Three stages of injuries regeneration on scleractinian corals

Titlyanov E.A.¹, ²*, Titlyanova T.V.¹, ², Yakovleva I.M.¹, ³, Sergeeva O.S.¹, ²

¹Institute of Marine Biology, Far East Branch of Russian Academy of Sciences, Vladivostok, 690041, Russia
²Tropical Biosphere Research Center, University of the Ryukyus, Sesoko Island, Okinawa 905-0227, Japan
³Department of Chemistry, Biology and Marine Science, University of the Ryukyus, Nishihara, Okinawa 903-0213, Japan

Abstract: Regeneration of artificial injuries on scleractinian corals of massive colonies Porites lutea and branching Porites cylindrica and algal/coral competition on newly formed substrate are the subject of investigation. It was shown that the injured coral areas recovered at three stages: (1) coral tissue recovery with the formation of a border between the regenerating live tissue and dead area, (2) growth and expansion of the live tissue on the substrate, and (3) new polyps development on the healed area. At the first stage of the regeneration, the rate of lesion healing was highest: it varied in respect to injury type and averaged 0.2–0.05 and 0.1–0.02 mm day⁻¹ for P. lutea and P. cylindrica, respectively. The regeneration rate mostly depended on morphology of corals and injury type. Coral entombed spores and thalli fragments of algae settled onto partially damaged live tissue and skeleton. At the second stage, the rate of lesion healing sharply decreased and varied from 0.1 to 0.03 mm day⁻¹ for P. lutea and from 0.05 to 0.02 mm day⁻¹ for P. cylindrica. Position of the injuries within the colony, light intensity, as well as the composition and abundance of algae and animals settled onto the damaged areas had a significant effect on the rate and duration of the recovery process. The algae growing on dead areas of the injuries acted as a physical and in rare cases as a chemical impediment for expansion of live tissue on the available substrate. At the second stage of healing, the live tissue overgrew twenty two algal species settled onto the lesions at winter and spring seasons. At the third stage of the regeneration, the recovery depended on external and internal conditions promoting the growth of coral polyps.

Key words: scleractinian corals; Porites lutea; Porites cylindrica; algae; artificial injuries; regeneration; algal-coral competition

*Corresponding author. Far East Branch of Russian Academy of Sciences, Institute of Marine Biology, Vladivostok-41, Vladivostok 690041, Russia. Tel.: +7-4232-310931; fax: +7-4232-310900.
E-mail address: etitlyanov@mail.ru

INTRODUCTION

Partial mortality in corals can occur due to lesions on the coral colony, where the live surface has died or been removed (Meesters et al. 1997a). Lesions are caused by natural processes such as diseases (Gladfelter 1982; Peters 1984; Hall 1997, 2001), prolonged coral bleaching (Brown 1997a, b; Brown et al. 2002; Bhagooli and Hidaka 2002), sedimentation (Rogers 1990; Stafford-Smith and Ormond 1992), bioerosion (Bruggemann et al. 1994; McCook et al. 2001), storms and cyclones (Glynn 1990) and by human activities (Grigg and Dollar 1990; Bruckner and Bruckner 2001). Hall (1997, 2001) has divided coral injuries into four major categories: partial tissue loss (grazing,
predation); tissue mortality (diseases, bleaching events); superficial tissue and skeleton loss (predation by excavating fish, and natural disturbances, such as turbidity, sand and rubble abrasion) and substantial tissue and skeleton loss (breakage due to storms, cyclones or human activity). These damages to colonies of hard corals sometimes reach extensive areas but do not lead to mortality of the colonies due to modularity of the corals, and to their high ability to regenerate by healing and recruitment (Hughes and Jackson 1985). Regeneration of injured areas depends on type and size of lesions on coral colony surfaces, and interspecific and environment-related differences (Kawaguti 1937; Meesters and Bak 1993, 1995; Meesters et al. 1996, 1997a, b; Hall 1997; Oren et al. 1997; Marshall 2000). It is also greatly affected by the physiological state of coral colonies (Hall 1997, 2001; Titlyanov and Titlyanova 2002). The ability of many corals to recover from injuries is energetically costly, and species differ in the allocation of resources between regeneration and other physiological processes (Meesters and Bak 1993; Meesters et al. 1994). Probably, algae and marine invertebrates may affect a process of healing of lesions because of their attachment to damaged areas and subsequent impediment to regeneration of coral tissue. However, although the regeneration mechanisms of various types of injuries to scleractinian corals were studied in some works (Meesters et al. 1997a; Hall 1997, 2001; Oren et al. 1997), the dynamics of regeneration and the influence of settled organisms on the recovery of injuries have been largely ignored.

In this paper, we examined the dynamics of regeneration of various types of artificial injuries on two coral species – massive colonies of Porites lutea and branching colonies of Porites cylindrica. We also studied the relationship between the regeneration rate of the injuries and their location within the colonies or light intensity in the habitats. Monitoring of colonization of the coral injuries by algae and animals allowed us to show the relation between the regeneration rates of coral tissue and composition and abundance of communities of these settlers.

**MATERIALS AND METHODS**

**Study specimens**

Massive colonies of Porites lutea Edwards and Haime, 1860 and branching colonies of Porites cylindrica Dana, 1846 were collected from open sites at a depth of 1–1.5 m from the fringing reef during low tide. Two types of fragments were cut from the colonies: small and large pieces with weight ranging from 2 to 60 g and from 80 to 200 g, respectively, from *P. cylindrica* and big fragments with a weight range from 200 to 800 g each from *P. lutea*. In some experiments, we used small (up to 1 kg) intact colonies of *P. lutea*.

**Study site, time and conditions**

All experiments were conducted in outdoor aquaria (50 L each) at Sesoko Station of Tropical Biosphere Research Center of University of the Ryukyus (Sesoko Island, Okinawa, Japan, 26°38' N, 127°52' E) from November 2002 to August 2003. In the winter period, water temperature in the aquaria was 19–24°C during the daytime and 18–22°C at night. In the spring period, the temperature was 25–28°C during the daytime and 22–24°C at night. In the summer period, the temperature was 28–30°C and 27–28°C, respectively. Mineral nutrition and zooplankton concentration in the aquaria were similar to natural conditions because the seawater was pumped from a depth of 2 m of the fringing reef and was not subjected to filtration or settling. The water in the aquaria was intensively aerated; water change was approximately 30% h\(^{-1}\). The light intensities in open aquaria were 70–90% of incident photosynthetically active radiation (PAR\(_{o}\)) or 800–1400 µmol m\(^{-2}\) s\(^{-1}\) at sunny midday during the winter period and 900–1800 µmol m\(^{-2}\) s\(^{-1}\) during the summer period. Some aquaria were shaded by gray or black plastic mesh.

**Experimental design**

Experiments were conducted on coral fragments acclimated to bright light (70–90% PAR\(_{o}\)) or to moderate light (30% PAR\(_{o}\)) for two months. Coral tissue was removed from the fragments with Water-Pik (WP injury) (Fig. 1A). Such treatment led to complete removal of the live tissue from the greater part of the injured areas or so called “partial tissue loss” (Hall 1997, 2001). At the area between healthy and damaged surfaces, the live tissue was removed partially and amounted to approximately 5–10% of whole injured area. Large and small fragments were also inflicted with injuries as follows: a chisel injury over the surface in the middle part of the fragment to remove superficial layer of tissue and skeleton 1–2 mm depth – “superficial tissue and skeleton loss” (Hall 2001) (Fig. 1B). Breakage or “tissue and skeleton loss” (Hall 2001) was simulated with pincers (for *Porites cylindrica*) or with a small hand-
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saw (for *Porites lutea*) (Fig. 1C). Osmotic shock (OS) injuries were made with a gentle jet of fresh water for five-ten min and live tissue was at once removed only from the middle part of the lesions (no more than 20% of the damaged area), and the rest of the tissue from the greater part of the lesions died and detached from the skeleton in a time course – “tissue mortality” (Hall 2001). Healthy areas of some coral fragments were partly covered with a 1 mm thick-layer of cement - cement injuries (Fig. 1F). This type of the injuries simulated an attachment of some animals or algae in nature. For further measurements of the recovery rate, wax lines or dots were marked in the middle part of the injuries. Usually, the lesions for all types of inflicted injuries were located at the middle part of fragments or at the upper, lateral or basal parts of small colonies. Injury size depended on the dimensions of the fragments and on average amounted no more than 10% of the living tissue area.

After the procedure with injuries, fragments or colonies were photographed under water and placed onto plastic grids in their natural position into aquaria. This series of the experiments were conducted during the winter-spring period from January 10, 2002 to May 6, 2003.

The next series of the experiments were conducted using small *Porites lutea* fragments pre-acclimated to light intensities 70–90%, 20–30%, 3–5% and <1% PAR, in the aquaria shaded by grey or black plastic mesh during 30 days. Before the experiment, WP injuries were made on the fragments. Then, these samples were fixed with cement to dead coral pebbles in three positions: at their upper part, perpendicular to solar rays, in the lateral part at angles to the rays and at the basis of colony turned to the bottom of an aquarium. The colonies were put into the aquaria with high, moderate and low light intensities. Light intensities near the surface of each fragment were similar to those experienced by fragments during their pre-acclimation. These experiments were conducted for a period of two summer months from June 10, 2003 to August 10, 2003.

Fig. 1. Colonies and fragments of the corals *Porites lutea* and *Porites cylindrica* with different injury types, and regeneration of tissue on damaged areas. A, *P. cylindrica* fragment with Water-Pik (WP) injuries. B, *P. lutea* fragment with chisel injuries. C, *P. lutea* fragment with breakage injury made at once. D, *P. lutea* fragment after breakage injury with a formation of the border between the live tissue edge and dead skeleton, and expansion of the live tissue on newly formed skeletal substrate. E, polyp development on the recovered tissue. F, cement injuries (*Porites lutea*) after two months of the recovery. Dots indicate the primary (initial) border between cement and live tissue.
Analytical procedure

The growth rate measurements

Undamaged coral fragments were blotted with a paper towel to remove excess seawater, weighed and placed back into the respective aquaria. This procedure took a few minutes and did not induce any damage to corals. The fragments were weighed again after 30 days of maintenance. The growth rate of samples was calculated using the formula:

\[ \mu = \frac{(m_1 - m_0)}{(m_0 \times \Delta T)} \times 100 \]

where, \( \mu \) is the average growth rate measured in mg g\(^{-1}\) day\(^{-1}\), \( m_0 \) is initial weight, \( m_1 \) is a weight at the end of the experiment, and \( \Delta T \) is the time between two measurements of the weight (Brinkhuis 1985). Means and standard deviations were calculated on the basis of eight fragments (n=8).

Measurements of the recovery rate of lesions

To determine the amount of regeneration of the injuries over time, the injured areas of the experimental fragments were monitored photographically with a digital camera “Olympus” C5050Z. The amount of regeneration within the experimental period was quantified from the color photographs by printing the image at its actual size or with a magnification and tracing the damaged and healed areas. On the basis of ten sporadic measurements for each fragment (distance from the center of the lesion to the edge of the lesion at the beginning of the experiments or to the border between dead area and live tissue during the maintenance), the average regeneration rate was calculated in mm day\(^{-1}\). In the summer experiments, the areas of initial lesions and the lesions after their partial healing were measured and the regeneration rate was calculated in mm\(^2\) cm\(^{-2}\) day\(^{-1}\). Means and standard deviations were calculated on the basis of five fragments (n=5).

Amount of algal and animal organisms settled onto the injury

To determine the area occupied by the algal and animal organisms, “weight” method was used. Color image of lesion was printed on a high quality Epson KA450PM paper at a magnification 5x. The image of the injured area was cut and weighed, and then the images of the algae and animals were similarly cut and weighed. The relative area occupied by the settlers was then calculated by the following formula:

\[ \%S = \frac{W_2}{W_1} \times 100 \]

where, \( S \) is the relative area of a projective cover of injury by settlers, \( W_1 \) is weight of paper with image of lesion, and \( W_2 \) is weight of paper with image of settlers.

Algal composition and abundance were determined under a stereoscopic microscope on the basis of ten fortuitous optical fields.

Light intensity measurement

Light intensity was measured at the water surface in the open aquaria and near the upper parts of coral fragments in both the open and shaded aquaria with a Li-Cor radiation sensor (Model LI-192 SB). The measurements were performed three times a day: at 9–10 a.m., 13–14 p.m. and 17–18 p.m. The relative light intensity near the coral surface was calculated from these measurements and represented in percent of PARs.

Statistical analysis

The raw data for the regeneration and growth rates were arcsine transformed prior to use of analysis of variance (ANOVA) procedures. Tukey Honest Significance Test was employed for multiple comparisons of means whenever ANOVA results were significant. Differences were considered significant at \( P < 0.05 \).

RESULTS

The recovery dynamics of damaged tissue and colonization of the injuries by algae and animals

Figure 2 shows the rate of growth and regeneration of lesions on the fragments of Porites lutea and P. cylindrica inflicted with the different injury types and maintained under 30% PAR\(_0\) during two winter months. The growth rates of coral fragments differed insignificantly between the species and time treatments and, amounted to an average about 1.2 mg fw g\(^{-1}\) fw day\(^{-1}\) (Fig. 2A).

In breakage, chisel and WP injuries of both coral species investigated, the regeneration rates were significantly (ANOVA, \( P < 0.05 \)) higher (2–3-fold) during the first month of the experiment compared to those during the second one (Fig. 2B-D). In OS and cement injuries, the regeneration rates did not differ significantly (ANOVA, \( P > 0.05 \)) between the first and the second month of the maintenance (Fig. 2E, F). For all the injury types, the regeneration rate was
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higher in *Porites lutea* than in *P. cylindrica* especially within the first month of the experiment. The formation of a clear border between the live tissue and the dead area of breakage injuries occurred during the first month of the experiment (Fig. 1D). In both coral species investigated, new polyps were formed only within the second month of the experiment (Fig. 1E).

The projective cover of injuries with settlers, their list and abundance are given in Table 1 and 2. After the first month of the maintenance, *Enteromorpha clathrata* (Chlorophyta), *Feldmannia irregularis* (Phaeophyta) and *Centroceras clavulatum* (Rhodophyta) were observed on the injuries of both coral species. A small amount of *Spyridia filamentosa* (Rhodophyta) and *Phormidium tenue* (Cyanobacteria) were found only on the injuries of *P. cylindrica*. Among marine animals, there were found only solitary tunicates (Urochordata). On all the types of injuries, the projective cover with settlers was insignificant: the algae and animals formed 2–7% and <1%, respectively (Table 1). After the second month of the maintenance, the algae and animals occupied 20-

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**Fig. 2.** Growth rate (A) and regeneration of lesions on fragments of the corals *Porites lutea* (B-F) and *Porites cylindrica* (B-D, F) inflicted with different injury types (breakage; chisel; WP - Water Pik; OS - osmotic shock; cement) and maintained in the aquaria under moderate light intensity (30% PAR) during two winter months. Means ± SD, n = 8.
### Table 1. Means and standard deviations of the relative algal and animal cover (%) on the injured areas after 30 and 60 d maintenance in the aquaria

<table>
<thead>
<tr>
<th>Coral species</th>
<th>Injury type</th>
<th>On February 10, 2003 After 30 days</th>
<th>On March 10, 2003 After 60 days</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Algae</td>
<td>Animals</td>
</tr>
<tr>
<td><strong>Porites lutea</strong></td>
<td>Breakage</td>
<td>4.5 ± 1.4</td>
<td>&lt;1</td>
</tr>
<tr>
<td></td>
<td>Chisel</td>
<td>7.4 ± 2.6</td>
<td>&lt;1</td>
</tr>
<tr>
<td></td>
<td>WP</td>
<td>2.4 ± 6.2</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Cement</td>
<td>1.8 ± 0.5</td>
<td>&lt;1</td>
</tr>
<tr>
<td></td>
<td>OS</td>
<td>3.8 ± 1.8</td>
<td>&lt;1</td>
</tr>
<tr>
<td><strong>Porites cylindrica</strong></td>
<td>Breakage</td>
<td>6.1 ± 2.0</td>
<td>&lt;1</td>
</tr>
<tr>
<td></td>
<td>Chisel</td>
<td>5.7 ± 1.2</td>
<td>&lt;1</td>
</tr>
<tr>
<td></td>
<td>WP</td>
<td>2.6 ± 1.4</td>
<td>&lt;1</td>
</tr>
<tr>
<td></td>
<td>Cement</td>
<td>2.3 ± 0.6</td>
<td>0</td>
</tr>
</tbody>
</table>

### Table 2. Species list and the abundance of algae and animals settled onto the corals *Porites lutea* and *Porites cylindrica* after the damages (WP injuries) under maintenance in aquaria within the winter-spring period from January 10, 2003 to March 10, 2003.

<table>
<thead>
<tr>
<th>Species</th>
<th>P. lutea</th>
<th>P. cylindrica</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>February</td>
<td>March</td>
</tr>
<tr>
<td></td>
<td>10, 2003</td>
<td>10, 2003</td>
</tr>
<tr>
<td><strong>BACILLARIOPHYTA</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Diatoma</em> sp.</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td><em>Navicula</em> sp.</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td><em>Nitzschia longissima</em> (Brebisson) Ralfs</td>
<td></td>
<td>++</td>
</tr>
<tr>
<td><strong>CYANOBACTERIA</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lyngbya</em> sp.</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td><em>Phormidium corium</em> (C. Agardh) Gomont</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td><em>Phormidium tenue</em> (Meneghini) Gomont</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Spirulina</em> sp.</td>
<td></td>
<td>++</td>
</tr>
<tr>
<td><strong>CHLOROPHYTA</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Enteromorpha clathrata</em> (Roth) Greville</td>
<td>++</td>
<td>++</td>
</tr>
<tr>
<td><em>Enteromorpha compressa</em> (Linnaeus) Nees</td>
<td>++</td>
<td>++</td>
</tr>
<tr>
<td><em>Rhipidiosiphon javensis</em> Montagne [Udotea javensis]</td>
<td>++</td>
<td>+</td>
</tr>
<tr>
<td><em>(Montagne) A. Gepp &amp; E. Gepp</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>PHAEOPHYTA</strong></td>
<td></td>
<td></td>
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<tr>
<td><em>Ectocarpus</em> sp.</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td><em>Feldmannia irregularis</em> (Kützing) G. Hamel</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Hincksia mitchelliæ</em> (Harvey) Silva in Silva et al.</td>
<td>++</td>
<td>+</td>
</tr>
<tr>
<td><em>Sphacelaria novae-hollandiae</em> Sonder</td>
<td></td>
<td>+</td>
</tr>
</tbody>
</table>
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Table 2. (continued)

<table>
<thead>
<tr>
<th>Species</th>
<th>P. lutea January</th>
<th>P. lutea February</th>
<th>P. lutea March</th>
<th>P. cylindr ica January</th>
<th>P. cylindr ica February</th>
<th>P. cylindr ica March</th>
</tr>
</thead>
<tbody>
<tr>
<td>RHODOPHYTA</td>
<td></td>
<td></td>
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<tr>
<td>Falkenbergia killebrandii (Bornet) Falkenberg</td>
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<tr>
<td>Hymnea sp.</td>
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<td></td>
</tr>
<tr>
<td>Centroceras clavulatum (C. Agardh) Montagne</td>
<td>±</td>
<td></td>
<td>±</td>
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<td></td>
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<tr>
<td>Ceramium sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spyridia filamentosa (Wulffen) Harvey</td>
<td>++</td>
<td></td>
<td>++</td>
<td></td>
<td></td>
<td>++</td>
</tr>
<tr>
<td>Herposiphonia secunda (C. Agardh) Ambronn f. tenella Wynne</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Laurencia obtusa (Hudson) J.V. Lamouroux</td>
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</tr>
<tr>
<td>Polysiphonia sp.</td>
<td></td>
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<tr>
<td>PROTOZOA</td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>Acervulina sp.</td>
<td>+</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>UROCHORDATA</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Tunicate sp. (solitary tunicates)</td>
<td>+</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>POLYCHAETE</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Spirorbis sp.</td>
<td>+</td>
<td></td>
<td>+</td>
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</tr>
</tbody>
</table>

Annotation: +++, for 1-10 individuals per cm²; +, for less than 1 individual occurred per cm². S, a single individual per injury.

80% and about 3%, respectively (Table 1). At the same time, cement injuries were covered only by 20% (Fig. 1F), whereas OS injuries were covered to more than 80%. Enteromorpha spp. (Chlorophyta) and Spyridia filamentosa (Rhodophyta) were common algae observed on the injuries. Hincksia mitchelliae (Phaeophyta), Rhipidosiphon javensis (Chlorophyta), Spirulina sp. (Cyanobacteria) and Nitzschia longissima (Bacillariophyta) represented appeared as new settlers. Moreover, WP injuries of both coral species significantly differed in the composition of the settlers but not in their abundance. The most common settlers were Phormidium tenue, Enteromorpha compressa, Feldmannia irregularis, Ectocarpus sp., Centroceras clavulatum and Spyridia filamentosa. New animals, which settled onto the injuries of both coral species, were Spirorbis sp. (Polychaete) and Acervulina sp. (Protozoa). In total, after the second month of the maintenance, twenty two species of algae were found: three species of Bacillariophyta; three species of Cyanobacteria; three species of Chlorophyta; four species of Phaeophyta and eight species of Rhodophyta.

The influence of location of injuries on colonies and light intensity on the recovery rates

Position of lesions within the fragments of Porites lutea colonies had a significant effect on the regeneration rates of WP injuries (Fig. 3). During the first month of maintenance (period I), the regeneration rate differed insignificantly between the lesions located at the upper, lateral and basal parts of the fragments. During the following two months of the experiment (period II), the regeneration rate of the injuries in all parts of the colonies significantly dropped, especially at the upper part (4–5 times). Injuries located at the upper parts of the colonies healed approximately two times slower than those located at the lateral and basal parts.

During summer two-month experiments, significant differences in the regeneration rates of WP injuries in relation to their position within the colony of P. lutea and to light intensity were observed (Fig. 4). The highest regeneration rate of WP injuries located at the upper and lateral parts of the fragments was observed under low light (20–30% PAR). The regeneration rate
significantly ($P < 0.05$) dropped with either an increase (70–90% PAR$_0$) or a decrease (3–5% PAR$_0$) in the light intensity. There was no significant difference ($P < 0.05$) in the regeneration rate of WP injuries located at the basal part of the coral fragments exposed to 20–30% and 3–5% PAR$_0$. A significant decrease in the regeneration rate was observed only under extremely low light (<1% PAR$_0$). The highest regeneration rate (2.6 ± 0.5 mm$^2$·cm$^{-2}$·d$^{-1}$) was
observed in the fragments of the basal parts of colonies exposed to low light.

**DISCUSSION**

*The dynamics of regeneration of tissue and skeleton of damaged corals*

For both the massive coral *Porites lutea* and the branching coral *P. cylindrica*, the regeneration of all injuries started from the partially damaged coral tissue and only after that the recovered tissue occupied dead parts of the lesions exposing on the dead area and formed new polyps. The partially damaged tissue started to recover immediately after the damage and healed 2-4 times faster than the dead area of wound. Earlier, Bak and Steward-van Es (1980) showed that the recovery of live tissue and skeleton of partially damaged polyps of the corals *Agaricia agaricites* and *Porites astreoides* occurred also at the beginning after the damage following by the recovery of the tissue on the dead areas of the lesions.

*Interspecific differences in the recovery dynamics for different injury types*

Previously, regenerative ability of injured colonies with different morphologies has been studied in eleven coral species (Hall 1997). The regenerative abilities could be ranked according to morphological attributes for these species as following: arborescent > bushy > tubular > massive > submassive. According to the Hall’s scheme, the recovery of injuries for *P. cylindrica* (bushy) must be faster than that for *P. lutea* (massive). However, our experiments clearly showed that the recovery from breakage, chisel, WP and cement injuries in *P. lutea* was two-three times faster than in *P. cylindrica* within the first month of the maintenance. Some explanations could be proposed for these differences. The structure (morphology) of the polyp affects the number of polyps damaged partially, and dimension of the mechanistic damage restricts mainly to the polyp size and the height of corallites (i.e. on depth of the spread of live tissue). Based on the morphological characteristics of the species investigated, the live tissue of *P. lutea* spreads approximately two times deeper (due to the greater height of the polyps) into the skeleton and has a relatively greater area of lesions with tissue damaged partially compared to that of *P. cylindrica*, which was damaged almost completely under the same type of injury. As it was shown above, partial damages of coral tissue recovered faster than dead areas. Therefore, we suppose that scleractinian corals with the live tissue spreading deeper into the skeleton are more resistant to the injuries with damaged polyps.

In the present experiments, lesions in both coral species with partially damaged polyps after breakage, chisel and WP (scraping) injuries healed significantly faster than those after OS and cement injuries (close to tissue injuries). Moreover, the recovery from OS and cement injuries did not display any significant differences in the regeneration rates between the first and the second months of the experiment for both coral species. Bak and Steward-van Es (1980) have reported similar results for the recovery of scraping and tissue injuries for *Porites astreoides*. The authors have shown that the rapid recovery was assisted by the regeneration of the partially injured polyps within the injured site. It might be possible that areas of the partially damaged tissue were minimal in the tissue injury type (OS and cement), and thus, the recovery has been started with the formation of new live tissue and with the expansion on newly formed substrate (dead skeleton, cement) that is energetically more costly and takes more time than to repair partially damaged polyps.

*Regeneration in relation to location of injuries within colony and to light conditions*

Variations in the regeneration of lesions, located at different positions within a colony, have been reported by many authors (e.g., Jackson 1979; Palumbi and Jackson 1982; Meesters et al. 1994; Meesters and Bak 1995; Hall 1997). Meesters and coauthors (1994) showed that the regeneration of artificial lesions was slower in the areas with high sedimentation. However, Hall (1997) did not find the differences between healing of lesions located at different parts in the colonies for six out of seven investigated species.

In the present experiments, the injuries healed with a high rate and did not depend on their location during the first month of the recovery. Subsequently, the injuries located at the upper parts healed approximately two times slower than wounds located on either side or at the base of the fragments. We suggest that at the first stage of the regeneration, the recovery of partially damaged coral tissue is not affected by external factors, such as sediments deposition and coral-algal competition.

Lesions located at the lower part of colonies and faced to the bottom, where light intensity
varied from 20% to less than 1% PARo, repaired 1.5–2-fold faster than those located at the upper and side parts of the colonies and experienced irradiation from 90% to 3% PARo. We suggest that sediment deposition affected the recovery rate of the lesions situated at various places, and thus impeded the repair of the inflicted injuries. These results allowed us to conclude that there is no significant effect of light intensity (in a range from 20–30% to 3–5% PARo) on the healing of lesions at the first stage of the recovery process. The latter supports the idea that the regeneration of live tissue in the damaged corals occurs with a large energetic cost (Hall 2000) and, thus, has a paramount significance for an organism, which spends for these needs the energy obtained by various manners: photosynthesis of zooxanthellae, predation, feeding by plant remnants, dissolved organic matters, and also digestion of own zooxanthellae (Titlyanov and Titlyanova 2002b).

**Coral-algal competition**

At the first stage of the recovery, algal colonizers, such as *Enteromorpha* spp. and *Centroceras clavulatum* attached to the damaged skeleton or to the coral live tissue, respectively, impeded healing. However at this stage, regenerating live tissue is able to overgrow the algae and to entomb them into the skeleton (Titlyanov et al., 2005). Subsequently, when newly formed live tissue occupies the substrate, algae and animals, which settled onto the substrate, act as a physical or sometimes chemical impediment for expansion of the coral tissue. Moreover, two species of the Cyanobacteria (*Lyngbya bouillonii* and *L. majuscula*) are able to act as poison for the corals, inhibiting their growth and bleaching the live tissue (Titlyanov et al., 2005).

Probably, it might explain a sharp decrease in the rate of coral regeneration. In winter season, the first colonizers that settled onto newly formed substrate were marine plants such as *Phormidium tenue* (Cyanobacteria), *Enteromorpha compressa* (Chlorophyta), *Ectocarpus* sp and *Feldmannia irregularis* (Phaeophyta), *Spyridia filamentosa* (Rhodophyta) and animals such as solitary tunicates (Chordata). New animals, which settled onto the injuries of both coral species, were *Spirorbis* sp. (Polychaete) and *Acervulina* sp. (Protozoa). By the second month after the injuries were inflicted, the wounds of *Porites cylindrica* and *P. lutea* were colonized by more than twenty species of algae. Nonetheless, the corals were able to overgrow all these species of algae. As it was shown previously (Titlyanov et al. 2005), more than one hundred algal species were overgrown by the corals after eight months of their recovery from injuries (Titlyanov et al. 2005).

It is interesting to note that OS and cement injuries had a maximum (80%) and minimum algal cover (20%), respectively. Probably, the OS injuries had better conditions and more suitable surface for the settlement and attachment of the algal spores and fragments (onto unchanged morphology of the skeleton) and also for the algal growth (remnants of dead tissue) compared to the cement injuries.

**CONCLUSION**

Our experiments showed that coral injuries recovered at three stages. At the first stage, partially damaged tissue healed forming a clear border between the recovered live tissue and the dead area. During this stage, the regeneration rate of polyps (tissue and skeleton) depended mainly on their damage, morphophysiological and anatomical features of the damaged coral. At the second stage, the newly formed live tissue gradually overgrew the dead area. During this stage, the rate of the formation of new tissue and expansion on substrate depended mainly on coral physiology, on features of the substrate (structure, sedimentation and overgrowth with algae), on the position of injuries (the upper, lateral and basal sides of colonies), and on environmental conditions in their habitat, especially on light intensity. At the third stage, the recovery of tissue and skeleton followed by the development of new polyps on newly formed substrate. The main conditions during this stage are optimal conditions for the coral growth.

**ACKNOWLEDGEMENTS**

The Russian authors thank the President of the University of the Ryukyus, Prof. Moshin Morita and the scientific leader of the Sesoko Marine Biological Station Prof. Minoru Murai for the invitation to work at the Sesoko Station of the Tropical Biosphere Research Center. We are also grateful to the staff of the Sesoko Station for use facilities, technical support, hospitality and the convenience of research work.
Three stages of injuries regeneration on scleractinian corals

LITERATURE CITED


(Received: 9 Dec. 2005/Accepted: 12 April. 2006)