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Community effects of the invasion of a new intertidal hydroid, *Samuraia tabularasa*, in the Gulf of California

Mangin, Katrina Leslie, Ph.D.

The University of Arizona, 1991
COMMUNITY EFFECTS OF THE INVASION OF
A NEW INTERTIDAL HYDROID, SAMURAIA TABULARASA,
IN THE GULF OF CALIFORNIA

by
Katrina Leslie Mangin

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY
In Partial Fulfillment of the Requirements
For the Degree of
DOCTOR OF PHILOSOPHY
In the Graduate College
The University of Arizona

1991
As members of the Final Examination Committee, we certify that we have read the dissertation prepared by KATRINA LESLIE MANGIN entitled Community effects of the invasion of a new intertidal hydroid, Samurais tabularasa, in the Gulf of California.

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.

James H. Brown 12/11/90

Donald A. Thomson 12/11/90

Conrad A. Istock 12-20-90

J. Bruce Walsh 12/11/90

Judith Bronstein 12/11/90

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

Dissertation Director

3/29/91
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ABSTRACT

In 1984, a previously unreported species of hydroid, *Samuraia tabularasa* Mangin, 1991, appeared in the rocky intertidal zone of the northern Gulf of California, Mexico. *Samuraia tabularasa*, whose common name is the samurai hydroid, is a new genus and species in the athecate family Hydrocorynidae, class Hydrozoa, phylum Cnidaria. A key character that refers this species to a new genus is its mode of sexual reproduction by eumedusoids. Additionally, *Samuraia tabularasa* is able to withstand extreme desiccation in the intertidal zone, an evolutionary novelty for hydrozoans. Since its appearance, the samurai hydroid has had a dramatic effect on the community by causing the death of barnacles (*Chthamalus anisopoma*), the dominant occupier of space in this system, and thereby increasing the amount of primary substrate available for use by other species. Each hydroid colony is surrounded by an elliptical clearing approximately 2.5 cm in diameter that is kept clear of adult barnacles by causing the death of all newly settled barnacles that settle within reach of its tentacles. The clearings are maintained free of barnacles for sufficient time to allow for the growth of crustose algae (*Ralfsia* sp., and others) and subsequent grazing by limpets (*Collisella strongiana*) that live in the clearings. The addition of the samurai hydroid thus has led to an increase in local abundance of these two native species. This study shows that communities can be very resilient to the changes caused by the
addition of a new species. Not only was there "room" for the samurai hydroid, but its activity promoted local species diversity by increasing habitat complexity. 

Hydroid mortality has exceeded recruitment from 1985-1990. This population decline, along with a 60% decrease in the average area of a hydroid clearing, may be associated with the hydroid's status as a recent invader and suggests that it is no longer favored in this region.
CHAPTER 1

INTRODUCTION

This dissertation is composed of two separate but related sections. It begins with a narrative history of the study (Chapter 2), meant for a general audience, and for those interested in the process of doing a field research study. This chapter is a slightly modified version of an article in Natural History Magazine (Mangin 1990). It is a story of the discovery of a new species, the samurai hydroid, *Samuraia tabularasa* (Fig. 1) and a previously unknown phenomenon, the killing of barnacles in such a way that long-lasting patches of bare rock are left exposed on rocks otherwise densely covered with barnacles. The first section also includes the taxonomic description of the samurai hydroid (Chapter 3), which is currently in press in a symposium volume from the 5th International Conference on Cnidarian Biology (Southampton, U.K.), and in the journal Hydrobiologia (Mangin 1991). This chapter includes a description of the life cycle and morphology of the samurai hydroid, and a justification for its referral to a new genus. It is a classical, taxonomic description and not a phylogenetic analysis.

Section two (Chapters 4 & 5) of the dissertation describes ecological field experiments done in the Gulf of California, near Puerto Peñasco, Sonora, Mexico. The experimental results describe both the evidence for the hydroids causing the
Fig. 1. The samurai hydroid, *Samuraia tabularasa*.

A colony of one polyp of the samurai hydroid, *Samuraia tabularasa*, with immature eumedusoids arising from the hydorhiza.
death of barnacles (Chapter 4), and the network of species interactions that were established upon the appearance of the hydroid (Chapter 5). Because the middle intertidal zone where the hydroid occurs is normally dominated by barnacles, the clearings formed by the hydroid have opened space for other species to use, particularly algae that grow in the absence of barnacles, and limpets that graze on the algae. This effect of hydroids is of interest for three main reasons. First, hydroids do not normally kill barnacles or live on exposed rock in the middle intertidal zone. Second, as this hydroid is only recently abundant, and perhaps newly invaded, into a previously-studied community, the effect on the community of the hydroid provides a model for what occurs when a species is added to a community. Third, interactions among sessile invertebrates in the marine intertidal have been a focus of many classic and current ecological questions that address the processes that allow species to coexist. This habitat has received unusual attention due to the largely two-dimensional nature of the rock surface, where space is the primary limiting resource that translates very directly into food for filter feeders, and to survival and reproduction.

This dissertation will not answer certain questions that will probably occur to the reader. These include the following: Do the hydroids kill barnacles directly or indirectly, and by what mechanism? The evidence is strong that the hydroid kill barnacles directly (Chapter 4); however, I have never seen a predation event. How can the hydroids withstand desiccation in the intertidal? I was unable
to address this question. Where did the hydroids come from, and where else do they occur? An interesting feature of studying a new phenomenon, and a previously unreported species, is that no baseline data exist, and the information emerges in pieces, whose significance is sometimes not clear until more of the whole is known. The hydroid has never been seen before and so I only know that it occurs where I have found it so far, along the NE coast of the Gulf of California. However, I presume that it occurs elsewhere and did not arise de novo in 1984 in the northern Gulf. It may play a less noticeable role in its source habitat. Its appearance in 1984 in the northern Gulf of California may be associated with unusual current conditions and ocean temperatures associated with the El Niño year of 1982-83 (Chapter 5).
CHAPTER 2

A POX ON THE ROCKS

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It was another baking hot summer day in Puerto Peñasco, on Mexico's Sonoran coast. Through the shimmering haze I could see the mountains of Baja California, sixty miles away across the Gulf. I was just about to take a break from the heat when a research colleague, Pete Raimondi, called me over to look at a strange pattern - one of the barnacle-covered rocks appeared to have a kind of "pox". Here and there, amid the dense growth of barnacles, were half-dollar sized patches of bare rock free of barnacles. The patches made a regular and distinct pattern, unlike anything we had ever seen before. We looked more closely at individual clearings and noticed that in the center of each clearing there was a tiny, coal-black spot about 2-3 mm in diameter, about the size of a pin-head. Although it seemed improbable to us at the time, we wondered if the black spots were somehow responsible for the clearings around them. Barnacles tend to monopolize space on rocks. Those species that do co-occur with barnacles tend to do so by either living in the interstices between between barnacles, or by occuring
transiently in small, ephemeral clearings which result from predation on barnacles, or from random, physical disturbance.

The pattern of clearings was unusual for a number of reasons. First of all, the clearings were round, suggesting that a non-random process had created them. They also were larger than most accidentally-caused clearings would be, and they had persisted for long enough to grow algae. It looked like a classic case of allelopathy, a phenomenon in which an organism inhibits the growth of its neighbors by releasing a toxin. This seemed unlikely, however, because it required a chemical to work at a distance to kill barnacles, and one that would not wash away in the water. And, why would the black spots be creating a large area which they did not then occupy?

We set up the following experiment to see if the black spots were actually responsible for the clearings. During a low tide when the rocks were exposed, we removed the black spots from the center of some clearings and left others intact. It was easy to remove the black spots by carving them out of the rock with a pen knife. We mapped the clearings onto plastic sheets so that we could keep track of their progress over time. A year later we found a striking result. The clearings had completely disappeared wherever we had removed the black spots, but had remained virtually unchanged in areas with the black spots left intact.

The results of a second experiment were even more surprising. We wanted to know if the black spots could create the clearings as well as maintain them. To
test this, we transplanted a few of the black spots, using Superglue, into dense patches of barnacles. We did the same with Superglue alone to control for possible toxic effects of superglue on barnacles. We did not expect this experiment to work, but a year later we saw that some of the transplants had developed clearings around them, while the areas with Superglue alone had disappeared. Now we had evidence that the black spots could actively create the clearings. However, we still had no idea what they were or even if they were alive.

By now I was so impressed with the power of the black spots to kill barnacles that I had decided to pursue the phenomenon as a dissertation topic. The effect of the black spots was absolute. All barnacles within a certain radius of the spot died. What were the black spots? Were they alive? And how were they managing to keep an area at least an order of magnitude larger than themselves free of barnacles, animals which are notoriously difficult to keep off of any hard surface in shallow seas?

A number of months later, I found that the black spots, which I had been calling "little black units" (or "LBUs") in the meantime, were actually tiny animals called hydroids, in the phylum Cnidaria, related to jellyfish, corals, and anemones. I was surprised to find that the LBU was an animal, and especially that it was a soft-bodied animal like a hydroid. I was convinced that it was a type of algae, partly because there was algae growing in the rest of the clearing, and because
many species of algae can survive being completely dried out when exposed at low tide. Hydroids, like anemones and other soft-bodied animals, are usually found subtidally, where they are always submerged in water, or in the lowest intertidal zone where they are only exposed to dry air for brief periods of time. This species of hydroid was occurring in the middle intertidal zone, where it could be exposed for up to six hours at a time, along one of the most hot and arid coastlines of the world. It is still a mystery how it is able to survive such harsh conditions.

It had taken me a year to figure out not only that the black spots were animals, but that they were alive. The reason for this is that I hadn’t expected the spot to be an animal, and I certainly hadn’t expected it to be a soft-bodied animal like a hydroid. For this reason, I wasn’t properly looking at the specimens I collected. I didn’t watch the spots carefully when they were submerged because I hadn’t expected them to move, and I didn’t collect them properly (by carefully digging them out of the granite intact, and keeping them cool until I could observe them under the scope) because I didn’t envision them as the fragile creatures that they are. I eventually learned how to collect an individual animal so that it was left intact, and I could then observe it alive, and submerged in water, under a microscope.

What I saw through the microscope was a beautiful, delicate animal formed of slender translucent stalks each of which had a crown of mace-like tentacles
(Fig. 1). The stalks were attached to a small, black cup-like base, the structure I had been calling the LBU. The black base is all I had ever seen because, when they are exposed on the reef during a low tide, the soft body of the hydroid retracts into the shallow cup at its base and dries out. In this state, the spot is indistinguishable as anything alive.

I could not find a description of the hydroid in any books on marine invertebrates, including one specific to invertebrates of the Gulf of California intertidal zone. Hydroid systematists work on specific families so I found the names of the appropriate people I needed to send specimens to, Jean Bouillon in Belgium and Ferdinando Boero in Italy. Both wrote back right away and told me that they had never seen a hydroid of its type before and that it appeared to be a new species, and probably a new genus, belonging to a small family of hydroids called the Hydrocorynidae.

Not only is the hydroid a new genus, but it also seems to have appeared only recently in the northern Gulf of California, probably not long before 1984 when Pete and I first noticed the clearings on rocks near Puerto Penasco. A number of other researchers worked in this region prior to 1984; yet none ever noticed the pattern of clearings created by the hydroid. Additionally, three of the researchers, Pete Raimondi, Curt Lively and Mike Dungan, had specifically studied aspects of the ecology of barnacles in the same general area prior to the appearance of the hydroid. The mosaic-like pattern created by the hydroids is
sufficiently striking that it is unlikely that it would have been missed by all previous workers in this region. Additionally, hydroids have appeared in some long-term sites that were established before 1984 and monitored since then.

Knowing the recent history of the hydroid in this particular region makes it an ideal candidate for understanding what happens when a new species invades a resident community. What has happened to other species in the community since the invasion? Have any native species become extinct? And, most interestingly, is there anything about this particular community that would suggest that one of the components is a recent addition?

The hydroid has found a new region in which it is highly successful. It can reach densities of 160 individuals per square meter. At one clearing per individual hydroid, approximately ten percent more space on the rocks is made available to other species that would otherwise tend to be crowded out by barnacles. The hydroids have had a dramatic effect on the community by creating a patchwork of islands of barnacle-free space, and by maintaining these islands long enough that they become miniature communities of their own. The clearings maintained by the hydroids grow a covering of algae (mainly Ralfsia sp.), which is then grazed upon by snails (the limpet, Collisella strongiana) that live in the clearings.

Algae and limpets do occur amid barnacles in the absence of the hydroids, but in much lower numbers and for shorter amounts of time. Barnacles are able to monopolize space on rocks by producing vast numbers of larvae that rain out of
the plankton throughout the spring and summer. These larvae settle out and quickly fill in any break that occurs in the barnacle cover when barnacles are eaten by a passing predator, or broken off by random physical disturbance. In the absence of the hydroids, limpets are largely restricted to rock crevices, in which predatory snails keep the rock surface free of barnacles by eating the barnacles that occur within or near the crevices. Here, as well as in the clearings maintained by the hydroids, there is enough algae and space to support limpets. Hydroids provide limpets with a suitable habitat away from crevices because hydroids are common on the flat upper surfaces of rocks. Thus, the introduction of the hydroids has allowed limpets to increase in abundance in an area where they used to be rare.

Hydroids appear to benefit limpets by providing them with space and food. I did experiments in which I followed the fate of limpets in clearings in which I had removed hydroids and found that, while limpets disappeared as barnacles covered the clearings, they persisted in clearings with hydroids still present. I also found that limpets persisted longer in clearings maintained by hydroids compared to clearings caused by random disturbance or by predation. Limpets in clearings not maintained by hydroids become completely surrounded by barnacles and eventually disappear.

I wondered what the reciprocal effect was of limpets on hydroids. I found that when I removed limpets from clearings around hydroids, a film of algae grew
over the clearings, and fewer barnacles settled in the clearings. If hydroids are eating young barnacles, as I suspect, then limpets are potentially benefiting hydroids by grazing algae in the clearings and increasing the amount of food (young barnacles) that settles in the vicinity of the hydroids.

The hydroids appear to kill young barnacles by "minesweeping" a circular area with their tentacles when submerged at high tide. I've watched this behavior when snorkeling, and it looks like the hydroids are using the surge of the waves to whip their tentacles around. The end result is that the clearings that surround them are not actually circular in shape, but elliptical in the direction of wave wash.

Other than observing the behavior mentioned above, I still do not know exactly how the hydroids kill barnacles, or why. It is likely that the hydroids are stinging barnacles with their tentacles. Each tentacle is heavily armed with stinging cells called nematocysts. The triggers of the nematocysts jut out of the surface of the tentacles, giving them the appearance of medieval mace. If the triggers are released, the nematocysts fire both a barbed spear and a toxin, which can paralyze other organisms. I suspect that the hydroids use this mechanism to sting newly settled barnacles, pull them off of the rock, and eat them.

Hydroids and limpets affect each other indirectly because each partner is responding to a resource provided by its partner, rather than to the partner itself. For example, the hydroid is responding to the presence of additional young barnacles in its vicinity, rather than to the presence of the limpet. And the limpet
is responding to the presence of space free of barnacles, and to algae growing there, rather than to the presence of the hydroid. It's not who is providing the resources, but the resources themselves, that is important to the persistence of the interaction between the two species. These sorts of indirect interactions are bound to be ubiquitous in all natural communities, and probably very important in the resilience of communities to changes in species composition.

I still do not know where the hydroids came from, or where else in the world they occur. There are a number of possibilities for their origin in the Gulf. They may have arrived on their own by currents, perhaps currents associated with the strong El Niño of 1982/1983; or they may have been introduced by human activities such as shipping or oyster farming. They also may have been present but so rare until recently that they were never noticed.

The hydroid's introduction in the Gulf may be related to the strong El Niño year of 1982/1983. El Niños are unusual current patterns that periodically occur in the Pacific Ocean. They can affect the Gulf of California by causing warm water currents to move farther north than they would in a non-El Niño year. Larvae from a more southerly population of the hydroids may have been transported northward into the Gulf in a warm-water mass associated with El Niño. Additionally, warmer than usual ocean temperatures may have favored their survival upon arrival.
Oyster farming began near Puerto Peñasco in 1980. A non-local species of oyster is farmed, primarily a species from northern California. However, the farmers experimented at first with oysters from various countries, including Peru. The oysters arrive on wooden flats that can have other associated fauna. The samurai hydroid could have come in on one of these batches.

Knowing that the hydroid is a recent addition to this community demonstrates how quickly a species can become integrated into a web of interactions in a new community. It argues against viewing communities as co-evolved entities in which all the interactions between species that make up the community are seen as products of evolution.

We generally assume that the species found in a particular community are long time residents with a history of association with one another. This shared history is predicted to have led to coevolution and consequent stability among species in the community. In contrast, newly introduced species are expected to disrupt communities, partly due to a lack of shared history with native species. However, all species were introduced at some point, either by speciation, or natural range expansion, or by human activity. We know very little about whether species in a community work together as a unit, and whether the specific identities of species are important in the functioning of that unit. At an extreme level, it would be interesting to know how many species there would be in the world if all species had a worldwide distribution.
The story of the hydroid's success in this community suggests that communities can be very resilient to the changes caused by the addition of a new species. Not only was there "room" for the hydroid in this community, but the hydroid's activity has promoted local species diversity by making the habitat more complex and allowing other species, limpets and algae, to increase in abundance in the vicinity of the hydroids. A clue to the ready integration of the hydroid could be that, by causing the death of barnacles, it plays a role already performed in the community by other processes. The community was thus primed for the activity of the hydroid. The interactions between species are no more or less finely tuned since the appearance of the hydroid. Many communities probably function in this way, as flexible composites of species whose number and identity can vary to produce equally viable combinations.
Summary

Samuraia tabularasa, the samurai hydroid, a previously unreported genus and species of athecate hydrozoan, family Hydrocorynidae, is described, based upon field and laboratory observations. Colonies live attached to rocky substrates in the middle of the intertidal zone in the northern and central Gulf of California, Mexico. The principal characters that allow this species to be referred to a new genus are associated with its mode of sexual reproduction by eumedesoids that can remain attached to the colony, or be released as ephemeral, rudimentary structures. This is in contrast to the feeding, free medusae produced by the two species of the other genus, Hydrocoryne, in the family Hydrocorynidae.
Introduction

The family Hydrocorynidae (W.J. Rees 1957) has previously included just two species: *Hydrocoryne miurensis* Stechow 1907, and *H. bodegensis* Rees, Hand & Mills 1976. The polyp stage of *H. miurensis* was described by Stechow (1907, 1909) followed by descriptions of the medusa by Uchida (1932) and Uchida & Nagao (1967). J.T. Rees *et al.* (1976) described the life cycle and morphology of *H. bodegensis* and compared them with those of *H. miurensis*. More recently Kubota (1988) surveyed the differences between the two *Hydrocoryne* species.

*H. bodegensis* and *H. miurensis* are both found in temperate waters. *H. bodegensis* was originally described from Bodega Bay, California (J.T. Rees *et al.* 1976) in the East Pacific. It was later reported by Margulis and Karlsen (1980) and Kubota (1988) from the West Pacific from Petra Velikogo (Peter the Great Bay), Sea of Japan, Soviet Union. *H. miurensis*, in contrast, is known only from the West Pacific from numerous sites along both coasts of northern and central Japan, Sea of Japan and the North Pacific (Uchida & Nagao 1967; Kubota 1988), and not from North American coasts. *H. miurensis* occurs in both the lower intertidal and subtidal zones (Kubota 1988), while *H. bodegensis* is exclusively subtidal (J.T. Rees *et al.* 1976).

The family Hydrocorynidae (W.J. Rees 1957) is notable for large hydranths (up to 6 cm) with a single ring of exclusively capitate tentacles; a hard, encrusting
base; a thick mesoglea; and medusa buds arising in groups on branched pedicels from the proximal half of the hydranth (Bouillon 1985). The present paper describes a new genus of hydroeorynid, *Samuraia tabularasa*, n.g., n.sp., the samurai hydroid, from the Gulf of California, Mexico, and emends the family diagnosis of Hydrocorynidae to include the unique characters of this new genus.

**Study Site**

Colonies of the samurai hydroid were collected intertidally from 0 to 0.3 m above mean low water at Pelican Point, 31°20'N, 113°40'W. Pelican Point is an exposed, granitic promontory 10 km NW of Puerto Peñasco, Sonora, Mexico, on the NE coast of the Gulf of California. The climate of the intertidal zone in this region is highly seasonal due to the influence of the adjacent Sonoran desert. Air temperatures range between monthly means of 11.8° C in January and 30° C in August; while sea surface temperatures range between monthly means of 13.8° C in January and 29.4° C in August (Thomson 1989).

Colonies were collected intact, using a pen-knife to carve the base of each colony out of small pits in the granite rock to which they were attached. They were placed loose in small containers in sea water prepared from a mix (Instant Ocean), maintained at 22° C, and aerated vigorously. They were fed two-day-old *Artemia*
nauplii every 1-2 days for 2-6 hours, the water being changed after each feeding period. Healthy, reproductive colonies were cultured for up to four months.

Materials and Methods

I initially sent preserved, reproductively mature colonies to two hydroid systematists: Dr. Jean Bouillon of Brussels, Belgium, and Dr. Ferdinando Boero of Lecce, Italy. Both independently concluded that the hydroid appeared to be a new, previously unreported genus in the family Hydrocorynidae. Each based his diagnosis of a new genus on two features of the reproductive structures unique to the family: gonozoids that 1) are retained on the parent colony until mature, and 2) originate on the stalk (hydrocaulus) of the polyp as well as off the base (hydrorhiza) of the colony. I later found that, upon reaching maturity, the gonozoids could either be retained on the parent colony through maturity and release of gametes, or be released from the colony as short-lived, non-feeding, rudimentary medusae called eumedusoids.

I derived the mean values for dimensions of the samurai hydroid from measurements of colonies collected in April-May, 1989. Hydranth and overall-colony dimensions were based on 37 separate colonies, measured in the field; while eumedusoid dimensions are based on 18 eumedusoids produced by 6 colonies collected infertile in the field and cultured in the laboratory until mature.
eumedusoids were produced. Student's t-test was used to analyze differences in size between mature male and female eumedusoids.

Three hydranths and ten mature eumedusoids (four attached, six released) were examined live for nematocyst type and distribution using light-transmission and phase-contrast microscopy. Student's t-test was used to determine if shared nematocyst types differed significantly in mean size between hydranths and mature eumedusoids. Not all the measurements were taken on all individuals.

I examined four preserved specimens of Hydrocoryne miurensis from Japan for comparison to the polyp stage of the samurai hydroid.

Taxonomic Diagnosis

The discovery of a new hydrocorynid has required a modification of the family diagnosis. That of Bouillon (1985) is now emended to include the presence of eumedusoids; their origin on the hydrorhiza; their lack of mouth, tentacles, ocelli, and gastric peduncle; and the position of gonads surrounding the manubrium.

Order Capitata Kühn, 1913
Superfamily Corynoidea Johnston, 1836
Family Hydrocorynidae W. J. Rees, 1957
**Emended diagnosis:** Corynoidea emerging from a thick encrusting base. Hydranths large (recorded up to 6 cm), columnar, mesoglea thick, with single ring of capitate tentacles. Medusa generation free and fully-formed, or eumedusoid and either retained or liberated. Medusa buds arising in clusters or singly from hydrorhizal pedicels or from proximal half of hydranth. Medusae and liberated eumedusoids small, 1-3 mm long, bell-shaped, enlarged at top. Gonads interradial in medusae, surrounding manubrium in eumedusoids. Manubrium conical to spherical, with or without a gastric peduncle. Marginal tentacles present in medusae, capitate, armed with hemispherical clusters of cnidocysts scattered irregularly. Abaxial ocelli when present situated on wide, clasping tentacle bulbs (After Bouillon 1985).

**Samuraia GEN. NOV.**

Figs 2-6, Tables 1-3

**Diagnosis:** A hydrocorynid with eumedusoids, which can be retained on the colony or be liberated, originating on unbranched pedicels on the hydrorhiza. Other characters are those of the single included species.

**Type species:** *Samuraia tabularasa* sp. nov., by monotypy.

**Etymology:** I have named the genus after the Japanese samurai warriors, due to the hydroid's presumed aggressive behavior towards barnacles which it appears to slay with a sword-like motion of its tentacles (Mangin 1990).
samurai were chosen as namesakes also due to the similarity of *Samuraia* to its Japanese relative, *Hydrocoryne miurensis*.

*Samuraia tabularasa* SP. NOV.

Figs 2-6, Tables 1-3

**Species description:** Colonies unbranched (Fig. 2), arising from a hard encrusting base, 2-6 mm across, usually shallow cup-shaped. Hydrorhizal plate circular. Colonies small, 1-3 hydranths/colony (Table 1). Hydranths highly extensile, from 1 mm to 3 cm. Single terminal ring of capitate tentacles (Fig. 3). Tentacle number varied, commonly 11-22 ($\bar{x} = 17$). Extended tentacles 0.4-0.6 mm long. Nematocysts of hydranth tentacles comprising two sizes of stenoteles, and two sizes and types of microbasic euryteles one with a solid inclusion (Table 2).

Colonies dioecious. Eumedusoids retained on the colony (Fig. 4) or liberated (Fig. 5), borne on unbranched pedicels arising directly from the hydrorhiza; round to bell-shaped, longer than wide, with four knobby, darkly-pigmented radial canals, each ending in a swollen marginal bulb; lacking tentacles, a mouth, and a peduncle. Manubrium varied in shape and size, conical and extending length of bell in attached eumedusoids, and 1/3 to 3/4 length of bell after release. In spent eumedusoids, manubrium long, slender and
TABLE 1. Morphological dimensions of *Samuaria tabularasa*.

<table>
<thead>
<tr>
<th>STRUCTURE</th>
<th>$\bar{X} \pm 1$ S.D.</th>
<th>RANGE</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Hydroid Colony</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Base length (mm)</td>
<td>3.73 ± 0.98</td>
<td>2.33 - 6.00</td>
<td>37</td>
</tr>
<tr>
<td>No. polyps/colony</td>
<td>1.63 ± 0.62</td>
<td>1 - 3</td>
<td>16</td>
</tr>
<tr>
<td>No. eumedusoids/colony</td>
<td>7.36 ± 5.75</td>
<td>0 - 17</td>
<td>14</td>
</tr>
<tr>
<td>No. tentacles/hydranth</td>
<td>17.55 ± 3.05</td>
<td>13 - 22</td>
<td>29</td>
</tr>
<tr>
<td>Tentacle length (mm)</td>
<td>0.50 ± 0.07</td>
<td>0.43 - 0.63</td>
<td>16</td>
</tr>
<tr>
<td><strong>Attached Eumedusoid</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length (mm)</td>
<td>0.65 ± 0.08</td>
<td>0.51 - 0.78</td>
<td>14</td>
</tr>
<tr>
<td>Width (mm)</td>
<td>0.63 ± 0.07</td>
<td>0.47 - 0.79</td>
<td>12</td>
</tr>
<tr>
<td><strong>Liberated Eumedusoid</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length (mm)</td>
<td>1.14 ± 0.12</td>
<td>0.90 - 1.30</td>
<td>18</td>
</tr>
<tr>
<td>Width (mm)</td>
<td>0.82 ± 0.13</td>
<td>0.55 - 1.01</td>
<td>17</td>
</tr>
</tbody>
</table>
TABLE 2. Dimensions of nematocysts found in hydranth tentacles and eumedusoids of *Samuralia tabularasa*. Numbers are length (μm ± 1 S.D.) × width (μm ± 1 S.D.) over the ranges and numbers of nematocysts examined. Three hydranth tentacles and six newly liberated eumedusoids were examined.

<table>
<thead>
<tr>
<th>LIBERATED STRUCTURE</th>
<th>HYDRANTH TENTACLES (3)</th>
<th>EUMEDUSOIDS (6)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>NEMATOCYST TYPE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small Stenoteles</td>
<td>15.14±0.86 × 8.2±0.68</td>
<td>14.35±1.0 × 10.10±0.85</td>
</tr>
<tr>
<td></td>
<td>(14.4-16.4) 16, (7.2-9.2) 10</td>
<td>(12.3-16.4) 17, (9.2-12.3) 11</td>
</tr>
<tr>
<td>Microbasic Euryteles</td>
<td>11.22±0.66 × 4.81±0.69</td>
<td>11.38±1.05 × 4.24±0.25</td>
</tr>
<tr>
<td></td>
<td>(10.3-12.3) 20, (4.1-6.2) 20</td>
<td>(10.3-13.3) 21, (4.1-4.9) 15</td>
</tr>
<tr>
<td>Large Stenoteles</td>
<td>24.56±0.33 × 15.40±0.83</td>
<td>none</td>
</tr>
<tr>
<td></td>
<td>(23.5-26.6) 17, (14.4-16.4) 10</td>
<td></td>
</tr>
<tr>
<td>Microbasic Euryteles</td>
<td>15.02±1.43 × 6.15±0.84</td>
<td>none</td>
</tr>
<tr>
<td>(with inclusion)</td>
<td>(14.4-16.4) 21, (5.2-8.2) 21</td>
<td></td>
</tr>
<tr>
<td>Basitrichous Haplonemes</td>
<td>none</td>
<td>8.82±1.10 x 5.42±0.56</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(6.1-10.3) 55, (4.1-6.2) 27</td>
</tr>
</tbody>
</table>
Fig. 2. A colony of *Samuraia tabularasa*.

A colony of the samurai hydroid with three hydranths arising from a shallow cup-shaped base. From life, and photograph of live individual.
Fig. 3. Tentacle crown of *Samuraia tabularasa*.

A single hydranth of the samurai hydroid with single tentacle enlarged. From photograph of live individual.
Fig. 4. Attached eumedusoids of *Samuraia tabularasa*.

a. Immature, with undeveloped gonads; sex unknown. b. Ripe female with eggs. From life, and from photographs of live individuals.
Fig. 5. Liberated eumedusoids of *Samuraia tabularasa*.

a. a newly liberated, releasing eggs. b. a spent, a few hours after liberation from colony. From photographs of live individuals.
hooked, less commonly small and round. Gonads completely surrounding the orange manubrium. Female eumedusoids containing c. 80 pale orange eggs, not in rows, with 6-8 eggs spanning height of manubrium. Male eumedusoids containing an opaque white to pale yellow mass surrounding manubrium. Mature attached eumedusoids 0.5-0.8 mm long; newly-liberated eumedusoids 0.9-1.3 mm long. Nematocysts of eumedusoids occurring in marginal bulbs and in clusters of 1-5 scattered over entire exumbrellar surface. Nematocyst types comprising a large stenotele, a basitrichous haploneme, and a microbasic eurytele (Table 2); stenoteles in liberated eumedusoids rare to absent.

**Type Locality:** Pelican Point, 31°20'N, 113°40'W, 10 km NW of Puerto Peñasco, Sonora, Mexico, NE Gulf of California. Colonies collected intertidally on granite bench substrate 0-0.3 m above mean low water.

**Range:** Known only from the coast between Puerto Peñasco and Guaymas, Sonora, Mexico.

**Type Material:** The following have been deposited at the United States National Museum of Natural History, Smithsonian Institution, Washington D.C.: Holotype: A single colony with two hydranths and numerous small, immature eumedusoids on the hydrorhiza. Collected and preserved in the field June, 1989, NMNH# 86835. Paratypes: 1) Attached eumedusoids (NMNH# 86836): Three separate colonies with mature eumedusoids off hydrorhizae and hydranths. Colonies collected in the field February, 1989, raised to eumedusoid maturity in
the laboratory, and preserved May, 1989. Female eumedusoids with eggs. 2) Five liberated eumedusoids less than 24 hours old (NMNH# 86837): Produced by colonies collected from the field in April and reared in the laboratory until eumedusoids were liberated in May, 1989. One eumedusoid with eggs. Different shapes of manubria are represented.

**Etymology:** *Tabularasa* is from the Latin phrase, *tabula rasa*, which means blank slate. The species is named for its most distinctive trait: the circular clearing of bare rock which surrounds each colony (Mangin 1990; and Chapter 2) on rocks otherwise covered with the acorn barnacle, *Chthamalus anisopoma* (Pilsbry 1916).

**Results and Discussion**

**Taxonomic Affinities.** *S. tabularasa* is referred to a new genus on the basis of several characters, both of the polyp and medusa stage (Table 3). However, a primary distinction from *Hydrocoryne* is that *S. tabularasa* reproduces sexually through eumedusoids which can remain attached to the colony or be liberated, while both species of *Hydrocoryne* reproduce sexually through free medusae. Traditionally, genera of hydroids have been distinguished on the basis of whether gonophores remain fixed or are liberated as free medusae (W. J. Rees 1957). However, some workers question this practice because of the apparent continuum
TABLE 3. Morphological characters that vary between *Samuraia* and *Hydrocoryne*. From Uchida & Nagao (1967), J.T. Rees et al. (1976), Kubota (1988), and this paper.

<table>
<thead>
<tr>
<th>Genus</th>
<th><em>Samuraia</em></th>
<th><em>Hydrocoryne</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Hydranth:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td># tentacles/hydranth</td>
<td>11-30 (46)</td>
<td>30-70</td>
</tr>
<tr>
<td>size of extended hydranths</td>
<td>up to 3 cm (10)</td>
<td>up to 6 cm</td>
</tr>
<tr>
<td><strong>Sexual stage:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>placement of gonozoids</td>
<td>fixed &amp; liberated eumedusoids</td>
<td>free medusae</td>
</tr>
<tr>
<td>arrangement of gonads on manubrium</td>
<td>off hydrorhiza &amp; proximal half of hydranth</td>
<td>proximal half of hydranth</td>
</tr>
<tr>
<td>tentacles</td>
<td>absent</td>
<td>4</td>
</tr>
<tr>
<td>ocelli</td>
<td>absent</td>
<td>4 abaxial</td>
</tr>
<tr>
<td><strong>Nematocysts of medusae or eumedusoid:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>desmonemes</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>atrichous isorhizas</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>small stenoteles</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>microbasic uryteles</td>
<td>present</td>
<td>absent</td>
</tr>
</tbody>
</table>
which exists between the two character states (e.g., Petersen 1979), and the presence in certain species of gonophores which can remain fixed or be liberated (hence termed eumedusoids); for example in *Orthopyxis integra* (see Stefani 1959), and as here described in *S. tabularasa*.

There are numerous morphological differences between the eumedusoids of *Samuraia* and the free medusae of *Hydrocoryne*, as well as developmental differences in the degree of retention of the medusa. The morphological differences are the following, found in the eumedusoids of *Samuraia* and not in the medusae of *Hydrocoryne*: 1) Origin on unbranched pedicels off the hydrorhiza, 2) Gonads surrounding manubrium, 3) Lacking tentacles, ocelli, mouth and peduncle, and 6) Irregular, knobby radial canals. In contrast, the free medusae of *Hydrocoryne* originate on the proximal half of the hydranth, have straight radial canals, tentacles, ocelli, a mouth, a peduncle (in mature medusae), and gonads placed interradially on the manubrium (Uchida & Nagao 1967, J. T. Rees *et al.* 1976, Kubota 1988).

Additionally, the eumedusoids of *Samuraia* are retained on the colony until gonads are fully developed, at which point they either remain attached, or are released to swim in the plankton. In both cases, all gametes are released over the next 24 hours. In contrast, in *Hydrocoryne* the medusae are released immature and the gonads develop in laboratory cultures within 3-4 days, with medusae living for up to 70 days (Kubota 1988); to 1 week, with medusae living for up to 32 days (J. T. Rees *et al.* 1976); to 12 days, with medusae living for up to one month (Uchida & Nagao 1967).
Comparing the cnidomes of the medusa stages of both genera, *Hydrocoryne* has desmonemes, basitrichous haplonemes, atrichous isorhizas and 2-3 size-classes of stenoteles (Uchida & Nagao 1967, J. T. Rees et al. 1976, Kubota 1988); while *Samuraia* has microbasic euryteles, basitrichous haplonemes, and one size class of stenotele. Thus, both genera have basitrichous haplonemes and stenoteles, but of different, though overlapping, size ranges.

The colony morphology of *Samuraia* is similar to that of *Hydrocoryne* except that *Samuraia* has: 1) Fewer hydranth tentacles (11-22 vs. 30-70), 2) Shorter extended tentacles (0.4-0.6 mm vs. 0.5-3.4 mm), 3) Less extended hydranths (3 cm vs. 6 cm), 4) Smaller colony size (1-3 vs. 2-20 hydranths/colony), 5) Capitate tentacle knobs bumpy vs. smooth, and 6) Same types of nematocysts, but different sizes of small stenoteles and microbasic euryteles with and without inclusion (Uchida & Nagao 1967, J. T. Rees et al. 1976, Kubota 1988) (Table 3).

Uchida (1927), Uchida & Nagao (1967) and Kubota (1988) noted that medusae of *H. miurensis* closely resembled *Sarsia resplendens*, which was described by Bigelow (1909) from Acapulco harbour, Mexico. The hydroid of *S. resplendens* is still unknown, and its taxonomic position not clear. The discovery of *S. tabularasa* has not resolved this since *S. resplendens* is more similar to the medusa of *H. miurensis* than to that of *S. tabularasa*. Both *S. resplendens* and *H. miurensis* have relatively long-lived, feeding medusae, in contrast to the rudimentary, non-feeding eumedusoids of *Samuraia*. 
**Cnidome.** The hydranth tentacles of *Samuraia* contain a rare nematocyst type, a microbasic eurytele with a large round inclusion. The inclusion remained intact in discharged nematocysts unless pressure was applied with a cover slip, causing the inclusion to break into fragments that appeared solid, similar to that described in the same nematocyst type in both species of *Hydrocoryne* (see J. T. Rees *et al.* 1976, Kubota 1988). This nematocyst type is found in only four species of hydroids in two families: *Samuraia*, the two species of *Hydrocoryne* (see J. T. Rees *et al.* 1976, Kubota 1988), and *Halocordyle disticha* (see Toppe 1910, Weill 1934, Brinckmann-Voss 1970, Bouillon 1985), in the family Halocordylidae Stechow 1921. The function of the inclusion is not known.

The five different nematocyst types found in *Samuraia* varied in abundance both between and within different parts of the colonies and eumedusoids (Table 2). In the tentacles of the hydranth small stenoteles were the most abundant followed by large stenoteles, microbasic eurytele with inclusion, and microbasic eurytele without inclusion. The hypostome was dominated almost exclusively by microbasic eurytele without inclusion. Mature eumedusoids contained, in order of decreasing abundance, basitrichous haplonemes, microbasic eurytele without inclusion, and small stenoteles. The latter were rare in or absent from older, liberated eumedusoids. Attached, immature eumedusoids lacked basitrichous haplonemes, even though these were the most abundant type in mature eumedusoids. There were no significant differences in
the mean sizes of shared nematocyst types in male and female eumedusoids, attached and released eumedusoids, and hydranth tentacles and eumedusoids.

**Sexual Reproduction.** Field-collected colonies had attached eumedusoids from March through early September. Notably, all eumedusoids on field-collected colonies were immature, and all arose singly from pedicels directly off the hydrorhiza. However, these same individuals readily produced mature eumedusoids when maintained in the laboratory; and the eumedusoids frequently arose on branched and unbranched pedicels off the proximal half of the hydranth, as well as off the hydrorhiza (Fig. 6).

Mature eumedusoids released eggs or sperm by pulsating either while remaining attached to the parent colony, or after liberation. In both cases all gametes were released within 12-24 hours, after which the eumedusoids disintegrated to shriveled transparent sacs. Although I never saw liberation of a eumedusoid, colonies with ripe attached eumedusoids produced swimming eumedusoids. It is not clear what determines whether a eumedusoid will be released or retained.

**Extension of hydranths.** The hydranths of *Samuraia* are highly extensile, seen to extend to a maximum of approximately 3 cm in the field and 10 cm in the laboratory. In the field, hydranth lengths of *Samuraia* ranged from fully contracted and barely visible when exposed to dry air for up to 6 hours during low tides, through
Fig. 6. Laboratory-maintained colony of *Samuraia tabularasa*.

Elongate hydranths and attached immature eumedusoids originating from both the hydorhiza and hydranths. From photograph of live colony.
1-2 mm when submerged in calm water, to a maximum of c. 3 cm when fully extended in strong wave surge. In the presence of an equally strong aeration current in aquaria, hydranths in laboratory cultures were commonly observed to extend 10 cm. The longer extension is probably a result of hydranths growing larger under laboratory conditions. When fully extended in a water current in the field or the laboratory, hydranths appeared as long, slender hairs with extended tentacle crowns. The current appeared to stretch the anchored hydranths away from the substrate, much as a kite catches the wind. Occasionally, in still water, particularly under the warmth of a microscope light, the hydranths extended 2-3 cm and lay tangled on the substrate (Fig. 6). The latter condition was not seen in the field.

**Laboratory and field morphology compared.** Discrepancies in the morphology of field-taken and laboratory-maintained colonies posed a problem for the choice of characters for the formal diagnosis of *Samuraia*. Specifically, the following characters, though not present in the field, appeared almost invariably in all colonies under laboratory conditions: 1) The origin of eumedusoids on the proximal half of the hydranth, 2) Eumedusoids borne in clusters of 2-4 on branched pedicels, and 3) Larger hydranths with more tentacles (25-30/hydranth). In contrast, in the field, eumedusoids originated exclusively off the hydorhiza, and they appeared singly on unbranched pedicels. Tentacle number was somewhat varied in the field as well as in
the laboratory, with rare occurrences of individuals with 22-30 tentacles/hydranth, and one with 46 (out of approximately 100 colonies measured).

I decided to base the diagnostic description of the colony, including the position of the eumedusoids, solely on traits observed in wild colonies. This was done to guard against confounding the diagnosis with morphological variation which appeared to be outside a normal response seen in the field. However, the diagnostic description of the life-cycle and characteristics of mature eumedusoids were based of necessity on laboratory observations (see above).

It is notable that the colony morphology of *Samuraia* is more similar to that of *Hydrocoryne* when colonies of *Samuraia* are maintained in the laboratory than when observed in the field. For example, the hydranths become larger, tentacle number increases to 25-30 (the range limit for *Hydrocoryne*), eumedusoids originate on the hydranth (as well as on the hydorhiza) and they originate on branched pedicels. It is possible that at least some of these traits are inhibited by the effects of desiccation during low tides in colonies of *Samuraia* in the field. If so, this is an interesting example of an environmental inhibition of taxonomically important traits in a hydrozoan.

Not enough is known to resolve the differing field and laboratory character differences, therefore it is best to provisionally propose a new genus for *Samuraia*. Though the differences in the sexual, medusa stage remain marked between the two genera; some characters of the colony vary under laboratory conditions and need to be investigated further to evaluate the degree of taxonomic relatedness between *Samuraia* and both species of *Hydrocoryne*.
CHAPTER 4

A NOVEL MODE OF SPACE PROVISION BY A ROCKY INTERTIDAL HYDROID

Summary

The samurai hydroid, *Samuraia tabularasa*, n.g., n.sp. (phylum Cnidaria, class Hydrozoa, family Hydrocorynidae) (Chapter 3), was recently discovered in a Gulf of California rocky intertidal zone. It has the ability to maintain rock substrate free of barnacles in areas that are otherwise dominated by the barnacle *Chthamalus anisopoma*. The activity of an individual hydroid colony results in a small, round to elliptical clearing, approximately 2.5 cm in diameter, of bare rock with the hydroid at its center. Experiments showed that hydroids were able to maintain rock substrate free of adult barnacles by causing the death of all newly-recruited barnacles that settled within range of their tentacles. Additionally, transplanted hydroids were able to enlarge smaller-than-average clearings. Hydroids were not found to prevent or reduce barnacle settlement in their vicinity.
Introduction

Space is a primary limiting resource for sessile organisms in the largely two-dimensional environment of the marine, rocky intertidal zone. In the absence of processes that open up primary substrate, or allow species to use one another as secondary substrate, intertidal communities tend to be dominated by a few species that monopolize space. Thus, diversity among sessile organisms in rocky intertidal communities is largely considered to be a function of processes that open up space and allow for coexistence among species (Paine 1966, Dayton 1971, Lubchenco & Menge 1978). The two general processes that create free space in the intertidal are physical disturbance (Connell 1978; Sousa 1979), and predation (Paine 1966, Lubchenco 1978).

This paper describes an unusual mode of space provision in the intertidal via space exclusion by the samurai hydroid, *Samuraia tabularasa*. This hydroid is able to maintain small patches of bare rock in a zone where rocks are otherwise covered with a dense stand of the acorn barnacle, *Chthamalus anisopoma* (Pilsbry 1917). This pattern of distribution is unusual in that elsewhere hydroids are not known to occur this high in exposed areas in the intertidal, or to be major predators of barnacles in any marine habitat. The way in which the hydroids maintain substrate free of barnacles also appears to be unique. They are sessile organisms that cause the death of all newly-settled barnacles in a circular area
within reach of their tentacles. Additionally, since the hydroids occupy only a minute fraction of the area they clear of barnacles, they provide long-lasting, and relatively large, areas free of barnacles in a zone where patches of open space are generally smaller and always more ephemeral.

The organism is a newly described genus and species of athecate hydroid in the family Hydrocorynidae (Chapter 3). Individual hydroid colonies are centrally placed within round to elliptical bare patches, approximately 2.5 cm in diameter (Fig. 7). Each colony has from one to three polyps, arising from a hard, black, encrusting base that is 1 to 3 mm wide. Sexual reproduction is by eumedusoids that can either remain attached to the parent colony or be released as short-lived, rudimentary medusae (Chapter 3). Though the hydroids are inconspicuous, the clearings they create are striking. When numerous, these "hydroid clearings" create a patchwork pattern in the barnacle zone that make the rocks appear to have a "pox" (Fig. 8).

I first noticed the samurai hydroids in 1984 on a single rock at Pelican Point. No previous researchers in the area (e.g., Brusca 1980; Dungan 1984, 1987; Lively 1984, 1986a,b; Raimondi 1987, 1990) remember seeing the hydroid or its clearings before then (pers. comm.), though Lively, Raimondi, and Dungan specifically worked on aspects of the ecology of the barnacle Chthamalus anisopoma in this area.
Fig. 7. A single hydroid clearing at low tide.

A clearing surrounding a single hydroid colony at low tide. Adult barnacles (*Chthamalus anisopoma*) are visible around the clearing, and the black spot in the clearing center is the hard base of the hydroid. Photograph taken at Pelican Point in 1984. Scale bar equals 1.5 cm.
Fig. 8. Multiple hydroid clearings in the barnacle bed at low tide.

Multiple clearings in the barnacle bed during low tide on a large granite boulder. Each clearing has a single hydroid colony in its center. Sharpie pen in foreground in 13.5 cm long. Photo taken in September 1984 at Pelican Point.
The hydroid may be recently introduced, or it may have been present but rare prior to 1984. This same region experienced the near extinction of the sea star *Heliaster kubinijii* in 1978 (Dungan *et al.* 1982) following a severe El Niño event. The appearance of the hydroid in 1984 may also be related to an El Niño event. The hydroid is unknown outside of the Gulf of California.

I used a combination of repeated observations and field experiments to document the role of the samurai hydroid in causing the death of barnacles and maintaining open space. The observational surveys illustrate the density and distribution of, amount of substrate affected by, and the average size and clearing size of, the samurai hydroid. The experimental data address the following questions: 1) Are the hydroids responsible for both maintaining and clearing the barnacle-free space that surrounds them? 2) What effects do the hydroids have on the density of barnacles in their vicinity? Specifically, how do hydroids affect barnacle settlement, survival of adult barnacles, and survival of newly settled barnacles in their vicinity?

**Study Site**

I conducted these investigations at Pelican Point (also known as Roca del Toro, 31°20'N, 113°40'W), 8 km northwest of the town of Puerto Peñasco, in Sonora, Mexico, on the eastern coast of the northern Gulf of California. Pelican
Point is a granitic promontory with an intertidal zone composed of outcrops of granite bedrock interspersed with boulder zones and tide pools. All observations and experiments were done on granitic bedrock in the middle intertidal zone, from 0 to 2.5 feet above mean low water (MLW), a zone that is continually exposed for up to six hours during low tides (Matthews et al. 1967, Matthews 1968, Thomson 1989). The coastline is exposed and subject to moderate to strong wave action, and to powerful tidal currents (Brusca 1980). Tidal amplitude is extreme, reaching 8 m (Matthews et al. 1967, Matthews 1968, Levinton 1982).

The northeastern Gulf of California is bordered by the Sonoran Desert and has an arid, subtropical, highly seasonal climate (Hendrickson 1973). Rainfall is sparse ($\bar{X} = 7.4$ cm/yr) (Thomson 1989), and temperatures range from 12° to 30° C air, and 14° to 29° C sea surface, at Puerto Peñasco (Maluf 1983, Thomson & Lehner 1976).

**Materials and Methods**

**General Methods.** Certain procedures were common to all experiments. I conducted all experiments and surveys while the reef was exposed during low tides, and once hydroid clearings had dried and were easily visible. I mapped hydroid clearings by placing acetate sheets, or plexiglass tiles, ranging from 10 cm$^2$ to 3150 cm$^2$, upon reef bedrock and marking the location of hydroids and their
clearings. I marked all adult barnacles on, and slightly away from, the perimeter of hydroid clearings. To allow me to return to the same sites for multiple samplings and remappings, I marked the corners of each map with shallow holes drilled in the rock and filled with epoxy cement. I measured clearing areas from the maps with a digitizer. Newly settled barnacles near hydroids were transitory and microscopic and were not considered to affect clearing size.

For experiments involving hydroid removals, I removed hydroids from experimental clearings by digging them out of the granite with a penknife; in control clearings I left hydroids intact and dug a small hole to one side of the colony as a control for the small disturbance spots caused by removals. Removals had to be thorough, because hydroids could re-grow from tiny amounts of residual tissue. I transplanted hydroids by digging them out of the rock and re-attaching them with superglue into small artificial nicks on the rock surface. A drop of superglue alone served as the control.

*Chthamalus anisopoma* (hereafter referred to as *Chthamalus*) settlement is seasonal and occurs in pulses; it peaks in the summer and virtually drops to zero from October through January (Raimondi 1990, and pers. obs.). At Pelican Point, during the course of my experiments, *Chthamalus* settled in pulses, with most settlement occurring from March through August. Newly settled *Chthamalus* less than 24 hours old are around 0.3 mm in basal diameter, increasing linearly to around 1.1 mm after 14 days and 2.2 mm after 44 days (Raimondi 1990). At this

I shall refer to different age classes of *Chthamalus*. I familiarized myself with the appearance of *Chthamalus* of increasing age (24 hours, one week, two weeks, and four weeks old) by making artificial clearings to allow for settlement, and by observing individuals of known age. "Young barnacles" refers to *Chthamalus* up to two weeks old. "Adult barnacles" refers to Chthamalus at least six weeks old. *Chthamalus* less than two weeks old are orange and barely visible with the naked eye. After two weeks, they turn grey.

I sampled *Chthamalus* less than two weeks old with a hand-held field microscope. This procedure allowed me to accurately count microscopic individuals. It also standardized the area sampled, since each view through the microscope covered 0.75 cm² of surface area. Samples consisted of one to three views per replicate. When I sampled with more than one view per replicate (an experimental clearing), I summed the number counted across views. The number of views per replicate was held constant within each experiment.

**Observational surveys.** On 24 April 1986, I measured hydroid density, hydroid size (maximum diameter of the base), hydroid clearing (average diameter), and number of hydroids per clearing, at each of three different tidal
heights: 0, 1, and 2.5 feet above MLW. The lowest (+0) is the lowest Cthamalus zone; below this level coralline algae predominates and the samurai hydroid no longer occurs. The other two intertidal heights (+1 to +2.5 ft.) are in a dense Cthamalus zone that continues higher than the hydroid occurs. Each tidal height was sampled by making ten random tosses of a 30.5-cm-diameter (730 cm² area) metal sampling ring within an approximately 10 m² horizontal strip parallel to the shore, keeping within the flat, consolidated reef where the hydroid occurs and not including any rings that landed in tide pools or boulder fields. Hydroid and clearing sizes within each ring were measured with a ruler.

Two days later (26 April 1986) at a nearby site over an area of approximately 0.75 m² at +1 ft. MLW, I mapped 32 haphazardly chosen clearings around hydroids, measured the maximum diameter of the base of the hydroid for each, and measured the areas of the clearings with a digitizer.

To create hydroid clearings for laboratory observations, I glued (with marine epoxy) small, bare rocks into areas of dense barnacle cover, glued hydroids onto the rocks, and left them undisturbed until barnacles settled and hydroid clearings had formed. I then chipped off the rocks and returned them to the laboratory for observation under the microscope. Hydroids do not occur naturally on moveable rocks.
**Experimental removal of hydroids.** To examine the ability of hydroids to maintain the clearings that surround them, on 17 August 1985, I randomly assigned 32 natural clearings to one of two treatments: hydroids removed (experimental, N=16) and no manipulation (control, N=16). The clearings were located at 0 MLW at a site called New Allelo. I censused the number of adult barnacles present in all clearings seven, nine, and 13 months (i.e., on 28 March, 8 May, and 10 October 1986) after the start of the experiment. No clearings had adult barnacles initially. Two years later, in September 1987, I remapped all original clearings for quantitative comparison with the original maps. Additionally, I qualitatively censused (by placing the maps over the sites and noting changes without remapping) the mapped clearings for changes in clearing size at least every six months during the two-year period between mapping dates.

I conducted a second hydroid removal experiment to measure the survival of barnacle recruits in hydroid clearings. The removal experiment described above was initiated in mid-August as the season for barnacle settlement was declining; the second was initiated in May at the middle of the season for barnacle settlement. I mapped 12 natural clearings with hydroids and randomly assigned six to controls and six to hydroid removals. All clearings began with high densities of newly-settled *Chthamalus*, which are characteristic of hydroid clearings during peaks of barnacle settlement in the spring and summer. For each clearing, I censused the density of barnacles (all newly-settled) on 27 May 1987, and three
and 14 days later (i.e., on 30 May and 11 June). I removed hydroids on 28 May, the day after the first census. Six and eight weeks later (on 11 and 25 July), I counted the number of both young and maturing barnacles per cm² in each clearing. Since all clearings started with high densities of newly-settled barnacles, the number of maturing barnacles present two months later provided a measure of the survival of young barnacles to adulthood in the vicinity of hydroids. No adult barnacles occurred initially in any of the clearings and barnacles continued to settle in the clearings throughout the experiment. As an independent measure of barnacle settlement, I created nine 2-cm²-in-diameter artificial clearings by scraping adult barnacles from the rock surface near experimental, natural clearings. I censused the number of barnacles that settled in the artificial clearings over the next three and 14 days, as well as the number of maturing barnacles that had accumulated in the clearings after 42 and 58 days.

Experimental transplant of hydroids. The experiments above were designed to evaluate the ability of hydroids to maintain clearings, and the survival of young barnacles in their vicinity. To determine the ability of hydroids to expand clearings, and their effect on adult barnacles, I created five pairs of clearings, which were much smaller than natural hydroid clearings, within areas of dense barnacle cover. Within each pair, I randomly assigned a transplant (experimental) and a control. Controls and transplants were paired to control for
possible microhabitat differences among sites, though all sites were on the same, relatively uniform 1 m² of rock surface. I mapped all adult barnacles within an approximately 1 cm radius of each control and transplant at the start of the experiment on 17 August 1985 and, seven months later, in March 1986, I recorded the survival rates of these original barnacles. I mapped all clearings initially and two years later in September 1987.

The experiment above tested the mortality rate of adult barnacles near hydroids. A second transplant experiment tested the mortality rate of young, two-week-old barnacles in the vicinity of hydroids. On 26 April 1986, I made eight artificial clearings in areas of dense barnacle cover by scraping adult barnacles off areas about the size of an average hydroid clearing, and sterilizing the bared rock surface with concentrated NaOH. I sterilized the clearings to ensure that all began equally clear of barnacles and algae. The clearings were mapped and left undisturbed for two weeks to allow for barnacle settlement, which was heavy during this period. Then, on 9 May, I sampled the density of barnacles (all microscopic) in each clearing and randomly assigned four clearings to be transplants (hydroid glued into clearing center), and four to be controls (drop of superglue alone). In this way, the experiment began with young barnacles of a known maximum age of two weeks, which is older than the average age, but within the range, of barnacles found in hydroid clearings. Twenty-six days later, on 6 June, I sampled all barnacles within a haphazardly chosen, 0.75-cm² area of
each clearing. Barnacles were assigned to one of two age classes: more or less than one month old. Only barnacles present before the experiment began could be one month old or older.

Experimental effects of hydroids on settlement of barnacles. Young barnacles can occur in hydroid clearings, so hydroids do not prevent barnacle settlement, but they may be able to reduce settlement. The following experiment was done twice, first on 8 September and second on 9 September, 1987. On 8 September, I mapped 27 hydroid clearings, sterilized a small spot (< 1 cm in diameter) with NaOH within each clearing to remove algae and any barnacle recruits present before the start of the experiment, and randomly assigned 14 to be hydroid removals and 13 to be unmanipulated controls. Hydroids were removed from the designated clearings with a penknife as described above. Twenty-four hours later, on 9 September, I censused the sterile spots within each clearing for barnacle recruits. I repeated the experiment by resterilizing the spots that same day, on 9 September, and measuring barnacle settlement 24 hours later, on 10 September.

A limitation of this experimental design was that any differences in the densities of barnacle settlers that occurred between treatment and controls after 24 hours could indicate either unequal settlement, or equal settlement but unequal mortality between controls and removals. This would not allow me to address the
question of hydroids limiting settlement. However, if I found no difference in the density of barnacle settlers after 24 hours, I could infer that settlement is probably independent of the presence of hydroids, and that mortality differences take longer than 24 hours to appear. This reasoning is flawed if barnacles preferentially settle near hydroids. I did not control for this possibility, but have never seen any indication that barnacles preferentially settle near hydroids compared to equivalent clear space without hydroids.

Results

Observational Surveys. Hydroids occurred from +0 MLW where Chthamalus begins, to the center of the Chthamalus zone at +2.5 ft. MLW tidal height. The average diameter of a hydroid clearing was significantly larger at +1 ft. tidal height (\( \bar{X} = 2.52 \) cm, \( s = 0.07 \), \( N = 53 \)) than at +0 tidal height (\( \bar{X} = 2.07 \) cm, \( s = 0.10 \), \( N = 38 \)) (\( t = 3.82 \), \( p < 0.0005 \)); while hydroid basal diameter was comparable at the two tidal heights (\( \bar{X} = 2.68 \) mm, \( s = 0.09 \), \( N = 55 \), at +1 ft. MLW). The basal diameter of a hydroid colony was not correlated with clearing diameter at either tidal height (\( R^2 = 0.018 \), \( p = 0.342 \), at 0 MLW). However, in a separate survey, done at +1 ft. MLW at a nearby site at the same time, the basal diameter of a hydroid colony was positively correlated with clearing area (\( r = 0.5852 \), \( p = 0.004 \), \( N = 23 \)).
Hydroid clearings sampled at randomly-chosen sites from +0 to +1 ft. tidal heights were most dense at +1 (X̄=73.9 hydroid clearings/m²) (Table 4). Each clearing contained on average 1.05 hydroid colonies (=individuals) at +1 ft. tidal height (t= 3.22, p=.005). I also censused densities at a site (New Allelo) located at +1 ft. MLW, specifically chosen for its unusually high density of hydroids. At New Allelo, densities reached 183 hydroid clearings per m², with an average of 1.23 hydroid colonies per clearing.

Hydroid Removal Experiment #1. Barnacle density increased and clearing area decreased with hydroid removals (Figs 9 & 10). When hydroids were removed, the clearings surrounding them virtually disappeared, as evidenced by the change in clearing area two years after hydroid removals compared to controls (Mann-Whitney U=225, p=.0000, N=16,15) (Fig. 9). Clearing areas did not differ initially (U=127.5, p=.985, N=16,15). Where hydroids had been removed from clearings, adult barnacles accumulated and covered the clearings. Adult barnacle density increased more than ten-fold seven months after hydroid removals (Mann-Whitney U=31.5, p=.0005, N=16,15) (Fig. 10). I found a comparable result after nine months (U=0, p=.0000, N=16) and 13 months (U=0, p=.0000, N=16,13).
TABLE 4. Densities of *Samuraia tabularasa* at three tidal heights. From a survey done on 24 April 1986 at Pelican Point, Sonora. The high density values are from 10 random tosses of a sampling ring within a site (New Allelo) selected for high density of hydroids.

<table>
<thead>
<tr>
<th>Tidal Height (+ ft. MLW)</th>
<th>Mean No. Hydroids/Clearing</th>
<th>Mean No. Hydroids/730 cm²</th>
<th>Mean No. Hydroids/m²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average Density</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>+0</td>
<td>1.05 (.036)</td>
<td>3.90 (1.29)</td>
<td>53.4</td>
</tr>
<tr>
<td></td>
<td>N=38</td>
<td>N=10</td>
<td></td>
</tr>
<tr>
<td>+1</td>
<td>1.06 (.032)</td>
<td>5.40 (1.48)</td>
<td>73.9</td>
</tr>
<tr>
<td></td>
<td>N=53</td>
<td>N=11</td>
<td></td>
</tr>
<tr>
<td>+2.5</td>
<td>-----</td>
<td>0.10 (.10)</td>
<td>1.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>N=10</td>
<td></td>
</tr>
<tr>
<td>High Density</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>+1</td>
<td>1.23 (.095)</td>
<td>13.36 (1.93)</td>
<td>182.9</td>
</tr>
<tr>
<td></td>
<td>N=65</td>
<td>N=11</td>
<td></td>
</tr>
</tbody>
</table>
Fig. 9. Adult barnacle density increases when hydroids are removed.

Seven months after hydroids were removed, there were significantly more adult barnacles/cm² of clearing in removal clearings (N=16) compared to unmanipulated, control clearings with hydroids (N=16). Subsequent samplings were even more significantly different. Number of replicates sampled on each date is indicated above data point on graph.
Fig. 10. Clearings disappear when hydroids are removed.

Clearings around hydroid removals (N=16) were significantly smaller than unmanipulated control clearings (with hydroids) (N=16) two years after removals. Control and removal clearing areas did not differ initially.
Qualitative inspection at least every six months from the start of the experiment showed that the control clearings fluctuated little in size during the two-year period between mappings. This indicates that hydroids not only affect the clearings that surround them, but that they are able to maintain the same clearing area for up to two years.

**Hydroid Removal Experiment #2.** Newly settled barnacles did not survive to adulthood in the vicinity of hydroids. The second hydroid removal experiment, initiated on 28 May 1987, began with equally high densities of barnacle recruits in control and removal clearings (Mann-Whitney $U=41$, $p=.748$, $N=6$) (Fig. 11). All clearings experienced high mortality of young barnacles in the next two weeks, but significantly fewer young barnacles survived in clearings with hydroids compared to those with hydroids removed after 14 days ($U=5$, $p=.037$, $N=6$). However, no difference appeared after only three days ($U=27.5$, $p=.128$, $N=6$). Few barnacles settled into the artificial clearings over the first 14 days, suggesting that the lower density of young barnacles in control clearings after 14 days was due to higher mortality rather than to differential settlement. Barnacles had very low survival rates in the vicinity of hydroids: 42 and 58 days later, maturing barnacles were significantly more dense in hydroid removal clearings than in controls ($U=2.5$, $p=.01$, after 42 days; $U=0$, $p=.0039$, after 58 days; $N=6$). The
Fig. 11. Effect of hydroid removals on survival of barnacle recruits.

Fewer young barnacles (approximately two-week-old) were present around control clearings (N=6) with hydroids compared to clearings with hydroids removed (N=6) 14 days after removals. Control and removal clearings began with equally high numbers of newly recruited barnacles. Forty-two and 58 days after removals, more adult barnacles were present in clearings with hydroids removed compared to control clearings. The dotted line represents barnacle settlement and accumulation in nine artificial clearings made at the start of the experiment in May 1987.
accumulation of growing barnacles in artificial clearings followed the pattern seen for the hydroid removals.

**Transplant Experiment #1:** Two-week old barnacles had higher mortality rates in the vicinity of hydroids (Fig. 12). In this experiment, I transplanted hydroids into patches of barnacles that I knew could be no more than two weeks old. Twenty-six days later, the density of that cohort of barnacles (those at least one month old) was lower in patches where hydroids had been transplanted compared to control patches with superglue alone (Mann-Whitney $U=16$, $p=.021$, $N=4$). At the start of the experiment, barnacle density did not differ significantly between control and transplant patches ($U=11$, $p=.3865$, $N=4$). This result was pronounced as no barnacles greater than one month old were present in the transplant clearings, indicating a zero survival rate of any barnacles present in the vicinity of hydroids two weeks earlier. Numerous barnacles less than one month old occurred in the clearings as a result of additional settlement. Mean area of the artificial clearings at the start of the experiment was 6.14 cm$^2$ (S.D.=1.64, $N=8$), which was similar to that of nearby natural hydroid clearings ($\bar{X}=6.06$ cm$^2$, S.D.=1.78, $N=32$).

**Transplant Experiment #2:** Hydroids were able to enlarge clearings (Fig. 13). In September 1987, two years after hydroids were transplanted into small
Fig. 12. Effect of hydroid transplants on survival of young barnacles.

Two-week-old barnacles (*Chthamalus anisopoma*) died faster near hydroid transplants (N=4) than controls (N=4). Hydroids were transplanted into artificial clearings with two weeks worth of barnacle settlement. One month later, barnacle mortality was higher near transplants compared to controls. Control and transplant clearings began with equal numbers of barnacles, all young.
Hydroids transplanted into the barnacle bed were surrounded by significantly larger clearings after two years than clearings around controls (N=4). Clearing size initially did not differ between control and removal clearings.
openings in the barnacle bed, they were surrounded by clearings that were approximately six times larger than the original openings ($U=256$, $p<.0001$, $N=3$ transplants), while control clearings without hydroids did not change in size ($U=128$, $p=.98$, $N=3$). A similar experiment done from 1986-87 at another site over a shorter period (10 months) had a similar result: All of the clearings around hydroid transplants increased in size, while all control clearings disappeared. The mean area of the clearings around transplants had increased to 5.95 cm$^2$ (S.D.=2.78, $N=4$ transplants) after 10 months, while control clearings had disappeared. The initial area of transplant clearings ($\bar{X}=1.98$, S.D.=.81) did not differ significantly from that of control clearings ($\bar{X}=2.3$, S.D.=.63) ($t=.685$, $p=.52$).

In two out of four cases, adult barnacles had higher mortality rates in the vicinity of hydroids (Table 5, Fig. 14). On 24 March 1986, seven months after the experiment was initiated, significantly more adult barnacles, of the original present, had died when around hydroid transplants compared to superglue controls for all four pairs combined ($X^2=5.39$, $p=.020$, d.f.=1). However, in an analysis done separately on each control/transplant pair, the mortality rate of adult barnacles was higher around transplants in two out of the four control/transplant pairs ($X^2=8.46$, $p=.004$; $X^2=3.87$, $p=.049$; d.f.=1). The transplants may have taken with varying degrees of success, causing the difference in effect among the four control/transplant pairs. Sample size varies at the two sampling dates (seven
TABLE 5. Mortality of adult barnacles in the vicinity of hydroid transplants compared to controls (no hydroids). In two out of four cases, significantly more adult barnacles died when hydroids were present compared to controls. The overall $X^2$ for the four transplants combined showed a greater mortality of adult barnacles in the vicinity of hydroid transplants.

### Individual Control/Transplant Pairs

<table>
<thead>
<tr>
<th>Number of adult barnacles that, 7 months later, were</th>
<th>Alive</th>
<th>Dead</th>
<th>$X^2$ (df 1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>16</td>
<td>4</td>
<td>8.46</td>
<td>(p=.004) **</td>
</tr>
<tr>
<td>6</td>
<td>12</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>9</td>
<td>3.87</td>
<td>(p=.049) *</td>
</tr>
<tr>
<td>2</td>
<td>20</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>8</td>
<td>2.55</td>
<td>(p=.110) NS</td>
</tr>
<tr>
<td>13</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>6</td>
<td>.606</td>
<td>(p=.436) NS</td>
</tr>
<tr>
<td>12</td>
<td>10</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### All Pairs Combined

<table>
<thead>
<tr>
<th>Alive</th>
<th>Dead</th>
<th>$X^2$ (df 1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>43</td>
<td>27</td>
<td>5.39</td>
</tr>
<tr>
<td>33</td>
<td>45</td>
<td>(p=.020) *</td>
</tr>
</tbody>
</table>
Fig. 14. Effect of hydroid transplants on survival of adult barnacles.

Adult barnacles present at the start of the experiment had higher mortality rates in two out of four cases around hydroid transplants compared to paired controls (See table 1).
months and two years) because I omitted transplants that died. Out of five original transplants, one had died after seven months and another had died after two years.

**Barnacle Settlement Experiments:** Hydroids do not appear to reduce barnacle settlement in their vicinity (Fig. 15). In two sequential 24 hour periods, barnacles settled at comparable rates in clearings with hydroids (controls) and in those with hydroids removed (Mann-Whitney U=88, p=.884, trial 1; U=111.5, p=.320, trial 2; N=13,14). I found a comparable result for a similar experiment done at a different site in 1988, but with scraped instead of sterilized spots used as sampling sites within clearings. Barnacle settlement was relatively low over the course of each experiment.

**Discussion**

The removal and transplant experiments demonstrate a powerful negative effect of *S. tabularasa* on all young barnacles, at least up to two weeks old, that settled in their clearings, and a significant, but less potent, negative effect on adult barnacles. Hydroids create and maintain their clearings by a combination of these two effects.
Fig. 15. Effect of hydroids on barnacle settlement.

Barnacle recruitment over 24 hours into sterilized spots within clearings did not differ in clearings with hydroids present (N=13) compared to those with hydroids removed (N=14) in either of two separate trials, the first on 9 September, the second on 10 September 1988.
Young barnacles in the vicinity of hydroids were less dense after 14 days compared to barnacles with hydroids removed from their vicinity in the second hydroid removal experiment (Fig. 11). These results suggest that young barnacles near hydroids had a higher mortality rate than those with hydroids removed from their vicinity. Alternatively, settlement could have been lower in clearings with hydroids. Arguing against this is the following. In this experiment, barnacles settled at low rates during the first 14 days, suggesting that new settlement contributed little to the total number of barnacles in the experimental and control clearings, particularly since settlement was low from day three to 14, when the significant difference in mortality occurred. Additionally, even if hydroids reduce settlement, adult barnacles should be less dense, but not absent, from their vicinity. Also, hydroids did not reduce barnacle settlement in another experiment (Fig. 15).

Mortality of newly settled barnacles was high in both control and removal clearings in the hydroid removal experiment above. This high mortality may have been independent of hydroids; however, a residual effect of hydroids could have increased barnacle mortality even in the hydroid removal clearings. For example, barnacles near hydroids could have been weakened (due to mechanical and/or chemical damage, or starvation) and thus have suffered higher mortality even after hydroids were removed. Regardless, fewer barnacles were present in clearings with hydroids after 14 days compared to those with hydroids removed.
When hydroids were transplanted into the vicinity of young barnacles, the barnacles suffered higher mortality over the next 26 days than in equivalent areas with no hydroids (Fig. 12). All clearings began with the same history in this experiment; thus hydroids could have had no residual effect (as in the hydroid-removal experiment above). Also, a direct measure of the survival of young barnacles was possible, without the confounding effects of further barnacle settlement, because all barnacles initially were of a known maximum age of two weeks. The two sets of results, removals and additions of hydroids, complement one another, and clearly show that when hydroids are either removed from or added to the vicinity of barnacles up to two weeks old, many fewer survive to adulthood compared to controls.

I have never seen a predation event between *S. tabularasa* and barnacles. However, I suspect that the hydroids are directly killing newly settled barnacles within a certain radius of their tentacles, probably by stinging them with nematocysts, which are notably concentrated in the tentacle caps of this species (Chapter 3, and Mangin 1991). A mechanical action of hydroids against barnacles is suggested by the notably elliptical shape of the clearings, with the long axis of the ellipse oriented parallel to the direction of wave wash. The asymmetry of clearing shape is perhaps a result of polyps of the hydroid being whipped back and forth by wave surge during high tides, a behavior I have observed in the field. Interestingly, the polyps seem to extend their hydranths and tentacles in response
to increased water turbulence, suggesting that they may be actively using the motion of the waves to feed more effectively. Alternatively, the hydroids may secrete a chemical that kills barnacles. However, if a chemical mechanism is involved, I would predict that clearings on vertical surfaces would appear to "droop"; yet this is not seen.

If the hydroids are killing barnacles, I suspect that they are picking them off the substrate and eating them. A related Pacific coast species, *Hydrocoryne bodegensis*, from Bodega Bay, California, is described as a substrate feeder on small invertebrates (Rees et al. 1976); therefore this mode of feeding is known for the family Hydrocorynidae and could be occurring in the Gulf of California species. Alternatively, *S. tabularasa* may only incidentally kill barnacles by interfering with their feeding, or by stinging but not consuming them.

It is also possible that *S. tabularasa* may only indirectly cause the death of barnacles by playing host to another organism that kills barnacles. However, in this case, I would expect to have found at least occasional instances of healthy barnacles near hydroids, for example at sites where the hypothesized, associated barnacle-predator was absent or rare. As I never saw this, I believe that this alternative, of an indirect, negative effect of hydroids on barnacles, is an unlikely explanation for the death of barnacles near hydroids.

Hydroids actively feed and survive on one-to-two-day-old brine shrimp in the laboratory, so they are capable of surviving on a crustacean diet and of eating
prey the size of a two-week-old *Chthamalus* (approximately 1.1 mm) (Malusa 1986). I observed hydroids to very effectively catch brine shrimp out of the water column and consume up to 10 brine shrimp per polyp per one hour feeding. Hydroids in the laboratory did not respond to barnacle larvae the one time I observed this. On the contrary, they allowed the larvae to crawl over their tentacle caps. Barnacle larvae may be too small for the samurai hydroid to eat, being smaller than the capitate end of a single tentacle. When hydroids in the laboratory made tentacle contact with young and old settled barnacles in their vicinity, the barnacles responded quickly by closing their apertures, but later reopened them. In many cases, when a barnacle was present in a hydroid’s clearing, the hydroid appeared to have more frequent "hits" of its tentacles with the barnacle compared to nearby, more abundant bare rock surface. However, these observations are anecdotal.

I know of two other cases of interactions between hydroids and barnacles. The first is that described by Standing (1976) for the subtidal, thecate hydroid, *Obelia dichotoma*. *O. dichotoma* mechanically interferes, but does not eat, barnacles attempting to settle beneath its dense, branching canopy. Additionally, a blanket of the hydroid’s stolons occupies the substrate below its canopy. Thus, in contrast to the Gulf samurai hydroid, *O. dichotoma* does not clear primary substrate or interact with settled barnacles. The second barnacle-hydroid interaction I know of is that observed by Leo Buss and Philip Yund (pers. comm.)
for the athecate, intertidal and subtidal hydroid *Hydractinia echinata*. *H. echinata* has specialized defensive polyps that it uses against, and whose development may be cued by, barnacles. Additionally, a close relative of the samurai hydroid, *Hydrocoryne miurensis*, from Japan, is described as occurring "intertidally, on rocks with barnacles" (Uchida and Nagao 1967). However, it does not appear to make clearings as does the samurai hydroid, and is not known to affect barnacles (Kubota 1988, and pers. comm.).

The action of *S. tabularasa* appears to be more specifically directed at barnacles than at other invertebrates that persist in the clearings, as evidenced by the occasional presence of other sessile organisms in the clearings. For example, I have seen vermetid tube worms and the tiny mussel *Brachiodontes semilaevis*; and mobile organisms, such as the limpet *Collisella strongiana* and juveniles of the snail *Cantharus elegans*. However, *Collisella strongiana* and young barnacles are the only animals that can be found reliably in hydroid clearings (Chapter 5).

An unusual aspect of the interactions of *S. tabularasa* with barnacles is that the hydroid clears rock surface that it does not then occupy but maintains as open clearings. This results in long-lasting free space that is then available for use by other species normally crowded out by barnacles (Chapter 5). In the absence of the hydroids, patches of space free of barnacles in this zone are rare, small, and ephemeral. For example, the average size of a disturbance clearing at this site ranges from 0.7 to 1.6 cm² (Chapter 5), and these clearings rapidly fill in with
barnacles during the season for barnacle settlement in the spring and summer. In contrast, individual hydroid colonies are long-lived and can maintain the same areas clear of adult barnacles for up to five years (Chapter 5). At a mean area of 6.8 cm² per clearing, hydroid clearings are larger than disturbance clearings (Chapter 5). At densities of 160 hydroids/m², 10 percent of the substrate is affected.

A second unusual aspect of the ecology of *S. tabularasa* is that the hydroids are sessile excluders of barnacles, rather than mobile consumers whose presence depends on refuges. In many middle and upper intertidal communities, predators are limited in time and space by the distance that they can safely travel from their refuges to feed (Paine 1974, Lubchenco and Menge 1978, Leigh *et al.* 1987, Lively 1986a, Dungan 1984).
CHAPTER 5

RAPID RESPONSE OF AN INTERTIDAL COMMUNITY TO A BARNACLE-EXCLUDING HYDROID

Summary

In this study, I describe the effects of the recent appearance of the samurai hydroid, *Samuraia tabularasa*, n.g., n.sp. (Cnidaria, Hydrozoa) (Chapter 3), in a subtropical, rocky intertidal community. This area was studied prior to the appearance of the hydroid by a number of investigators specifically interested in interactions among species in the "barnacle zone" of the middle intertidal rocky reef, the area where the hydroid now occurs in densities reaching 160 hydroid colonies per m². Thus it has been possible to compare the community before and after the hydroid was added. By excluding barnacles, the hydroid provides relatively large and long-lasting clear space on rock surface otherwise densely covered with the barnacle *Chthamalus anisopoma*. This opened space is then used by species otherwise crowded out by barnacles: various species of crustose algae (*Ralfsia, Ulva*) and the grazing limpet, *Collisella strongiana*. This study provides a classic case of how interactions of "keystone" species can lead to higher local species diversity. The incorporation of the hydroid into the resident community is particularly interesting because, if the hydroid is a new addition, its interactions are not likely to be the product of coevolution.
The network of direct and indirect interactions rapidly established between members of the resident community and the recently abundant hydroid has persisted relatively unchanged since 1984 when the hydroid was first noticed and its effects documented. However, the hydroids have declined in both density and vigor since their appearance, particularly since 1987. The most pronounced evidence for the decline in vigor of the hydroids is a decrease in the average size of a hydroid clearing. Rather than declining due to their new dependence on hydroids, limpets have increased in overall numbers and in mean number per hydroid clearing. This suggests that though species interactions, particularly with hydroids, are important in influencing the distribution and abundance of limpets on open rock surfaces, limpet abundance in this region is strongly influenced by other, unknown factors as well.

Introduction

The ecological consequences of invasions and extinctions of species are of interest because, as large-scale natural additions and removals of species, they can indicate the responses and resilience of communities to changes in species composition. Studies of invasions in particular can be used to address the following questions: Are communities saturated in terms of a) the number of species they can support, and b) the number of niches they contain? Are the
specific identities of species important in the functioning of a community, or just the functional roles that they play? If communities are saturated with species, then an addition should either be unsuccessful or cause the extinction and replacement of a native species. Additionally, if identities of species, rather than their functional roles, are important, then successful replacements of native with exotic species should be rare. The answers to these questions have implications for conservation as well as for a general understanding of natural community structure.

This paper presents a case study of an apparent, natural invasion of a hydroid into a rocky intertidal zone, whose community structure and dynamics had been well-studied prior to the invasion. The result of the invasion has been the rapid incorporation of the hydroid into a web of direct and indirect interactions with native species in such a way that there is little indication that the hydroid was a recent addition.

Background

The invader. The samurai hydroid, *Samuraiia* tabularasa, belongs to a newly described genus (Chapter 3) in the athecate family Hydrocorynidae (W. J. Rees 1957). This family contains one other genus and two species: *Hydrocoryne miurensis* (Uchida and Nagao 1967), described from the West Pacific from the
The hydroids of *Samuraia tabulurasa* are tiny and inconspicuous, but they create conspicuous clearings of bare rock in the barnacle bed (Chapter 4, Fig. 8). Hydroid colonies appear as small, black spots averaging 2.7 mm in diameter (S.E. = 0.09, N = 55) cemented within surface pits in the granite. Each hydroid is centered in a patch of bare space that averages 2.5 cm in diameter (S.E. = 0.067, N = 53) (Chapter 4, Fig. 7).

I first noticed the samurai hydroid in August 1984 on a single rock in the middle intertidal zone at Pelican Point, near Puerto Peñasco, Mexico. In 1986 and 1987, I searched for and found the samurai hydroid at three of five localities along a 250-mile stretch of the northwestern coastline of Sonora, Mexico: 1) In the northern Gulf of California in the vicinity of Puerto Peñasco, Sonora (at Pelican Point, Sandy Beach, and Puerto Peñasco), and in the central Gulf at 2) Caleta Venecia and 3) San Carlos Bay, Sonora. In each locality, colonies of the samurai hydroid occurred in the middle intertidal zone in clearings amid the barnacle *C. anisopoma* on either granite, or basalt, but not on coquina rock. I did not find the hydroid at Puerto Lobos or Bahia Kino, Sonora.
The samurai hydroid may be recently invaded for the first time in this region, or recently reinvaded, either from within or outside of the Gulf of California. It also could have invaded the intertidal from a subtidal habitat, or have been present but rare prior to 1984. I cannot rule out any of these alternatives, particularly as the hydroid is a previously unreported species whose biology and geographic range is unknown outside of this study. However, whether it is new to this region or only recently abundant, the ecological effects of the hydroid will be that of an invader.

The middle-intertidal community. No investigators noticed the hydroid or the clearings it creates prior to 1984; although many worked intensively from 1970 to 1986 in areas where the hydroid now occurs. Their studies addressed aspects of the biology of the dominant barnacle *Chthamalus anisopoma*, including its life history (Malusa 1986), processes that open up space in the barnacle zone (Lively 1986a, Dungan 1987, Raimondi 1990), and the maintenance of a dimorphism in the barnacle in response to predation by the snail *Acanthina angelica* (Yensen 1979, Lively 1986b). Additionally, Brusca (1980) produced a comprehensive field guide to the invertebrates of the intertidal zone of this region. Yensen (1973) studied the ecology of two intertidal limpets which now co-occur with the hydroid. Boyer (1987) documented the community effects of the natural disappearance of a major barnacle predator in this region, the starfish *Heliaster kubinijii*. 
Additionally, since 1984, the hydroid and its clearings have appeared in the long-term sites, monitored since 1982, of Raimondi and Lively (Raimondi, pers. comm.).

**Response to invasion.** The network of interactions for this same community prior to the appearance of the hydroid was described by Dungan (1984, 1987) (Fig 16). The dynamics consist primarily of interactions between barnacles, limpets and a different barnacle predator, the thaid snail *Acanthina angelica*. However, the coexistence of all these species in substantial abundance was dependent on the snails, which provided open space by killing barnacles in the vicinity of rock crevices where they took refuge during high tides. During low tides *A. angelica* traveled only a limited distance from the crevices.

Like the snail, the samurai hydroid promotes diversity in this intertidal community by causing the death of barnacles and creating barnacle-free space. *Samuraia tabularasa* maintains bare patches of rock surface on rocks otherwise densely covered with *Chthamalus anisopoma*. These are maintained for at least six months, long enough that algae can grow and limpets can reside in the clearings and graze the algae. In the absence of the hydroids, space free of barnacles on the open surfaces of rocks away from crevices consists of infrequent, small, ephemeral patches (Dungan 1987, Raimondi 1990).
Community Structure Before Addition Of The Hydroid:
M.D. Dungan (1984)

Community Structure After Addition Of The Hydroid In 1984:

Fig. 16. Community structure before and after addition of *S. tabularasa*.

*S. tabularasa* has established a similar network of interactions with barnacles, limpets, and algae as was found by Dungan (1987) to exist in a different microhabitat for other local barnacle-predators, *Acanthina angelica* and *Morula ferruginosa*, prior to the appearance of the hydroid.
In this chapter, I shall present the results of manipulative field experiments that address the following questions: What are the direct and indirect interactions of the hydroid with resident species of barnacles, limpets, and algae? How has the hydroid population changed since 1984? How have its interactions changed as the amount of space affected by the hydroid has decreased? The results provide a framework for assessing the resilience of this community to the addition of a highly successful invader, and for a comparison of the network of interactions in the community before and after the invasion of the hydroid.

Study Site

I conducted these investigations at Pelican Point (also known as La Roca del Toro, 31°20'N, 113°40'W), near Cholla Bay, 8 km northwest of the town of Puerto Penasco, in Sonora, Mexico, on the eastern coast of the northern Gulf of California. Pelican Point is a granitic promontory with an intertidal zone composed of outcrops of granite bedrock interspersed with boulder zones and tide pools. I carried out all observations and experiments on granitic bedrock in the middle intertidal zone, from 0 to 2.5 feet above mean low water (MLW), a zone that is continually exposed for up to six hours during low tides (Matthews et al. 1967, Matthews et al. 1968, Thomson 1989). The coastline is exposed and subject to moderate to strong wave action, and to powerful tidal currents (Brusca 1980).
Tidal amplitude is extreme, reaching 8 m (Matthews et al. 1967, Matthews 1968, Levinton 1982).

The northeastern Gulf of California is bordered by the Sonoran Desert and has a highly seasonal, arid, subtropical climate (Hendrickson 1973, Brusca 1980). Rainfall is sparse (\(\bar{X}=7.4\) cm/yr) (Matthews et al. 1968), and temperatures range from 12\(^\circ\) to 30\(^\circ\) C air and 14\(^\circ\) to 29\(^\circ\) C sea surface at Puerto Penasco (Thomson & Lehner 1976, Maluf 1983).

Materials and Methods

General Methods

Certain procedures were common to all experiments. I conducted all experiments and surveys while the reef was exposed during low tides once hydroid sites had dried and were easily visible. I mapped hydroid clearings by placing acetate sheets, or plexiglass tiles, ranging from 10 cm\(^2\) to 3150 cm\(^2\), upon reef bedrock and marking the location of hydroids and their clearings. I marked all adult barnacles on, and slightly away from, the perimeter of hydroid clearings. To allow sites to be sampled repeatedly, I marked the corners of each quadrat with shallow holes drilled in the rock and filled with epoxy cement. I measured clearing areas from the maps with a digitizer.

For experiments involving hydroid removals, I removed colonies from experimental clearings by digging them out of the granite with a penknife. In
control clearings I left hydroids intact and dug a small hole to one side of the colony as a control for the small dug-out spots caused by removals. Removals had to be thorough because hydroids could re-grow from tiny amounts of residual tissue. I transplanted hydroids by digging them out of the rock and re-attaching them with superglue into small nicks I made on the rock surface. A drop of superglue alone served as the control.

*Chthamalus anisopoma* settlement is seasonal and occurs in pulses; it peaks in the summer and virtually drops to zero from October through January (Raimondi 1990; and pers. obs.). At Pelican Point, during the course of my experiments, *Chthamalus* settled in pulses, with most settlement occurring from March through August. I familiarized myself with the appearance of *Chthamalus* of increasing age (24 hours, one week, two weeks, and four weeks old) by making artificial clearings to allow for settlement, and by observing individuals of known age. Newly settled *Chthamalus* less than 24 hours old are around 0.3 mm in basal diameter, increasing linearly to around 1.1 mm after 14 days and 2.2 mm after 44 days (Raimondi 1990). At this point, around six weeks after settlement, *Chthamalus* reaches reproductive maturity (Malusa 1986, Lively 1986), and its growth rate declines considerably (Malusa 1986, Raimondi 1990). "Young barnacles" refers to *Chthamalus* up to two weeks old. "Adult barnacles" refers to *Chthamalus* at least six weeks old. *Chthamalus* less than two weeks old are orange and barely visible with the naked eye. After two weeks, they turn grey.

I sampled *Chthamalus* less than two weeks old with a hand-held field microscope. This procedure allowed me to count microscopic individuals. It also
standardized the area sampled, since each view through the microscope covered 0.75 cm² of surface area. Samples consisted of one to three views per replicate. Except for percent cover measurements I used total counts, rather than means, across views. The number of views per replicate was consistent within an experiment, and usually consisted of three views per replicate.

Experiments

What is the effect of experimental removal of hydroids on the persistence of limpets in hydroid clearings? On 13 June 1988, I mapped 15 natural hydroid clearings that contained limpets. I randomly assigned seven to be hydroid removals and eight to be unmanipulated controls. Hydroids were removed as described above. I then recorded the number of limpets per clearing initially, and 14, 33, and 104 days after the start of the experiment until its end on 24 September 1988.

What is the effect of experimental removal of limpets from hydroid clearings on: a) crustose algae, and b) barnacle settlement? On 18 May 1988, I mapped 36 hydroid clearings, that were occupied by limpets, and randomly assigned (in an interspersed design using clusters of clearings) 18 as experimental removals of limpets and 18 as unmanipulated controls. I measured the mean percent cover of algae per 0.75 cm² (mean of three microscope views) and number of young barnacles per 2.25 cm² (sum of three microscope views) at the
start of the experiment and 26, 41, and 58 days later (i.e., on 13 June, 28 June, 15 July).

What are the individual and combined effects of hydroids and limpets on settlement and survival of young barnacles? On 28 May 1987, I removed hydroids and limpets from 21 natural clearings (which initially contained both) in each of three treatment combinations: hydroids removed (5), limpets removed (4), and both removed (6), plus unmanipulated control clearings (6). Hydroid removals were assigned randomly by individual clearing, while limpet removals were assigned randomly by clusters of hydroid clearings in an interspersed design. This procedure reduced migration of limpets from control into removal clearings.

Initially, each clearing contained limpets and hydroids, a very thin coat of algae, and a dense covering of microscopic newly settled barnacles, as is typical of hydroid clearings during barnacle settlement. Clearings were censused for number of young (less than 2-week-old) barnacles initially and after one, three, 14, 28, 44 and 58 days (i.e., on 30 May, 11 June, 11 July, and 25 July 1987). All barnacles present initially were less than 2 weeks old, and most no more than 1-3 days old. On days 44 and 58 I censused adult and subadult (greater than two-week-old) barnacles. Percent cover of algae was measured once, on day 44. As a separate measure of barnacle settlement, independent of the experimental and control clearings, at the start of the experiment I made nine artificial clearings, about the size of average hydroid clearings, by scraping adult barnacles off the rock surface within the experimental site.
Observations

At what densities does the hydroid occur, and how much space does it clear relative to other processes? In August 1985 I began recording densities at a single site (New Allelo) with a high density of hydroids. Since then I have recorded densities at New Allelo at least twice a year. I measured density by ten random tosses of a metal 30.5-cm-diameter sampling ring over an area approximately 2 m². New Allelo is a flat area of reef substrate, with a dense covering of Chthamalus, bordered to the east by a 0.5-m-deep tidepool, and set within a larger area of consolidated granite bedrock at +1 ft. MLW.

Additionally, I followed 97 individual hydroids and their clearings in two 3150-cm²-quadrats (Long-term sites 1 & 3) from May 1987 until May 1990. These sites are located just above and northeast of the New Allelo Site. Long-term site 3 is bordered to the west by the same tidepool as New Allelo. I mapped the sites initially, and then each February and May from 1987 to 1990. At each sampling date I mapped the outlines of hydroid clearings and all limpets inside and outside of clearings associated with hydroids. I also mapped all free space not associated with hydroids that was larger than approximately 0.05 cm². This I shall call "disturbance space". It refers to free space in the barnacle bed not associated with hydroids. The two most likely processes to have created this space are physical disturbance and predation by non-hydroid predators. Additionally, from February 1989 to May 1990, I measured maximum basal diameter of hydroids (with the use
of calipers). I did not map disturbance space at either site in May 1987, at site 1 in February 1988, or at site 3 in May 1990.

What is the relative persistence time of limpets in hydroid clearings vs. disturbance clearings? In this region, the limpet *C. strongiana* requires bare rock; it does not occur upon barnacles. On 2 May 1989, I mapped all limpets (*Collisella strongiana*) within a 1890 cm² area (at +1 ft. MLW) chosen for the presence of limpets both with hydroids and in disturbance clearings nearby. Forty-seven limpets were in association with hydroids (in hydroid clearings) and 26 were in disturbance clearings in the barnacle bed. I followed the persistence of individual limpets two, six, eight, and 10 and one half weeks after the initial mapping until the final sampling on 15 July 1988. I marked location and size of individual limpets on the maps. I assumed that I was monitoring the same individual limpets in most cases throughout the experiment, since they were approximately the same size (or slightly larger due to growth) and in the same place, particularly in the hydroid clearing. This is a reasonable assumption, because *C. strongiana* is known to home to the same sites (Yensen 1973; and pers. obs.). However, a small proportion of limpets disappeared or migrated into or out of the observational area during the course of the experiment.
Results

Short-term Patterns

**Effect of hydroids on limpet persistence**

Experimental removal of hydroids: Limpet densities declined in both control (N=8) and hydroid removal (N=7) clearings from the start of the experiment on 13 June 1988 until its completion on 24 September (Repeated Measures ANOVA, F=8.63, p=.001, d.f.=3,23); however limpet persistence was higher in the presence of hydroids (F=9.9, p=.005, d.f.=1,23) (Fig. 17).

Observations: The following observations compare the persistence of limpets in disturbance clearings versus hydroid clearings (Fig. 18). Observations were initiated on 2 May 1988, and repeated on 16 May, 13 June, 27 June, and 15 July 1988. As in the experiment above, limpet densities declined over the summer in both types of clearings; however limpet persistence was higher in clearings with hydroids compared to nearby disturbance clearings ($X^2=3.84$, d.f.=1, p<.005, on 13 June; $X^2=8.97$, d.f.=1, p<.005, on 15 July).

**Experimental Removal of Limpets**

The experimental removal of limpets from hydroid clearings resulted in a significant increase in percent cover of algae (Fig. 19), and a significant decrease in the density of newly recruited young barnacles (Fig. 20). I removed limpets on 18 May 1988, and removed any limpet recruits that appeared after during the
Fig. 17. Effect of the experimental removal of hydroids on the persistence of limpets.

Limpets showed a significant decline over the summer in both control (N=8) and experimental (N=7) clearings; however, the decline was significantly greater in clearings where hydroids had been removed.
Fig. 18. The persistence of limpets in clearings around hydroid compared to disturbance clearings.

Significantly more limpets remained in clearings with hydroids than nearby disturbance clearings 42 and 58 days after observations began on 2 May 1988 (i.e., on 13 June and 15 July) (See $X^2$ Table 1).
On 13 June 1988, 26 days after I removed limpets from experimental hydroid clearings significantly more algae covered experimental clearings (N=15) than in un-manipulated control clearings (See Fig. 20 for the corresponding results for density of barnacle recruits).
Fig. 20. The effect of the experimental removal of limpets from hydroid clearings on the density of barnacle recruits.

On 25 July 1988, 58 days after I had removed limpets from experimental hydroid clearings (N=15), significantly more young barnacles occurred in experimental clearings (N=15) than in control clearings (N=16) (See Fig. 19 for the corresponding effects on % cover of algae).
course of the experiment), and sampled all clearings 26, 41, and 58 days later, until the completion of the experiment on 25 July. On Day 26 (13 June), significantly more algae covered clearings with limpets removed compared to control clearings ($t=3.25, p=.003, N=15,16$). Barnacle settlement was low in both controls and removals through day 41, and there was no significant difference in settlement. However, in the following two weeks there was a pulse of settlement and, by day 58, significantly more barnacles were present in clearings with limpets present than in those in which limpets had been removed ($t=2.72, p=0.01, N=16,15$).

**Experimental Removal of Hydroids and Limpets**

Fifty-eight days after experimental removal of limpets and hydroids, the density of young barnacles was highest where both limpets and hydroids were present, and the density of adult barnacles was highest where hydroids had been removed (Fig. 21). In an ANOVA on the density of young barnacles on Day 58 (on 25 July 1987), more barnacles occurred in the presence of hydroids ($F=17.11, p<.01, d.f.=1,16$); in the presence of limpets ($F=6.36, p=.02, d.f.=1,16$); and in the presence of both hydroids and limpets, i.e., an interaction effect ($F=5.48, p=.03, d.f.=1,16$). In contrast, by Day 58, more maturing barnacles (> two-week-old) occurred in clearings with hydroids removed ($F=4.73, p=.04, d.f.=1,16$), i.e., fewer barnacles survived to maturity in the presence of hydroids. Though there was no direct effect of limpets on the density of mature barnacles, the density of maturing barnacles was lower where both hydroids and limpets had been removed,
Fig. 21. Effect of experimental removal of hydroids and limpets on the survival of young barnacles in hydroid clearings.

All clearings began with nearly equally high densities of young barnacles (less than 2 weeks old). Significantly more young barnacles, and few adult barnacles, occurred on 25 July 1987, on Day 58 of the experiment, in clearings where hydroids had been removed. This result was magnified when limpets were removed as well (i.e., a direct effect of hydroids and an interaction effect of limpets). Legend: L = Limpets removed (N=4), H = Hydroids removed (N=5), LH = Limpets and hydroids removed (N=5), C = Controls (N=6).
i.e., an interaction effect \((F=172.07, p<.005, \text{d.f.}=1,16)\). Although the density of young barnacles was greater in clearings with hydroids compared to those with hydroids removed, barnacles that settle in the vicinity of hydroids do not survive to maturity. Additionally, I sampled the percent cover of algae in all clearings on Day 44 (Fig. 22), and found that algal cover was highest when limpets were removed \((F=36.81, p<.005, \text{d.f.}=1,16)\). There was no effect of hydroid removals on the percent cover of algae.

Long-term Patterns

**Population densities of hydroids**

Mortality of hydroids significantly exceeded recruitment from 1987-1989 at the two long-term sites combined. Out of 97 hydroid colonies present in May 1987, 31 had died and 12 new had recruited by May 1990 \((X^2=7.54, p=.006, \text{d.f.}=1)\). However, hydroid densities at New Allelo (high density site) did not change significantly from 1985 to 1990 from a mean of 11.6 hydroids/730.24 cm\(^2\) quadrat in August 1985 (S.E.=0.94, N=10 quadrats over an 1 m\(^2\) area). This density is equal to 158.8 hydroids/m\(^2\).

**Hydroid Size**

Hydroid basal diameter decreased significantly from 1986 to 1990 \(2(F=19.24, p<.0005, \text{d.f.}=4,155)\) (Fig. 23). Multiple comparisons (Duncan Newman Keuls) showed all dates to be significantly different except for March
Fig. 22. Effect of the experimental removal of hydroids and limpets on the % cover of algae.

On 11 July 1987, Day 44 of the experiment, algal cover was greatest in all clearings where limpets had been removed (N=9). Hydroid removals did not affect the % cover algae. Legend: L = Limpets removed (N=4), H = Hydroids removed (N=5), LH = Limpets and hydroids removed (N=5), C = Controls (N=6).
Fig. 23. Average basal diameter of hydroid colonies over time.

The average diameter of a hydroid base has decreased over time from 1987 to 1990. Multiple comparisons (Duncan Newman Keuls) showed all dates to be significantly different except March 1986 and June 1988.
1986 and June 1988. To control for variability across tidal height or season, only sites from the same tidal height (+ 1 ft. MLW) and general time of year (spring to early summer) are included.

**Clearing Size**

In August 1984, the average size of a hydroid clearing at Old Allelo, the first site where the hydroids were noticed, was 20.5 cm² (S.E.=1.97, N=10) (Fig. 24). By September 1985, mean clearing size at Old Allelo (site 1) had decreased by 50% to 9.59 cm² (S.E.=1.16, N=4) (paired t=3.33, p=.006). The mean size of hydroid clearings at New Allelo (site 2) was 6.28 cm² (S.E.=.25, N=16) in August 1985, which had not changed significantly by August 1987, but decreased significantly to 3.96 cm² by September 1988 (paired t=5.415, p >.001, N=13). This was not significantly larger than 3.34 cm² in April 1989. Clearing area declined again at New Allelo from 1989 to 2.80 cm² in May 1990 (paired t=2.40, p=.047, N=8). At both unmanipulated long-term sites 1 & 3 (site 3 & 4 in Fig. 24), clearing area decreased significantly from 1987 to 1988, and from 1988 to 1989, with no significant decrease from 1989 to 1990.

Disturbance clearings were significantly smaller than hydroid clearings at each sampling date in May and February of 1987-1990 at long-term site 1 (Fig. 25a, Table 6). The same pattern appears to hold for long-term site 3 as well (Fig. 25b), though this data is not analyzed here. The average size of a disturbance clearing was not continuous from one sampling date to the next, as openings in the barnacle bed soon filled in with new barnacle recruits. However, the average
TABLE 6. Hydroid and disturbance clearing sizes from 1987-1990 at long-term site 1. Sampling was done each year in late May (1990) or early June. For each year, the Student’s t-statistic represents a comparison of hydroid and disturbance clearing sizes, above the t-statistic for a comparison of disturbance clearing sizes with and without limpets.

Mean Clearing Area (cm$^2$)

<table>
<thead>
<tr>
<th>Year</th>
<th>Hydroid w/ L</th>
<th>Disturbance w/o L</th>
<th>t</th>
<th>p</th>
</tr>
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<tr>
<td>1988</td>
<td>4.5</td>
<td>1.6</td>
<td>4.28</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>1.0</td>
<td>.054</td>
</tr>
<tr>
<td>1989</td>
<td>2.6</td>
<td>1.3</td>
<td>5.14</td>
<td>.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>.70</td>
<td>.083</td>
</tr>
<tr>
<td>1990</td>
<td>2.6</td>
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<td>.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>.90</td>
<td>.000</td>
</tr>
</tbody>
</table>

Legend: w/ L = with limpet, w/o L = without limpet
Fig. 24. Average size of hydroid clearings over time.

The mean size of a hydroid clearing decreased by 50% from 1984 to 1985 at Old Allelo (site 1), the original site of discovery of S. tabularasa. At New Allelo (site 2), the average area of a hydroid clearing declined by 45% from 1985-1990 (-40% from 1987-1988, and -20% from 1989-1990). Long-term sites 1 & 3 (sites 3 & 4) show a similar decline. The same clearings were sampled at each site on each sampling date.
The mean area of a hydroid clearing decreased from 1987-1989, but was consistently larger than the mean area of a disturbance clearing, at both a. long-term site 1 (Also, see Table 6). A similar pattern is apparent in b. long-term site 3. The average size of a hydroid clearing was larger than that of a disturbance clearing across sites at the majority of dates sampled at site 1 (Table 6). Both sites were sampled from 1987-1990 in February and late May or early June of each year (except site 1 was not mapped in February 1988, and disturbance clearings were not mapped at site 3 on May 1990).
size of a disturbance clearing remained remarkably constant through time, ranging between 0.7 and 1.06 cm² at both long-term sites 1 & 3. Disturbance clearings containing limpets were significantly larger than those without limpets in long-term site 1 (Table 6).

Figure 26 shows changes in the total amount of barnacle-free space due to hydroids and disturbance in long-term sites 1 & 3. Disturbance space increased with the decline in hydroid-cleared space, i.e., barnacle density is lower than in past years. At each of the two sites, the total amount of disturbance space increased significantly from 1989 to 1990, with no significant difference between 1987 and 1989. A combination of a decrease in mean area and density of hydroid clearings led to a significant decline in the total amount of free space due to hydroids for the same periods.

**Distribution and Abundance of Limpets**

Despite shrinkage of clearings, at least as many limpets were associated with hydroids in 1990 as shortly after their appearance in 1985-86 (Table 7 & 8). On three out of seven sampling dates at long-term site 1 & 3 combined, limpets occurred in higher proportions in hydroid than in disturbance clearings relative to the amount of free space each provided (Table 7).
TABLE 7. Proportion free space, and limpets associated with, hydroid clearings and disturbance clearings. On three of seven sampling dates, limpets occurred in significantly higher proportions, relative to the amount of space contributed by each, in hydroid clearings than in disturbance clearings. Each date represents the sum of Long-term sites 1 & 3, except Feb. 1988 is missing for site 3 and May 1990 is missing for site 1.

<table>
<thead>
<tr>
<th>Date</th>
<th>Proportion Clear Space</th>
<th>No. Limpets</th>
<th>X²</th>
<th>p</th>
</tr>
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<tr>
<td></td>
<td>H</td>
<td>D</td>
<td></td>
<td>H</td>
</tr>
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<tr>
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<tr>
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</tr>
<tr>
<td>Feb. 1990</td>
<td>.27</td>
<td>.73</td>
<td>93</td>
<td>192</td>
</tr>
<tr>
<td>May 1990</td>
<td>.30</td>
<td>.70</td>
<td>39</td>
<td>77</td>
</tr>
</tbody>
</table>

Legend: H = clear space around hydroids, D = disturbance space

<table>
<thead>
<tr>
<th>Site 1</th>
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<th>Limpets/cm²</th>
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</thead>
<tbody>
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<td>Year</td>
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<td>D</td>
<td>Sum</td>
</tr>
<tr>
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<td>16</td>
<td>2</td>
<td>18</td>
</tr>
<tr>
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<td>66</td>
</tr>
<tr>
<td>1989</td>
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</table>

<table>
<thead>
<tr>
<th>Site 3</th>
<th>No. Limpets</th>
<th>Clearing Area(cm²)</th>
<th>Limpets/cm²</th>
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</thead>
<tbody>
<tr>
<td>Year</td>
<td>H</td>
<td>D</td>
<td>Sum</td>
</tr>
<tr>
<td>1987</td>
<td>5</td>
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<td>95</td>
</tr>
<tr>
<td>1990</td>
<td>85</td>
<td>141</td>
<td>226</td>
</tr>
</tbody>
</table>

Legend: H = clear space around hydroids, D = disturbance space
Fig. 26. Total barnacle-free space due to hydroids versus disturbance processes over time.

The total free space around hydroids in long-term sites 1 & 3, sampled from 1987-1990, decreased from 1987 to 1989, and the total disturbance space, sampled from 1988-1990, increased from 1989 to 1990. Data from two sites 0.03 m² mapped biannually from May 1987 to May 1990.
Density of limpets per hydroid clearing increased from 1987 to 1990 to varying degrees in the two long-term sites (Fig. 27). Limpet densities were significantly higher at both sites from 1987 to 1988 (site 1: $t=5.58$, $p<.001$; site 3: $t=5.15$, $p<.001$), and at site 3 from 1988 to 1989 ($t=2.79$, $p=.007$), and 1989 to 1990 ($t=2.27$, $p=.03$).

Summary Interpretation of Results

The samurai hydroids are able to maintain patches of bare rock free of adult barnacles throughout the year. This activity provides space for crustose algae to grow and for limpets to persist in the clearings (Figs 22 & 17). By maintaining space free of adult barnacles where algae can grow, hydroids appear indirectly to benefit limpets. Limpets do occur in the absence of the hydroids; but they occur in lower numbers and are resident for shorter periods of time (Fig. 18).

How do limpets affect hydroids? Limpets reduce the cover of algae that grow in the clearings that surround hydroids (Fig. 19), and thereby apparently increase barnacle settlement in the vicinity of hydroids (Fig. 20). If hydroids kill and eat young barnacles as I suspect (Chapter 4), then limpets should benefit hydroids by increasing the food supply in their vicinity.

The mean size of a hydroid clearing in 1990 decreased to one-third of its size in 1985 (Fig. 24). This led to a concomitant decrease in the total space cleared by hydroids in this community (Fig. 26). Perhaps because of an increase in space cleared in the barnacle bed by disturbance processes (physical and
Fig. 27. Average density of limpets per hydroid clearing over time.

Limpet densities in hydroid clearings increased significantly from 1987 to 1989 at both long-term sites sampled bi-annually in February and late May or early June. Limpet densities were significantly higher at both sites from 1987 to 1988, and at site 3 from 1988 to 1989.
biological) over the same time (Fig. 26), however, limpets have not decreased as expected. Instead limpets have increased in total numbers and in mean number per hydroid clearing (Table 7 & 8, & Fig. 27).

Discussion

As ecologists, we often assume that communities are composed primarily of species that are long-term residents with a shared history and the potential for coevolved interactions. In this study of the samurai hydroid, a recently invaded species became integrated into a network of interactions with resident species to such a degree that nothing about its present relationships would indicate that it is a recent addition. These results demonstrate that species can be very resilient to the addition of a new, invading species. Specifically, there was room for the hydroid to insinuate itself in this community without causing the extinction of any native species. Without knowledge of the recent invasion of the hydroid it would be easy mistakenly to infer that the samurai hydroid had always been abundant and playing its "keystone" role in providing barnacle-free space in this community.

We also often assume that the species present in a community during a particular study constitute the total community, and that those present comprise some sort of an equilibrial, closed assemblage. In reality, we cannot know how long individual species have been present without historical knowledge of the community. Many marine communities are probably open, non-equilibrial assemblages (Roughgarden et al. 1986). They are probably composed of many
more species than we see in any particular year, including some that are absent or rare temporarily. For these reasons, the total complement of species that make up a particular community and determine its resilience to change may only be apparent after years or decades of observation. Included in these "hidden" species are chance invasions of novel species. Invading, alien species; species that have increased after a period of rarity; and species that have reinvaded the region after suffering a range contraction; all represent species temporarily and effectively out of the community. It is only important to make a distinction between the different classes of such hidden species if communities contain coevolved species, and specific identities influence their interaction with other components in the community.

I do not know which category of invaded species applies to the samurai hydroid in the northern Gulf of California. The hydroid may be recently invaded or reinvaded in this region, or it may have been present but rare prior to 1984. Possible sources for the invasion or human-caused introduction of the hydroid could be at least one of the following, each of which is discussed further below: 1) Temperature and/or current change associated with the El Niño of 1982/83, 2) inadvertent introduction associated with oyster farming or shipping, or 3) a subtidal origin.

Warm water masses associated with the severe El Niño of 1982/83 may have carried planktonic larvae of the hydroid farther north than usual and extended the northern limit of its range, in or out of the Gulf. This same region experienced the near extinction of the sea star Heliaster kubinjii in 1978 (Dungan
et al. 1982) following a severe El Niño event. Warm than usual water temperatures could also have allowed the hydroid to increase in abundance, if it was present but rare prior to 1984.

Oyster farming began in both Puerto Peñasco and Cholla Bay in the early 1980s, and farmers experimented initially with oyster stock from different regions; for example, stock was received from Peru (pers. comm., local fisherman). Oyster spat arrives on wood planks which may have inadvertently carried the samurai hydroid as well. The oyster spat now comes from Monterey Bay, California, where the samurai hydroid is not known to occur.

Puerto Peñasco is an active shipping and fishing port and the hydroid may have been imported to the region in bilge water, or on ship hulls. I looked on ship hulls in the harbor and found no evidence of the samurai hydroid or its clearings; however this remains a possibility.

The hydroid may occur subtidally and only recently have invaded the intertidal zone. This seems the least likely source for the hydroid because it would require special adaptations to survive stresses in the intertidal. Additionally, hydroids transplanted into the lower intertidal either disappeared or became overgrown with coralline algae (Chapter 4).

If the hydroid is a recent invader, a key to its success in this community may be that it plays a role already performed both by other predators and by disturbance: the killing of barnacles and freeing of space. Therefore it can benefit from the indirect effects that had already been established in the community - those between grazing limpets and any process that clears space of
barnacles (Dungan 1987). Indirect interactions in general are probably easily transferable among species because they require no adaptation to a specific species but only a response to a resource, regardless of who or what is providing the resource.

Interestingly, the hydroid appears to have an unusual strategy for obtaining and holding space in the rocky intertidal. First of all, the intertidal tends to be dominated by solitary forms (Jackson 1979); yet the hydroid is clonal. It is long-lived like a clonal organism (surviving for multiple years by budding and replacement); yet individual colonies are limited in clonal growth, more like a solitary organism with determinate growth; individual colonies rarely increase beyond three polyps per colony. However, the hydroids do not appear to recruit very successfully in this zone, perhaps because of limited sexual reproductive output. For example, I have never seen a reproductively mature individual in the field despite extensive sampling; though colonies commonly had immature reproductive structures during the spring and summer, and the same individuals could rapidly reach reproductive maturity in the laboratory. Thus, the hydroid’s clonal habit in a solitary zone may be contributing to its decline (by restricting its ability to reproduce sexually) as well as its success (by allowing it to persist as a perennial form over multiple seasons in a space limited habitat).

Similarly, though the hydroids may benefit from limpets due to their indirect, positive effect on barnacles via space provision, the recent increase in limpet densities may be having a negative effect on the hydroids and leading to the decrease in the average size of a hydroid clearing. Limpets may harm
hydroids by crawling over them and causing mechanical damage, or by interfering with their feeding, or by some other unknown factor.

What allows this community to be so resilient to change in species composition? Part of the answer may lie in the redundancy in this community in the number of species playing the same functional role as is characteristic of rocky intertidal shores, at least in temperate zones (Dayton 1984). Two species of thaid snail, *Acanthina angelica* and *Morula ferruginosa*, the crab *Eriphia squamata*, the starfish *Heliaster kubinijii*, and now the samurai hydroid all prey on the barnacle *Chthamalus anisopoma* in this community. One of the snails, and now apparently the hydroid, appear to have a mutualistic interaction with a limpet through their interaction with barnacles; and potentially the same interaction occurs between limpets and the other predators on barnacles. As one predator declines (for example the recent decline of the starfish *Heliaster kubinijii*, (Dungan et al. 1982)), another is present to increase in abundance (Boyer 1987). It may be important to the long-term stability of the species diversity of a community to have a certain number of species waiting in the wings. On this level communities may be coevolved in terms of numbers of species, but only through a long enough study with sufficient variability could this coevolution be measured.
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