ABSTRACT: Settlement and growth of the pedunculate barnacle *Pollicipes polymerus* was studied within an intake seawater system at the Scripps Institution of Oceanography, La Jolla, California. Over a 47-day period (September–October 1983), following a thorough cleaning of this system, cypris larvae settled, metamorphosed, and grew into juveniles with a mean size of $5.49 \text{ mm} \pm 2.32 \text{ SE rostro–carinal length}$, reaching a maximum size of $11 \text{ mm}$ after 47 days. During this period, the barnacles were constantly immersed in seawater at $20^\circ\text{C}$. Settlement plate experiments using terra-cotta tiles indicate that the larvae preferentially settle on scratched and pitted regions of the tile. Greatest settlement and survival to 2–3-mm stages were seen on the peduncles and capitula of adults affixed to tiles placed in the flume for 3 weeks. No settlement of larvae was observed on the valves of mussels placed into the flume for the same time period.

The pedunculate barnacle *Pollicipes polymerus* Sowerby is usually found in distinctive aggregations or clumps along the western coast of North America wherever there is a stretch of rocky cliff exposed to the open Pacific (Ricketts and Calvin 1968). The distribution of this species is quite broad, ranging from British Columbia to as far south as Punta Abreojos, Baja California (Newman and Abbott 1980). The gregarious nature of this barnacle is reportedly due to the tendency of the cypris larvae to settle and attach preferentially to the stalks of adult conspecifics. Aggregations formed from such settlement patterns purportedly afford the recently settled recruits protection not only from predation and desiccation, but also from the surging waters required for adults to feed (Barnes and Reese 1959, 1960).

Presently, there is little information concerning the larval settlement and growth rates of the juvenile stages, especially in populations from the southern end of the distributional range. Cimberg (1981) documented records that brooding activity of *Pollicipes* reveal two geographically disparate races; the boundary between races corresponds to the cold and warm temperate zones located north and south of Point Conception, California. Also, there is a lack of information concerning the specificity of substrate selection of this stalked barnacle, taking into account that it preferentially settles on adult conspecifics. If, indeed, this is the case, how are new aggregates established, especially on open substrates?

I had the opportunity to study settlement and growth of *Pollicipes* at the Scripps Institution of Oceanography under a fairly controlled situation, specifically the seawater intake system that supplies the institution. This system afforded easy access to the barnacles since there was neither tidal fluctuation nor personal danger from the large surf that washes the rocky headlands along the southern California coastline. In addition, it was possible not only to observe the settlement of *Pollicipes* larvae on terra-cotta tiles and other organisms, but also to determine the survivorship and growth of metamorphosed...
barnacles under the conditions within this seawater system.

MATERIALS AND METHODS

Study Area

The seawater intake flume is approx. 305 m in length and runs along the top length of the Scripps Pier. The system is constructed of wood (cross-sectional area approx. 0.25 m$^2$) and lined with fiberglass. The flume gradually slopes to the landward end of the pier, facilitating the flow of water to the laboratories and aquarium. The flume is covered for the most part by plywood boards that are easily removed to facilitate cleaning out fouling organisms. Water is pumped up and into the seaward end with great force. It is at this end that large numbers of Pollicipes larvae settle and grow into such large aggregations that they must be regularly scraped out to prevent the obstruction of water flow through the flume. All observations and experiments were undertaken within the first 5 m of the seaward end.

Growth Measurements

Pollicipes growth rates were measured from two 10-cm-square randomly selected samples taken from the seaward end of the flume, 14 days after the flume had been thoroughly scraped clean of barnacles and other fouling organisms (personal communication with the Scripps Maintenance Supervisor). Similar samples were removed and counted on a weekly basis over the next 40 days, until an unannounced cleaning of the flume curtailed the study. The barnacles were measured in terms of their rostro–carinal length (after Lewis and Chia 1981) using a calibrated ocular micrometer in a dissection microscope. From these weekly data, size–abundance histograms were generated. Juvenile barnacles less than 1 mm in rostro–carinal length were pooled into one size group, $R$, for recent recruits, primarily found attached to the peduncles of other juvenile individuals. From these data, a growth curve was generated. The flume remained covered, the barnacles were completely immersed in water, and the seawater temperature remained at approx. 20°C during the time interval these growth data were taken.

Settlement Plate Experiments

Some of the Pollicipes juveniles within the flume appeared to be affixed to the valves of the balanomorph Chthamalus fissus. In a sample of 34 individuals, approximately half were attached to living Chthamalus, while the remainder were attached to the fiberglass wall of the flume. From this observation, I hypothesized that Pollicipes larvae may settle preferentially on the skeletal plates of such acorn barnacles and that this selection may serve to establish new aggregations of Pollicipes on hard substrates.

An experiment was designed to test whether settlement of Pollicipes larvae onto newly metamorphosed acorn barnacles could be observed. Terra-cotta tiles (approx. 8 cm square) were chosen as settlement plates. After cleaning in a bath of dilute nitric acid and rinsing in running tap water, the tiles were affixed to a plastic frame that supported them inside the flume by $\frac{1}{2}$-in. nylon bolts. Each plate was scored in a grid pattern with an electric etcher and also pitted with the tip of a $\frac{1}{2}$-in. masonry drill to test for rugophilic behavior (Crisp and Barnes 1954).

Four plates were placed within the flume 2 m from the seaward end, at approximately the same depth from which previous growth samples were taken. The tiles were placed in the flume on 3 January 1984, checked on a daily basis for barnacle settlement, and removed on 13 February, approx. 6 weeks later. The seawater temperature remained a constant 15.5°C.

Settlement on Adult Con specifics and Other Organisms

To determine settlement rates and survivorship of recently settled cypris larvae on adult conspecifics, two 5-cm-square sections of Pollicipes aggregates were affixed by monofilament line to terra-cotta plates and placed into the flume on 1 February 1984. Two ag-
aggregate sections of similar size were concurrently placed as controls in an aquarium supplied with running seawater from the flume. These sections of barnacle aggregates were taken from aggregations growing on Dike Rock, a rocky headland located about 350 m north of the Scripps Pier. On day 1 of the experiment, the mean number of juveniles per adult *Pollicipes* was determined from a sample taken from Dike Rock. The number and sizes of juveniles affixed to adults could not be accurately determined prior to placing the section in the flume, since the adults were too closely applied to each other, obscuring numerous small juveniles. When the settlement experiment ended on 21 February, the mean number of juveniles per adult was determined for both the flume and aquarium-maintained sections by disarticulating the aggregate sections into individual adult barnacles. Finally, a section of a barnacle aggregate from Dike Rock was disarticulated into individuals to determine the mean number of juveniles per adult in order to arrive at a measurement of settlement and growth of juveniles along the open coast.

Concurrently, four living sea mussels, *Mytilus californianus* (mean length 4.5 cm), were affixed to terra-cotta tiles with monofilament line. In addition, four empty *Mytilus* valves were affixed to tiles in a similar manner. The tiles were placed into the flume for the same duration and examined with a hand lens on a daily basis for the presence of recently settled and metamorphosed *Pollicipes*.

**RESULTS**

**Growth Measurements**

The growth of *Pollicipes* juveniles within the Scripps flume is shown in Figure 1. Over a period of 47 days (1 September–17 October,
Barnacle Settlement and Growth—HOFFMAN

TABLE I
RESULTS OF SETTLEMENT OF Pollicipes polymerus CYPRID LARVAE ON BARNACLE AGGREGATES

<table>
<thead>
<tr>
<th>GROUP</th>
<th>NUMBER, n, PER AGGREGATE</th>
<th>MEAN NUMBER, X, OF ATTACHED JUVENILES PER ADULT ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>E₁</td>
<td>67</td>
<td>35.58 ± 6.02</td>
</tr>
<tr>
<td>E₂</td>
<td>75</td>
<td>32.48 ± 4.67</td>
</tr>
<tr>
<td>C₁</td>
<td>85</td>
<td>14.43 ± 1.88</td>
</tr>
<tr>
<td>C₂</td>
<td>49</td>
<td>7.18 ± 1.62</td>
</tr>
<tr>
<td>I</td>
<td>113</td>
<td>4.18 ± 0.61</td>
</tr>
<tr>
<td>X</td>
<td>130</td>
<td>9.45 ± 1.10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1–3 mm LENGTH</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11.57 ± 2.66</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8.88 ± 1.77</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.94 ± 0.18</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.44 ± 0.35</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.43 ± 0.08</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.33 ± 0.06</td>
</tr>
</tbody>
</table>

Note: Barnacle aggregates were taken from Dike Rock and placed in the Scripps flume for 3 weeks (January–February 1984). E, aggregates in flume; C, aggregates in aquarium in laboratory; I, initial aggregate from Dike Rock; X, aggregate sampled from Dike Rock at end of experiment. Attached juveniles given in terms of rostro–carinal lengths.

1983) at 20°C, Pollicipes juveniles attained a mean rostro–carinal length of 5.49 mm ± 2.32 SE. By the end of this time period, the maximum size attained by some of the barnacles reached 11 mm.

Settlement Plate Experiments

Initial settlement of Pollicipes larvae on terra-cotta tiles occurred on 31 January, 20 days after they had been placed in the flume. The newly settled barnacle spat measured 500 μm in diameter and were directly attached to the scratched regions of the tile. Acorn barnacle spat were first evident 5 days prior to the settlement of the Pollicipes. Within 7 days after observing initial colonization by Pollicipes, it became apparent that the Pollicipes were settling in a nonrandom pattern, forming distinctive aggregations with a maximum recorded number of 15 per aggregation. The barnacles settled within the scratched portions of the plate, within the pits made by the masonry bit, and also at the interfaces between the tiles and the nylon bolts that affixed them to the frames. At the end of the experiment—approx. 2 weeks after initial settlement was recorded—the juveniles had attained a maximum rostro–carinal length of 4 mm, although a mean rostro–carinal length of a random sample of 113 individuals was 1.5 mm.

The results of settlement and survivorship of the juvenile Pollicipes on adult barnacle aggregates within the Scripps flume are given in Table 1. In comparison to field samples taken at the beginning and end of the experiment, the mean number of recently settled barnacles per adult is relatively large. A large number of the juveniles from the flume sample were able to attain rostro–carinal lengths up to 4 mm, a length not achieved in juveniles from field samples or from aggregates maintained as controls in an aquarium. In addition, numerous juveniles were able to establish themselves on the capitular plates and valves of adult barnacles placed in the flume, a phenomenon that was rarely evidenced in field samples.

There was no evidence that the larvae of Pollicipes would settle and grow on the valves of Mytilus that were placed within the Scripps flume.

DISCUSSION

It is well known that cypris larvae of acorn barnacles are rugophilic, in that they preferentially settle in cracks, grooves, and pits, resulting in aggregative settlement patterns (see Crisp 1961, 1976 for a general review of the literature). It is not surprising, then, that the larvae of the pedunculate barnacle Pollicipes polymerus also demonstrate this preferential settlement behavior, especially since they are highly gregarious. However, the larvae will settle and metamorphose on such hard sub-
strates as terra-cotta tile, indicating that they are able to establish themselves on primary substrata. Within the first 2 weeks of initial settlement, the typical settlement pattern had been established; that is, the presence of conspecifics does induce the settlement of cypris larvae forming the distinctive barnacle aggregate, but on a microscopic level.

The initial settlement of *Pollicipes* larvae on terra-cotta tiles occurred 28 days after they had been placed in the flume. This was 5 days after acorn barnacle spat had been first observed on them. Although there is no conclusive evidence, perhaps the presence of these balanomorphs influenced the settlement of the *Pollicipes* larvae. This could have been tested by cleaning away any metamorphosed acorn spat and returning the tiles to the flume to determine whether *Pollicipes* larvae would then settle in the same amount of time. Unfortunately, time constraints prevented this experiment from being carried out. However, this is one of the first reported observations of settlement and metamorphosis of *Pollicipes* cypris larvae. Although Lewis (1975) proposes that a combination of chemical and tactile responses is necessary for the specific settling behavior of *Pollicipes* cypris larvae, she did not observe settlement of larvae within beakers of aerated seawater. In these laboratory experiments, the larvae failed to settle and attach to etched glass plates, to plates coated with extracts of adult barnacles, or to rocks taken from the field. Although no attachment of *Pollicipes* larvae was observed on the valves of mussels and acorn barnacles in the flume, attachment to these surfaces is common in natural populations. Within one large, mixed barnacle–mussel aggregate taken from Dike Rock in October 1983, 44% of the *Pollicipes* (*n = 125*) were attached directly to numerous specimens of *Mytilus californianus*. The presence of some *Pollicipes* adults attached to *Mytilus* may stimulate the attachment of larvae to the valves of the mussel. However, the greatest number of settling larvae was evident on the peduncles of adult *Pollicipes* placed within the flume. Not only did the cypris larvae settle in large numbers, but the overall survivorship to the 2–3-mm size class was greater than in control and field samples. Here, too, numerous juveniles settled and survived on the capitular plates, indicating that desiccation pressures experienced in tidally exposed aggregates may limit this part of the adult anatomy to colonization by juveniles.

*Pollicipes* reportedly has a rapid growth rate after settlement. In northern populations, Lewis and Chia (1981) note that barnacles from San Juan Island, Washington, grew to a mean size of 15 mm in a single year. After settling in the spring and summer, these animals grew rapidly, as much as 0.2–1 mm in rostro–carinal length per month. Once they attained a size of 13 mm, the growth rate slowed to 1–2 mm/year. Paine (1974) also observes that *Pollicipes* from the open coast of Washington initially grew slightly faster, 0.7–1.2 mm in rostro–carinal length per month, generally averaging 4.2 mm/year after their first year. Barnes and Reese (1960) attribute differences in growth rates to greater wave action and more abundant food in the open coastal environment (Lewis and Chia 1981). The growth rates of *Pollicipes* within the Scripps flume appear to be much greater than those of the northern representatives. This increase in growth rate may be due in part to being continuously submerged, thus receiving a steady supply of food. Within the flume, *Pollicipes* reached a mean size of 4 mm after only 28 days at 20°C. In contrast, barnacles from northern intertidal populations were exposed to fluctuating tidal changes, and lower water temperatures, 6.2–13.6°C (Lewis and Chia 1981). But these data also may corroborate the reports of Cimberg (1981) that there are two distinctive geographical races of this widely distributed barnacle.

Other species of pedunculate barnacles demonstrate rapid growth rates. The opportunistic *Lepas anatifera* and *Conchoderma virgata* require from less than 17 to 50 days, respectively, to complete a life cycle at tropical water temperatures (MacIntyre 1966). Seventeen days after a newly painted marker buoy was laid off the east coast of Australia, reproductive specimens of *Lepas* (23 mm capitular length) were recovered. The rapid growth rate evidenced in recently settled *Pollicipes* juveniles also may be an opportunistic strategy.
selecting for survival in the rocky midtidal zone and giving *Pollicipes* a competitive edge in establishing their aggregative patterns.

ACKNOWLEDGMENTS

I wish to thank William A. Newman of the Scripps Institution for the facilities and favors afforded me during the course of this investigation. Also, my appreciation to Don Wilkie, Director of the Scripps Museum and Aquarium, for allowing me the opportunity to pursue investigations within the Scripps flume. I am most grateful to Cindy Lewis and Bryan Burnett for making themselves available to discuss and exchange ideas, to read drafts of papers, and for their friendship. Finally, I dedicate this paper to my wife, Marcia, whose tireless support and love helped make this project a reality.

LITERATURE CITED


