one specimen, I8
Lysidice ninetta Audouin & Milne Edwards N7, N9, E10, I2, I8, I15
Nematonereis unicornis (Grube) one specimen, E10, August 1979
Lumbriconereis latreilli (Audouin & Milne Edwards) one specimen, N6/7
Dorvillea rubrovittata (Grube) (*Staurocephalus* in Fauvel (1923)) N6/7; E10 north, I8, I15, S3, W12
Polydora ciliata (Johnston) N2, N9
† *Polydora flava* Claparède E10 north, I2, W18
† *Polydora caeca* (Oersted) N9, E10 north, I2
Polydora hoplura Claparède N9
† *Polydora giardi* Mesnil N2, N9, E10 north, table 2
Polydora armata Langerhans E10 north
Chaetopterus variopedatus (Renier) E11, July 1973; I15
† *Dodecaceria concharum* Oersted N2, N9, E10 north, I2, I8, I10; table 2
Capitella capitata (Fabricius) E10 north
Capitomastus minimus (Langerhans) E10 north
Macrochaeta clavicornis (Sars) S5
Branchiomaldane vincenti Langerhans N2, N9, E10 north, S5
Micromaldane ornithochaeta Mesnil N2, N9, E10 north, S5
Petaloproctus terricola Quatrefages I15, 1 specimen
Amphitritides gracilis (Grube) (*Amphitrite* in *Plymouth Marine Fauna* (Marine Biological Association 1957)) I15, one specimen
Trichobranchus glacialis Malmgren N6/7, one specimen
Sabella crassicornis Sars (*S. fabricii* Kröyer in Fauvel (1927)) I15, one specimen, September 1979
Potamilla incerta Langerhans (5) E10 north
* *Amphiglena mediterranea* (Leydig) E10, E11, S2/3, S3
† *Fabricia sabella* (Ehrenberg) (4) N2, N9, E10 north, S5, E11, table 2
Oriopsis armandi (Claparède) (5) E10 north, S5
* *Oriopsis* sp. undetermined E10, E11, S5
Myxicola aesthetica (Claparède) E10, I2
† *Pomatoceros* spp. found all around the lough, tables 1, 2 and 3, text §6*a*. Collections from N9, E10 north and S15 proved to be entirely *P. triqueter* (L.) as defined by Zimbrowius (1968) except for two specimens of *P. lamarcki* (Quatrefages) from E10 north
Spirorbis spirorbis (L.) E11, on *Laminaria saccharina*
Spirorbis tridentatus Levinsen on rocks at N9, E9/10, S5
Spirorbis cuneatus Gee on rocks at N9
Circeis armoricana Saint-Joseph ssp. *fragilis* Knight-Jones & Knight-Jones, 1977 (6) on *Laminaria saccharina*
* *Janua pagenstecheri* (Quatrefages) E11, on *Laminaria saccharina*; S2/3, S4, in large numbers on *Stilophora rhizodes*, table 2; on rocks at N9, E9/10, S5
Janua (*Dexiospira*) *pseudocorrugata* (Bush) E11, on *Laminaria saccharina*

SIPUNCULA

Phascolosoma granulatum Leuckart I15, September 1979

NEMERTINI: ANOPLA: PALAEONEMERTINI

Cephalothrix linearis (Rathke) (7) E10

NEMERTINI: ANOPLA: HETERONEMERTINA

* *Lineus longissimus* (Cunnerus) (7) E10, E11, E12, S6
Lineus viridis (Müller) (7) E12
Paradrepanophorus crassus (Quatrefages) (7) S2

ARTHROPODA: CRUSTACEA: CIRRIPEDIA

† *Verruca stroemia* (O. F. Muller) N2, N7, N9, E6, I6; table 2
Sacculina carcini Thompson frequently seen on *Carcinus maenas*

ARTHROPODA: CRUSTACEA: TANAIDACEA

Tanais cavolini Milne Edwards (8) N2, E11, S2, S3, S5/6
Leptochelia savignyi Kröyer (8) N2, N9, E10 north, S5, table 2

ARTHROPODA: CRUSTACEA: ISOPODA

Gnathia dentata Sars (9) ♂♂ from S15, September 1978; ♀♀ and immature *Gnathia* sp., undetermined, N9, E10 north, S5
Janira maculosa Leach N2, E10 north, S5, S15
Jaera (*albifrons* group) S2
* *Munna armoricana* Carton (9) E10, E11, S5

ARTHROPODA: CRUSTACEA: AMPHIPODA

Lysianassa ceratina (A. O. Walker) S15
Metaphoxus fultoni (T. Scott) (9) S5, one specimen, July 1980
* *Stenothoe monoculoides* (Montagu) N9, E10 north, E10, E11, S2, S3, S5/6, table 2; S15
Perioculodes longimanus (Bate & Westwood) S5, one specimen
Apherusa jurinei (Bate) S2, S9
Gammarus sp. (9). Some specimens approach *G. locusta* (L.) and others *G. insensibilis* Stock; 2 ♂♂ from S5 (July 1980) identified as *G. insensibilis* (9, 20)
* *Dexamine thea* Boeck on algae at E10, E11, I8 Ent., S2, S3, S5/6, S9, S15, W18/19; N9; table 2
Aora typica Kröyer N9, S5
* *Microdeutopus anomalus* Rathke (9) on algae at E10, E11, S2, S5/6, S9, S15
Lembos websteri Bate N9, E10 north, S5, S15
* *Microprotopus maculatus* Norman E10, E11, I8 Ent., S5
* *Amphithoe neglecta* Lincoln E10 north, S5, S15; table 2
Gammarella fucicola (Leach) E10, S5
Erichthonius brasiliensis (Dana) S5
* *Corophium bonnellii* G. O. Sars N9, E10 north, S5, table 2

Phtisica marina Slabber E10, I8
* *Caprella acanthifera* Leach S3, July 1971; S2, S4, S5/6

ARTHROPODA: CRUSTACEA: MYSIDACEA

Siriella clausi G. O. Sars S5, 1 specimen

ARTHROPODA: CRUSTACEA: DECAPODA

Hippolyte varians Leach E10, S3, S4, among algae
Spirontocaris cranchi (Leach) S3, July 1971; S15
Alpheus macrocheles (Hailstone) 10) E10 north, one specimen, August 1979
Palaemon serratus (Pennant) very common in lough
Galathea squamifera Leach E2
Porcellana platycheles (Pennant) N6/7, E2, E6, E10, I2, W18
Porcellana longicornis (L.) E2, W18
Eupagurus bernhardus (L.) E12
Cancer pagurus L. I12, I15, W18–W24, all July 1971
Liocarcinus arcuatus Leach (*Portunus* in Plymouth Marine Fauna; see Ingle 1980) E12; S8, W18, July 1971
Liocarcinus puber (L.) all around lough, but especially in South Basin and near Rapids (Muntz *et al.* 1965); E19, I12, I15, S3, S8, S14–S15, July 1971
Carcinus maenas (L.) all around lough, specially in North Basin and Goleen (Muntz *et al.* 1965); E10 E12, E19, I15, S3, S8, S14, S15, July 1971
Xantho incisus Leach N2, E2
Xantho pilipes Milne Edwards E2
Maia squinado (Herbst) I14, W18, W22, W38, all July 1971
Macropodia rostrata (L.) (11) E2

ARTHROPODA: PYCNOGONIDA

Endeis laevis Grube E12, E20

ARTHROPODA: INSECTA: DIPTERA

Halocladius fucicola (Edwards) (*Cricotopus* in *Plymouth Marine Fauna* (Marine Biological Association 1957)) larvae, N2, N9, E10, E11, S2, S3, S5/6, S9; many among algae, table 2
Clunio marinus Haliday larvae, N2, N9, E10 north, E10, E11, I8, S2, S3, S5/6, S9, many among algae, table 2

BRACHIOPODA

Crania anomala Müller E11, July 1973; I15, S3, W17

MOLLUSCA: POLYPLACOPHORA

Lepidopleurus asellus (Gmelin) (12) N6/7, E12, I16
Tonicella rubra (L.) (12) I16, S3, W18
Lepidochitona cinereus (L.) (12) N6/7, I18
* *Acanthochitona crinita* (Pennant) (12) E11, E12, S3, S15

Mollusca: Gastropoda: Prosobranchia

Emarginula reticulata Sowerby N7, I15
Acmaea virginea (Müller) E10 north, I2, I8, I15, S6, S15
Patella vulgata L. N7, sublittoral; common all around lough intertidally
† *Patella aspera* Lamarck sublittoral (see figure 4 and table 3; see also Ebling *et al.* 1962)
Patina pellucida (L.) S5, S15 (see also Sloane *et al.* 1961)
Gibbula cineraria (L.) N6/7, N7, E6, E7, E10 north, E11, E12, I6, I8, I12, I15, S3, S6, S15, W18
Lacuna vincta (Montagu) S15 (12)
Cingula semicostata (Montagu) (12) E10, S15
Alvania beani (Thorpe) (12) S5
* *Rissoa parva* (da Costa) (12) N9 (a few), E10 north (a few), E10, E11, I8 Ent., S2, S3, S4, S5, S5/6, S9, W18/19; table 2
* *Barleeia unifasciata* (Montagu) (*B. rubra* in *Plymouth Marine Fauna* (Marine Biological Association 1957)) (12) S2, S2/3, S4, S5, S5/6, S9, S15
* *Cingulopsis fulgida* (Adams) (12) E10, E11, I8, S2, S2/3, S5/6, S9, S15, table 2
Skeneopsis planorbis (Fabricius) S4
* *Omalogyra atomus* (Philippi) E10, E11, I8 Ent., S2, S2/3, S4, S5/6, S9, S15
Rissoella diaphana (Alder) S5
Rissoella opalina (Jeffreys) S5
* *Bittium reticulatum* (da Costa) N9, E10 north, E10, E11, I1, I8 Ent., I15, S2, S3, S4, S15, table 2
Trivia arctica (Montagu) E10 north, one specimen
Ocenebra erinacea (L.) N2, N6/7, N7, E2, E10, E11, I6, I15
Nassarius incrassatus (Ström) N7, E2, E7, E10, E11, E12, I6, S3; S5, S15. *Nassarius* sp. eggs at N2, N9, E10 north.
Nassarius reticulatus (L.) 17, one specimen

Mollusca: Gastropoda: Opisthobranchia

Onoba aciculus Gould (12) S15, one specimen
Odostomia plicata (Montagu) (12) N9, one specimen
Retusa truncatula Bruguière S15
Stiliger bellulus (Orbigny) (13) S4, 2 specimens, July 1974
* *Elysia viridis* (Montagu) E10, S2/3, S3, S9, table 2; E11, I12, S4; on *Codium*
Archidoris pseudoargus (Kapp) S7

Mollusca: Lamellibranchia

Modiolula phaseolina (Philippi) spat, S15
Musculus marmoratus (Forbes) small, N9 (a few); I8, S5, S15
Mytilus edulis L. (*sensu lato*) spat, N9, a few; S5, S15
† *Anomia ephippium* L. figure 4 and table 3
Monia patelliformis (L.) I8, 1 specimen
Heteranomia squamula (L.) S15

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† *Chlamys varia* (L.) N7, N9, E1–E2, E6, E7, E10 north, E11, I2, I6, I8, S5 (1 specimen); table 3

Venus verrucosa L. N1; E2–E3, and in Goleen, all buried in soft sediment

Venerupis rhomboides (Pennant) E2–E3 and in Goleen, all buried in soft sediment

Hiatella arctica (L.) N9, S5, I8, S15

Mollusca: Cephalopoda

Sepiola atlantica d'Orbigny S4, one specimen taken at surface at night, April 1978

Chaetognatha

Spadella sp. N9; S5

Phoronida

Phoronis hippocrepia Wright S2, July 1977

Entoprocta

Pedicellina cernua (Pall.) var. *hirsuta* Jull. (see Marcus 1940, p. 15) E20

Bryozoa

Filicrisia geniculata (Milne Edwards) S5

Tubulipora sp. E20, on *Laminaria saccharina*

* *Aetea truncata* (Landsborough) E20, S2/3, S6, S15

Scruparia chelata (L.) E20

Membranipora membranacea (L.) E20, on *Laminaria saccharina*

* *Scrupocellaria reptans* (L.) E10, E20; S2/3 on *Codium*; S5, S6

Callopora rylandi Bobin & Prenant (14) E3, N7

Hippothoa distans MacGillivray (14) N7, under rock

Hippothoa hyalina (L.) N7, I1, E20, S15, on *Laminaria saccharina*

Cryptosula pallasiana (Moll) (14) N7, under rock

Chorizopora brongniarti (Audouin) (14) N7, under rock

Microporella ciliata (Pallas) (14) N7, under rock

Escharoides coccineus (Abildgard) E12

Celleporaria pumicosa (Pallas) E20

Echinodermata: Asteroidea

Luidia ciliaris (Philippi) I10, I19–I20, S4, S7

Asterina spp. (*A. gibbosa* (Pennant) and *A. phylactica* Emson & Crump not separated, but both are present) all around lough

Henricia sanguinolenta (O. F. Müller) E20

Asterias rubens L. occasional all around lough

Marthasterias glacialis (L.) all around lough but small sizes mainly in South Basin, figure 4

Echinodermata: Ophiuroidea

Ophiothrix fragilis (Abildgard) all around lough

* *Amphipholis squamata* (Delle Chiaje) E10, E11, E12, S4, S5, S6, S15, W18

ECHINODERMATA: ECHINOIDEA

Echinus esculentus L. E1, W19, W20, W21, W37, W38, all July 1971; regularly seen on sublittoral cliffs up to s.l. in South Basin, especially in E19 and E20

Paracentrotus lividus (Lamarck) graze patches in figure 4 (see also table 4); seen spawning in July

ECHINODERMATA: HOLOTHUROIDEA

* *Cucumaria saxicola* Brady & Robertson (15) E10, E12, S6

CHORDATA: TUNICATA

† *Morchellium argus* (Milne Edwards) N9, E2, E6, E7, E10 north, E12, I6, I2, I8, I15, S3 one specimen, W18; table 3

Aplidium pallidum (Verrill) E20

Diplosoma listerianum (Milne Edwards) (16) N2, N9, E20, on *Laminaria saccharina*

† *Ciona intestinalis* (L.) N2, N7, E6

Ascidiella aspersa (O. F. Müller) E20, W23–W24

Ascidia conchilega O. F. Müller (16) N2, one specimen

Botryllus schlosseri (Pallas) E20

† *Botrylloides leachi* (Savigny) N6/7, N9, E7

Pyura squamulosa (Alder) (16) N2, two specimens

CHORDATA: PISCES

Nerophis lumbriciformis Pennant E12

Lepadogaster candollei Risso (17) N4, I2, July 1964; I1

Gobius niger L. (17) E3, July 1968; E2, I1, S11, July 1971

Gobius paganellus L. (17) E11, E19, I15, S9, W18–W20, all July 1971; E9, S4, S5

Gobius cruentatus Gmelin (17) S9, August 1980

Gobius couchi Miller (17) E15, July 1980; S2/3, S4, September 1976; S5, July 1980; S9, August 1980; S11, July 1971 (18)

Chaparrudo flavescens (Fabricius) (17) (*Gobius* in *Plymouth Marine Fauna* (Marine Biological Association 1957)) S11, July 1971

Pomatoschistus pictus (Malm) (17) (*Gobius* in *Plymouth Marine Fauna* (Marine Biological Association 1957)) E3, July 1968; E9

Pholis gunnellus (L.) S6

Crenimugil labrosus (Risso) (*Mugil* in *Plymouth Marine Fauna* (Marine Biological Association 1957)) shoals frequent in South Basin

Taurulus bulbalis (Euphrasen) (17) (*Cottus* in *Plymouth Marine Fauna* (Marine Biological Association 1957)) S11, July 1971

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