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PRIMARY AND SECONDARY SETTLEMENT IN *MYTILUS EDULIS* L. (MOLLUSCA)

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INTRODUCTION

In 1942 Maas Geesteranus postulated that the annual spatfall of mussel larvae in the vicinity of Den Helder, Holland, was scattered over a wide area, that these young mussels subsequently detached themselves from the substrate and that they then entered upon a migratory phase during which further attachment and detachment occurred many times. Eventually the mussels made contact with a substrate suitable for the adult way of life and then final attachment occurred. Verwey (1952) restated this view and stressed the importance of water currents and current-velocity in transporting the young mussels and in determining the site of final attachment. De Blok & Geelen (1958), also working at Den Helder, showed that the larvae of *Mytilus edulis* attached preferentially to artificial filaments which simulated the naturally occurring filamentous algae on which young mussels were found. They also observed that these young mussels subsequently disappeared from the filaments.

Up to the present, however, it has not been demonstrated that the mussel larvae pass successively from the plankton to temporary sites of attachment and thence to their final place of settlement. Population studies therefore have been made to follow the sequence of young stages in the field to confirm that the observed settlement on filamentous algae was the natural prelude to permanent settlement and not a wasteful settlement of larvae on unsuitable substrata.

The incidence of various age-groups of *M. edulis* in the Menai Straits, North Wales, was studied by observing the distribution of (a) the planktonic larvae, (b) the first settlement stages, and (c) the final settlement stages. The first settlement stages will be called early plantigrades and the final settlement stages late plantigrades, after the terminology of Carriker (1961).

METHODS

(a) During April, May, June and July 1963, quantitative plankton samples were obtained weekly from the Menai Straits with a Clarke-Bumpus plankton sampler, calibrated and used according to Yentsch & Duxbury (1956). The samples were obtained from the surface in the vicinity of the Marine Science Laboratories. The size-distributions of the *Mytilus edulis* larvae were recorded. These samples may be regarded as typical of the Menai Straits waters as a whole since the strong tides lead to almost complete mixing.

(b) Preliminary observations had revealed that young plantigrades were to be found attached to some of the common filamentous red algae, especially *Polysiphonia lanosa* (L.) Tandy, which grows epiphytically on *Ascophyllum nodosum* (L.) Le Jol, and *Ceramium rubrum* (Huds.) Ag. From February to August 1963, weekly samples of these algae from mean tide level on a rocky shore of the Menai Straits were examined for

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M. edulis plantigrades. The numbers of plantigrades counted were related to the weight of the thallus examined, each thallus having been dried with a cloth prior to weighing.

(c) Weekly samples were also obtained from mean tide level on a mussel bed at Tal-y-Foel in the Menai Straits. The numbers of plantigrades less than 3·0 mm in shell length were counted. The samples were obtained and treated as follows: random quadrats of 20 cm^2 area were taken, including the substrate to a depth of 3 cm. After careful examination of the byssal threads and shell surfaces of adult mussels, the samples were washed through a series of sieves of the following mesh-sizes: 2·057, 1·405, 1·003, 0·497 and 0·211 mm. The content of each sieve was examined for plantigrades.

To interpret these results it was necessary to arrive at a value for the rate of increase in shell length of young *M. edulis*.

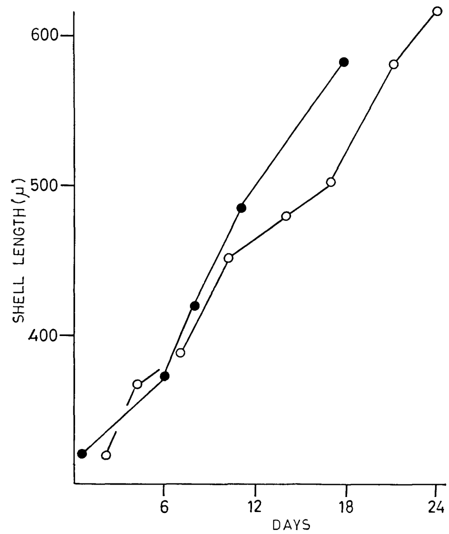

FIG. 1. The growth of *Mytilus edulis* plantigrades in the laboratory. ●, 16° C; ○, 11° C.

Although many authors have recorded the growth of mussels of shell lengths greater than 2·0 mm, there is little information on the growth of plantigrades immediately following settlement. Spärck (1919) found that young *M. edulis* in the Limfjord reached a length of 4·0 mm within 1 month of attachment and Warren (1936) reported a similar rate of length increase for young mussels constantly submerged in Passomoquoddy Bay, Canada. Warren also noted that mussels exposed for about 4 h daily reached a length of 1·0 mm in 28 days (*c.* 26 μ/day) and hardly 4·0 mm in 72 days. De Blok & Geelen (1958) recorded that plantigrades at 450–500 μ length grew about 38 μ/day, and plantigrades at 600 μ grew about 45 μ/day.

Observations on the rate of increase in length of *M. edulis* plantigrades were made in the laboratory and in the Menai Straits. Larvae were cultured in the laboratory and allowed to settle on filaments of *Ceramium rubrum.* Every 48 h they were fed on a culture of *Isochrysis galbana* (forty cells/mm^3); the water in the culture vessels was also changed every 48 h. The increases in shell length at 11 and 16° C are plotted in Fig. 1. There was an increase of about 14 μ/day at 16° C. Other measurements of plantigrades kept in running sea-water in the laboratory indicated an average length increase of 23 μ/day. During the growth of these plantigrades there is a gradual change in the shape of the shell. The height/length ratio alters from 0·802 at a shell length of 340 μ to 0·681 at 750 μ, so that increase in shell length is not an entirely satisfactory measure of growth rate. Nevertheless it is this measurement that is appropriate to this communication.

On 17 July 1962 thalli of *P. lanosa* with many early plantigrades of average

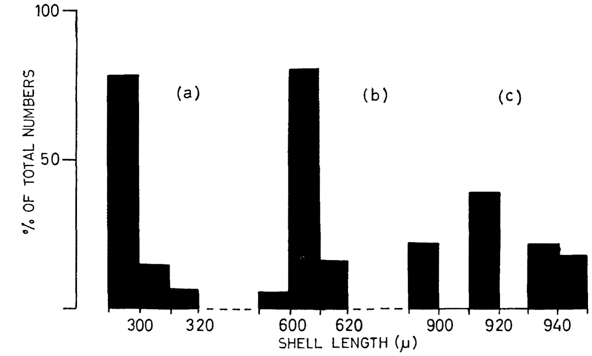

FIG. 2. The growth of *Mytilus edulis* plantigrades in the Menai Straits. Average lengths at (a) 0 days, 296 μ; (b) 10 days, 602 μ; (c) 22 days, 918 μ.

size 296 μ attached, were tied to a wooden frame which was then enclosed in coarse-mesh plankton netting and suspended from a raft in the Menai Straits. The plantigrades were remeasured on 27 July and 8 August (Fig. 2). These measurements showed an average daily increase in length of 30·6 μ between 296 and 602 μ shell length, and 26 μ between 602 and 918 μ, over a period when water temperatures were between 15 and 16° C.

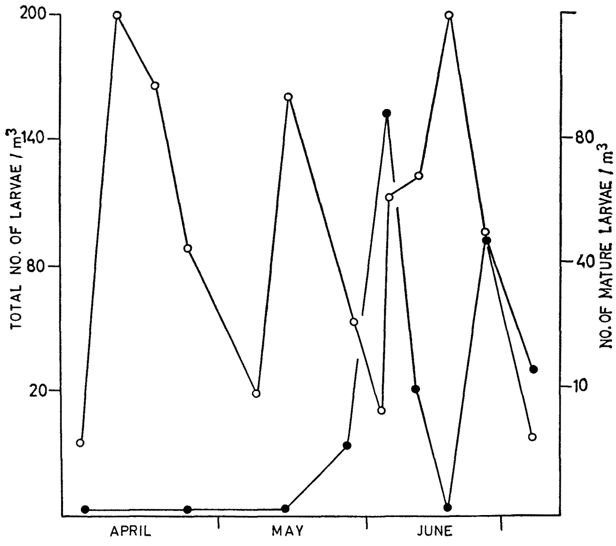

FIG. 3. The occurrence of *Mytilus edulis* larvae in the Menai Straits. ○, Total larvae; ●, mature larvae.

It is to be expected that growth in the laboratory would be slower than in the field and also that the growth of intertidally attached individuals would be slower than those attached sub-littorally. Therefore, on the basis of the above measurements, the figure of 25 μ/day was accepted as the average daily increase in shell length of newly-settled mussels in the Menai Straits in the summer months.

RESULTS

The occurrence of Mytilus edulis *larvae in the plankton*

Observations during 1960–61 showed that adult mussels in the Menai Straits spawned in April, May and June and that mussel larvae were present in the plankton from April to early July. Previous observations had also shown that in the area sampled most frequently the larvae had a uniform vertical distribution and that their numbers remained relatively constant throughout a tidal cycle.

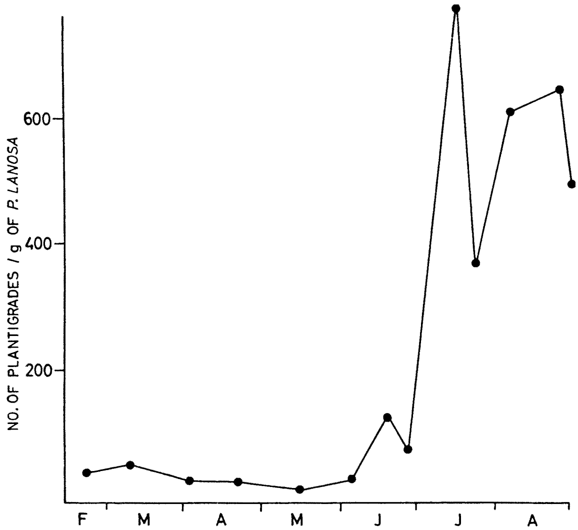

FIG. 4. The occurrence of *Mytilus edulis* plantigrades on *Polysiphonia lanosa* in the Menai Straits.

Fig. 3 shows the total number of larvae and the number of mature larvae (>250 μ in length) per m^3 that were counted on various occasions in 1963. There were three distinct periods of maximum larval density, in mid-April, mid-May and mid-June, but the incidence of mature larvae indicated that only the two later peaks of larvae reached maturity; the larvae that were present in the plankton in April disappeared before reaching maturity. These samples suggested that there should be two main periods of settlement, in early June and early July.

The occurrence of plantigrades on the algae

The numbers of early plantigrades found attached to *Polysiphonia lanosa* remained low through the early part of the year but increased from 5 June to 16 July (Fig. 4). If these plantigrades are grouped according to size (Table 1) it becomes clear that the increase in numbers from 5 to 19 June and the population present on 16 July contained a large proportion of plantigrades 250–350 μ in length, corresponding to the size of the larvae at settlement (Jørgensen 1946, and personal observation). Indeed, many of the plantigrades observed on 5 June had remains of the velum in the mantle cavity, indicating that attachment had occurred less than 24 h previously. The time of their occurrence corresponded closely with the dates of settlement expected from the incidence of mature larvae in the plankton.

Table 1. *The size distribution of small plantigrades on thalli of* Polysiphonia lanosa *in the Menai Straits,* 1963

Date	No. of plantigrades per g of *P. lanosa* within the size-range 250–350 μ	350–450 μ	450–550 μ
1 April	–	–	–
8 April	–	–	–
16 April	–	0·5	1·2
21 April	0·4	2·2	–
28 April	–	–	–
7 May	–	–	–
14 May	–	–	–
21 May	–	–	–
29 May	–	–	–
5 June	6·0	–	–
12 June	40·0	6·2	0·6
19 June	62·5	46·2	7·5
26 June	1·6	18·3	13·3
16 July	106·6	126·6	133·3
24 July	8·0	40·0	4·0
6 August	7·6	–	15·5
26 August	–	–	33·3

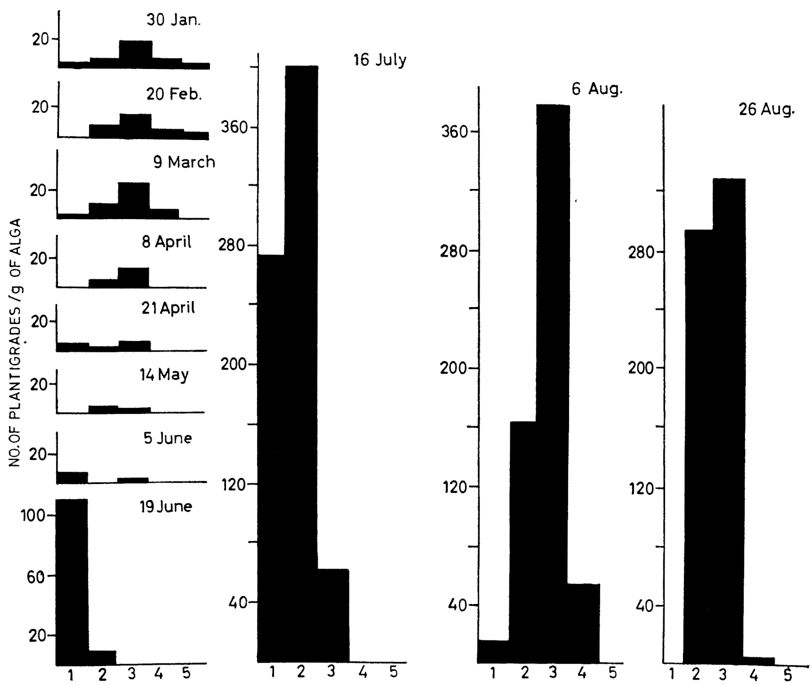

FIG. 5. The size distribution of *Mytilus edulis* plantigrades on *Polysiphonia lanosa,* 1963. Horizontal scale: 1, <500 μ length; 2, 500–999 μ; 3, 1·0–1·49 mm; 4, 1·5–1·99 mm; 5, >2·0 mm.

Fig. 5 shows the size distribution of these early plantigrades on *P. lanosa* in more detail. From January to April most of the plantigrades were in the third size group (1·0–1·49 mm). During June and early July there was a sharp increase in the numbers of plantigrades in the first size group (<500 μ long). From 16 July to 26 August the numbers

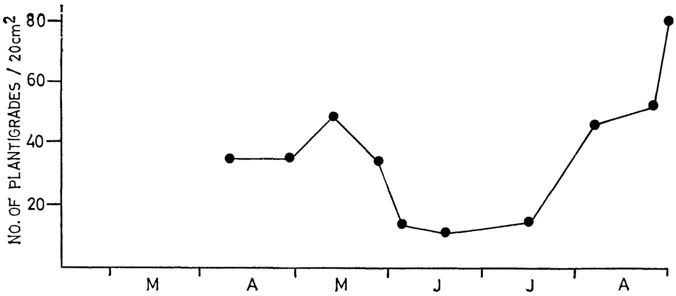

FIG. 6. The occurrence of *Mytilus edulis* plantigrades less than 3·0 mm in length on a mussel bed in the Menai Straits.

of these small plantigrades decreased (on 24 July the size distribution was: <500 μ, 48/g; 500–999 μ, 204/g; 1·0–1·49 mm, 100/g; >1·5 mm, 4/g). Over the same period the numbers in the larger size groups increased. If the daily average increase in length is 25 μ the small plantigrades observed on 19 June would have grown to 900–1000 μ by 16 July and 1·4–1·5 mm by 6 August.

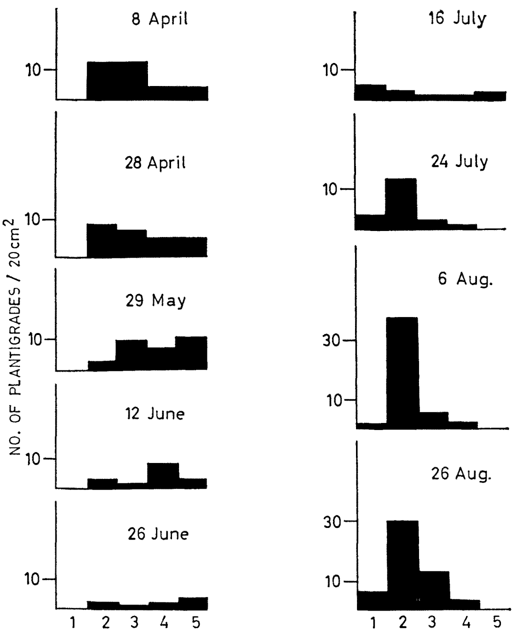

FIG. 7. The size distribution of *Mytilus edulis* plantigrades on the mussel bed, 1963. Horizontal scale: 1, 500–999 μ; 2, 1·0–1·49 mm; 3, 1·5–1·99 mm; 4, 2·0–2·49 mm; 5, 2·5–3·0 mm.

The occurrence of plantigrades on the adult mussel beds

Fig. 6 shows the density of plantigrades less than 3·0 mm in length recorded from the adult mussel beds at Tal-y-Foel in 1963. During April and May these numbers fluctuated considerably, due largely to heterogeneities of the substratum in the sampling area. From the middle of May onwards, however, all samples were taken from areas of similar substratum. The size distributions within these samples are presented in Fig. 7. During June and much of July few plantigrades less than 3·0 mm were present in these samples, and at no time were plantigrades less than 750 μ in length observed. The smaller plantigrades of up to 2·0 mm began to appear in numbers in late July and they became

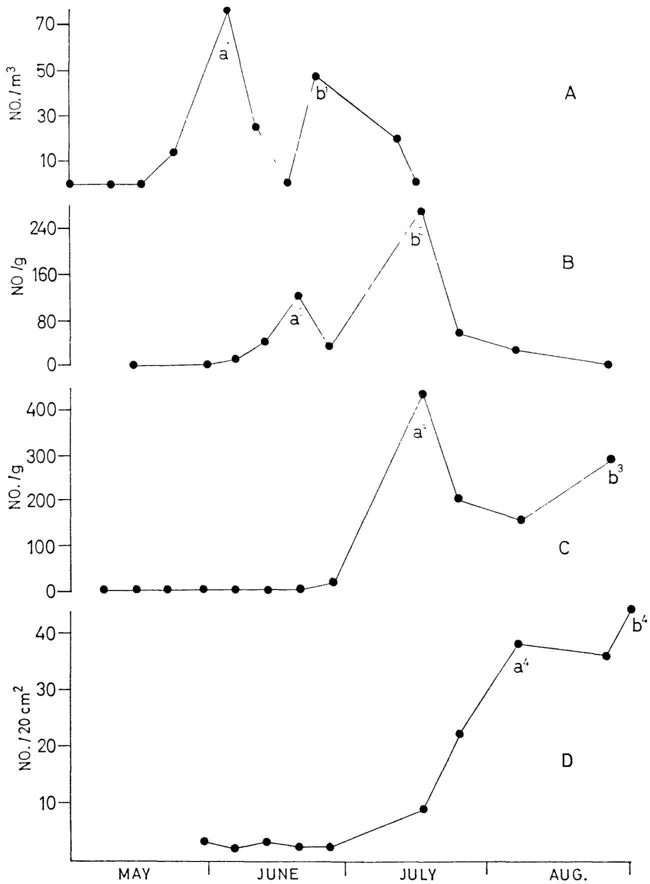

FIG. 8. The occurrence of the four stages of *Mytilus edulis* in the Menai Straits in the summer of 1963. A, mature larvae; B, early plantigrades <500 μ on *Polysiphonia lanosa*; C, late plantigrades 500–999 μ on *P. lanosa*; D, late plantigrades $<1·5$ mm on the adult mussel bed.

more numerous and grew through August. Thus, a period of more than 30 days elapsed between the first definite spatfall of larvae in the Menai Straits (early June) and the appearance of young mussels on the mussel beds (late July). Whilst settlement was occurring on the filamentous algae in early June, there was no settlement on the mussel bed. The main recruitment onto the mussel bed occurred in size group 2 (1·0–1·5 mm). The time interval involved between the first settlement on the algae and the first increase in numbers on the adult beds (*c*. 12 June to 31 July) would have resulted in a growth from 250 μ to *c* 1·5 mm shell length at a rate of 25 μ/day.

Some of these data are summarized in Fig. 8. This shows the abundance of mature larvae in the plankton and of three different size groups of plantigrades on the algae and on the mussel bed. The two settlements of larvae on the algae are apparent and the increase in the numbers of late plantigrades on the algae is reflected by a similar increase in the number of late plantigrades on the mussel bed.

It is possible to follow two age-groups of young mussels from larvae, through primary settlement, growth and subsequent appearance on the adult mussel bed (a_1, a_2, a_3, a_4 and b_1, b_2, b_3, b_4). By the time the late plantigrades had reached the mussel beds the two groups were not completely distinguishable. The two sequences of peaks represented as a_1, a_2, etc., and b_1, b_2, etc., correspond to a daily growth of *c.* 20 μ (growth of 1·25 mm from early June to early August and early July to early September).

The occurrence of plantigrades in the plankton

According to the original postulate of Maas Geesteranus (1942) and Verwey (1952), in the interval between the first settlement of mussel larvae and the recruitment of plantigrades onto the mussel beds, the early plantigrades pass through a migratory phase during which they are transported by currents between successive acts of attachment and detachment. If this is so it is to be expected that (a) plantigrades would be found in the plankton, and (b) if 'virgin' surfaces that are known to be attractive to the plantigrades were to be placed in the water, a transitory population of early plantigrades would be found attached to them.

Table 2. *Numbers of* Mytilus edulis *plantigrades taken in surface plankton hauls in the Menai Straits*, 1962

Date	No. taken	Numbers in size groups (percentage in parentheses)			
		< 500 μ	500 μ–1·0 mm	1·0–1·5 mm	> 1·5 mm
17 July	23	10 (43·5)	9 (39·1)	4 (17·4)	–
27 July	19	7 (36·8)	9 (47·3)	3 (15·9)	–
7 August	36	12 (33·3)	20 (55·5)	4 (11·2)	–
18 August	31	5 (16·1)	22 (70·9)	4 (13·0)	–
Total	109	34 (31·1)	60 (55·0)	15 (13·9)	–

In July and August 1962 four non-quantitative surface plankton hauls of 10 min duration each were taken in the Menai Straits with a tow-net. The samples were examined for the plantigrades of *Mytilus edulis* (Table 2). These samples showed that plantigrades in the size range 500 μ to 1·0 mm were present in the plankton in appreciable numbers.

Nelson (1928) reported that young *M. edulis* could remain pelagic after metamorphosis by the secretion of gas into the mantle cavity, by secretion of the byssus onto the surface film of water and by the attachment to the surface film by means of the foot or tentacles of the inhalent siphon. In the present study no plantigrades were observed with gas in the mantle cavity, but young mussels are capable of adhering to the surface film in a dish of still water as described by Nelson. Much more important, however, plantigrades possess a relatively very long and ciliated foot. They frequently protrude this foot fully, so exposing more surface to water friction. This, together with the active beating of the pedal cilia, permits the plantigrades to be transported very readily by water currents even of very low velocity. In this way plantigrades are able to enter upon a second pelagic phase after metamorphosis.

The attachment of plantigrades to a 'virgin' experimental surface

On 20 July 1962 a wooden panel with many thalli of the alga *Ceramium rubrum* attached was suspended just below the water surface from a raft moored in the Menai Straits. The thalli had been checked previously to ensure that no young mussels were attached. The panel was left undisturbed for 3 days and then re-examined and the numbers of plantigrades found was recorded (Table 3).

Table 3. *The size distribution of plantigrades attached within* 3 *days to tufts of* Ceramium rubrum *suspended in the Menai Straits* (*the tufts were suspended* 1 *m below the water surface*)

Size (μ)	No. counted	Size (μ)	No. counted
275–300	2	550–575	9
300–325	4	600–625	9
325–350	2	675–700	4
350–375	15	800–825	9
375–400	4	850–875	12
425–450	8	925–950	4
475–500	12	950–1000	4

Of the plantigrades that were found attached only those less than 375 μ in length could have settled onto the algae as larvae; the remainder must have done so as plantigrades. This observation is typical of many in which no plantigrades larger than 1000 μ were found to have migrated onto experimental surfaces.

DISCUSSION

An association between newly-settled *Mytilus edulis* and various filamentous substrates has been observed by many workers. Delsman (1911, Plate III, Fig. 21) shows a newly-metamorphosed mussel attached to *Polysiphonia* sp. Colman (1940) found young mussels attached to *Gigartina stellata* Butt. Wieser (1952) reported young mussels on *Gelidium corneum* Lamour (15/g) and *Ceramium rubrum* (24/g). Gislén (1930), Coe (1932), Harris (1946), Korringa (1951), Chipperfield (1953), Verwey (1954) and Brienne (1960) all observed young mussels attached to various filamentous algae and hydroids during their studies. Further, the field experiments of De Blok & Geelen (1958) have shown a preference for filamentous substrates by settling mussels. The importance of this as a factor in the ecology of *M. edulis* cannot be doubted.

It has also been observed that larvae seldom settle on existing beds of mussels (Verwey 1952, 1954). The so-called 'spatfall' which led to smothering of adult mussels by younger ones (Savage 1956) would presumably have been a heavy settlement of plantigrades. Thorson (1957) discussed the difficulty that the newly-settled young of lamellibranchs may have in competing with the adults. Referring to the genera *Tellina*, *Spisula* and *Cardium* he stated '. . . observations seem to indicate that an attraction of larvae to areas where the adults of their own species occur in large quantities is far from being desirable and may often be catastrophic'. The same would apply to *Mytilus*. A phase during which young *Mytilus* could grow in size before entering into direct competition with adult mussels for food and oxygen may be considered to have adaptive value. Primary settlement away from the adults, followed by growth and subsequent migration, is regarded as such an adaptive mechanism. There may also be another mechanism that acts more directly to prevent the settlement of *Mytilus* larvae on adult beds. Observations by the author have shown that adult mussels readily take in larvae that swim 'within range' of the inhalent current. In clear, filtered sea-water many larvae may then be exhaled alive, but with only a slight amount of silt in the water, and with the adults therefore producing pseudofaeces, the larvae become entangled in mucus and die. Thorson (1946) has calculated theoretically that an adult *Mytilus*, whilst filtering normally, may filter water containing 100 000 invertebrate larvae in 24 h.

ACKNOWLEDGMENTS

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SUMMARY

1. In the Menai Straits, North Wales, the mature larvae of *Mytilus edulis* settle on filamentous substrates away from the adult mussel beds. Newly-settled plantigrades have been found in large numbers attached to the filamentous red algae *Polysiphonia lanosa* and *Ceramium rubrum*. Very few plantigrades larger than 1·5 mm have been found attached to these algae.

2. Following this primary settlement the early plantigrades pass through a migratory phase during which they are transported by water currents. During this phase they may more than once attach and detach themselves from filamentous substrata. These plantigrades have been taken in plankton samples from the surface waters of the Menai Straits.

3. On reaching a size between 900 μ and 1·5 mm these young mussels attach themselves to adult mussel beds.

4. It is suggested that primary and secondary settlement in *Mytilus* is a mechanism that may reduce competition between very young and adult mussels.

REFERENCES

Brienne, H. (1960). A trial of mussel culture on ropes in the Breton pertius. *Science et Pêche*, No. 83–84.

Carriker, M. R. (1961). Interrelation and functional morphology, behaviour and autecology in early stages of the bivalve *Mercenaria mercenaria*. *J. Elisha Mitchell Sci. Soc.* **77,** 168–242.

Chipperfield, P. N. J. (1953). Observations on the breeding and settlement of *Mytilus edulis* (L.) in British waters. *J. Mar. Biol. Ass. U.K.* **32,** 449–76.

Coe, W. R. (1932). Season of attachment and rate of growth of sedentary marine organisms at the pier of the Scripps Institute of Oceanography, La Jolla, California. *Bull. Scripps Instn Oceanogr. Tech. Ser.* **3,** 37–86.

Colman, J. (1940). On faunas inhabiting intertidal seaweeds. *J. Mar. Biol. Ass. U.K.* **24,** 129–83.

De Blok, J. W. & Geelen, H. J. (1958). The substratum required for the settling of mussels (*Mytilus edulis* L.). *Arch. néerl. Zool., Vol. Jubilaire*, pp. 446–60.

Delsman, H. C. (1911). De voortplanting van der mossel. *Versl. Staat. Nederl. Zeevisch., extra bijlage* 3, pp. 75–88.

Gislén, T. (1930). Epibioses of the Gullmar Fjord. *Kristenebergs Zoologiska Station* 1877–1927, Nos. 3 and 4.

Harris, J. E. (1946). Report on antifouling research, 1942–44. *J. Iron and Steel Inst.* **150,** 143P–56P.

Jørgensen, C. B. (1946). Lamellibranchiata. In G. Thorson: 'Reproduction and larval development of Danish marine bottom invertebrates.' *Medd. Komm. Danmarks Fisk. Havundersøg. Kbh. Ser. Plankton*. Bd. 4, N.R.1.

Korringa, P. (1951). The shell of *Ostrea edulis* as a habitat. *Arch. néerl. Zool.* **10,** 32–152.

Maas Geesteranus, R. A. (1942). On the formation of banks by *Mytilus edulis* L. *Arch. néerl. Zool.* **6,** 283–325.

Nelson, T. C. (1928). Pelagic dissoconchs of the common mussel, *Mytilus edulis,* with observations on the behaviour of allied genera. *Biol. Bull., Woods Hole,* **55,** 180–92.

Savage, R. E. (1956). The great spatfall of mussels (*Mytilus edulis* L.) in the river Conway estuary in Spring 1940. *Fish. Invest.* Ser. 2 **20,** No. 7.

Spärk, R. (1919). Nogle bemaerkninger angaende yngleforhold hrs *Mytilus edulis* L. *Ved. Medd. Dansk. Naturh. Foren.* **71,** 161–4.

Thorson, G. (1946). Reproduction and larval development of Danish marine bottom invertebrates. *Medd. Komm. Danmarks Fisk. Havundersøg. Kbh. Ser. Plankton,* **4,** N.R.1.

Thorson, G. (1957). Bottom communities (sub-littoral or shallow shelf). *Mem. Geol. Soc. Amer.* **67**(1), 461–534.

Verwey, J. (1952). On the ecology and distribution of cockle and mussel in the Dutch Wadden Sea, their role in sedimentation and the source of their food supply. *Arch. néerl. Zool.* **10,** 171–239.

Verwey, J. (1954). De mossel en zijn eisen. *Faraday,* **24,** 1–13.

Warren, A. E. (1936). An ecological study of the sea mussel (*Mytilus edulis*). *J. Biol. Bd. Can.* **2,** 89–94.

Wieser, W. (1952). Investigations on the microfauna inhabiting seaweeds on rocky coasts. *J. Mar. Biol. Ass. U.K.* **31,** 145–74.

Yentsch, C. S. & Duxbury, A. C. (1956). Some of the factors affecting the calibration number of the Clarke-Bumpus quantitative plankton sampler. *Limnol. and Oceanogr.* **1,** 268–73.