Autotrophy and Predation in the Hermatypic Coral Stylophora pistillata in Different Light Habitats

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Abstract

The influence of light conditions in natural habitats on autotrophic function and also effects of light intensities, ammonium additions and feeding with zooplankton on predation of the coral *Stylophora pistillata* in aquaria experiments were studied. Coral colonies were collected in the Gulf of Eilat (Israel) from depths 2 m, 20 m and 40 m. Some branches were maintained in aquaria during two weeks under different light regimes from 5% to 90% of PAR₀ and with different feeding treatments: seawater; seawater enriched with (NH₄)₂SO₄; and seawater with the *Artemia salina* nauplii additions.

It was shown that in exterior branches of the colonies zooxanthella population density and chlorophyll concentration (calculated as per polyp as per 106 zooxanthellae) increased with gradual reducing light intensity from 90% to 5% PAR0, while the level of dividing zooxanthella frequency declined. With reducing light intensity from 20% to 5% PAR0 an average volume of zooxanthellae and the ratio of values of maximal gross photosynthesis and dark respiration of corals decreased.

It was elucidated that ingestion rates as well as killing rates increased with reducing light intensity in the field and in the experimental aquaria. In most cases the value of the ratio of ingestion rate to killing rate was increased. Feeding of corals with inorganic nitrogen as well as with zooplankton stimulated the ingestion rate. When corals incubated under 90% and 20% PAR₀ in all feeding treatments the

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highest daily rate of predation observed at morning hours and lesser – at evening hours. Under light intensity 5% PAR0 the rate of predation was high during the day in all feeding variants of the experiments.

We conclude that with reducing light intensity in habitat the production capacities of autotrophic function of corals increased by accumulation of algal-symbionts in exterior branches of corals and by increasing photosynthetic pigment concentration in the algae. In all probabilities, it depended on intensification of predation under shade. We assume that corals are capable of adapting to dim light not only by maximization of light absorption and its effective use, but also by intensification of heterotrophic function, at least predation.

Keywords: Stylophora pistillata, hermatypic corals, symbiosis, zooxanthellae, photoacclimation, predation, feeding, photosynthesis, respiration, chlorophylls

1. Introduction

Scleractinian reef-building corals are characterized by four types of feeding:

- 1. Autotrophic feeding on the photosynthate produced by endocellular symbiotic dinoflagellates
- 2. Predation on zooplankton
- 3. Capture and digestion of organic remains of animal origin and bacteria accumulated in the mucus on the surface of the coral colony
- 4. Uptake of dissolved organic carbon (DOC) from water (Sorokin, 1990).

Corals do not usually utilize food of plant origin (Yonge, 1930, 1973; Sorokin, 1973, 1990). We have shown that degradation (probably digestion) of zooxanthellae by coral hosts is a fundamental process of interaction between algae and host in coral organisms and it is one of the mechanisms of regulation of zooxanthellae density in the polyp endoderm (Titlyanov et al., 1996, 1998, 1999). The importance of each type of feeding on the energy and carbon budget of a coral will vary depending on morphological and physiological features of the coral species, and on its environmental conditions. The relative contribution of each type of feeding for some common scleractinian species inhabiting depths down to 10 m on Heron Island Reef, the Great Barrier Reef, Australia was determined by Sorokin (1984). Zooxanthellae photosynthesis made up 60% of the income portion of the energy budget, predation: 20%, consumption of organic sediments (mainly bacteria): 10% and DOC uptake: 10%.

The relation of autotrophic and heterotrophic feeding of different coral species in various habitats, and of reefs in general is one of the main problems in

coral reef ecology and energetics (Odum and Odum, 1956; Yonge, 1968; Goreau et al., 1971; Muscatine, 1973; Achituiv and Dubinsky, 1990; Sorokin, 1990; Dubinsky and Jokiel, 1994; Ribes et al., 1998). The idea that corals with big polyps and well developed tentacles are heterotrophs rather than autotrophs, suggested by Porter (1976) has not been supported by subsequent work (Sorokin, 1981, 1990). Sorokin (1990) rejects the possibility of trophic specialization of scleractinian corals and suggests that availability of nutrition (autotrophy, zooplankton, bacterioplankton, DOC) determines the ratio of autotrophy/heterotrophy and the importance of the various feeding modes in a coral species.

During the investigation of feeding of Astrangia danae, a coral inhabiting temperate waters, it was found that although this coral is characterized primarily by a heterotrophic type of feeding, it nevertheless changes the type of feeding to an autotrophic one during periods unfavourable to this type of feeding, whenever surrounding waters are poor in zooplankton (Szmant-Froelich and Pilson, 1980; Szmant-Froelich, 1981). There are some clear examples of trophic specialization of scleractinian corals. Thus, two morphological forms of the coral Montastrea cavernosa differ considerably not only in their predation activity, but also in their daily dynamics of this process (Lasker, 1976). Although availability of nutritional sources actually determines both autrophic and heterotrophic activities in a given coral species, we think that major changes in their ratios can occur only in coral species possessing sufficient trophic flexibility and capable of adaptive reactions to light and to quantity of biogenic nutrition: zooplankton, bacteria, and DOC. We found from the data of Sorokin (1990), that scleractinian species as Stylophora pistillata, Pocillopora damicornis, Fungia scutaria and also some species of Acropora have both, high photosynthetic, and predatory capacities, whereas other species such as Porites lobata and Cyphastrea seralis possess clearly predominant autotrophic capacity, while Goniastrea pectinata is mainly predatory. The first group of species is found to have a broad range of adaptation to light intensity, and to zooplankton availability in the water. From the second group it is hard to expect major shifts towards heterotrophy, even under conditions of plentiful supply of zooplankton combined with light limitation.

High irradiance does not always ensure maximal photosynthetic rates in zooxanthellae, even for such physiologically flexible as *Pocillopora verrucosa*; the highest level of primary production of this coral was found at medium depths and irradiance levels around 60% of subsurface photosynthetically active radiation (PAR₀) (Titlyanov, 1991a). It may well be that in this case under maximal irradiance levels photosynthesis is depressed due to photoinhibition. This species, as well as *P. damicornis* and *S. pistillata*, may sustain near-maximal, stable, primary production under a wide range of

illumination, from 90 to 30% of subsurface PAR₀. Below this irradiance, photosynthesis begins to decline at light intensities about 10% of PAR₀, autotrophic level of these species drops steeply to 20–30% of P_{max} (Titlyanov, 1991b). In all cases the zooxanthellae and the host coral respond with a coordinated series of photoacclimative mechanisms which mitigate the effects of reduced irradiance, limiting reduction in photosynthesis to only five fold, even in cases when the reduction in irradiance was 100–200 fold. The photoacclimative mechanisms of corals and zooxanthellae operate differently under various light ranges for different ecological and morpho-functional groups of corals. Photoacclimation of the autotrophic function of corals and zooxanthellae was recently well documented (Helmuth et al., 1997; Stimson, 1997; Rowan, 1998; Beer et al., 1998). Furthermore, there are no data on adaptation processes of heterotrophic feeding of symbiotic coelenterata as responses to the range of irradiances encountered in their habitats.

In the most general terms, we aimed at examining the interactions between autotrophy and heterotrophy in zooxanthellae corals. While autotrophy provides carbon and energy, heterotrophy may provide nitrogen as well as carbon. Indeed, one of the main reasons for the dependence of corals, at least under high light, on zooplankton stems from the need to obtain the nitrogen required to satisfy Redfield ratios allowing balanced growth (Muscatine et al., 1989; Dubinsky et al., 1990). We hypothize that by modifying light level and nitrogen supply, we might elicit compensatory changes in heterotrophic feeding, aimed at stabilizing the flux and ratios of carbon and nitrogen.

More specifically:

- 1. Will low light induce the polyps to intensify food capture activity?
- 2. We also aimed at examining the converse question: will enrichment with inorganic nitrogen or sufficient supply with zooplankton influence the rates of killing and eating of *Artemia salina* nauplii?

2. Material and Methods

Biological material

Experimental work was conducted in the Gulf of Eilat, Red Sea, at the Interuniversity Institute (IUI) of Eilat, H. Steiniz Marine Laboratory in Eilat, Israel. Corals were collected near IUI from a shallow platform at 2 m depth and from a reef slope at 20 m depth and deep-water platform at 40 m depth. Seawater temperature during our study was 24–25°C. Gulf of Eilat water is clear enough and corresponds to Type II ocean water (Jerlov, 1968). The waters of the Gulf of Eilat are poor in nutrients, and their concentrations varies between a summer minimum of >0.1 μ M NH_4^+ , 0.08 μ M ($NO_3^- + NO_2^-$), and >0.02 μ M

 PO_4^{-3} , to a winter maximum of >0.1 μ M NH_4^+ , 2.25 μ M $(NO_3^- + NO_2^-)$, and >0.25 μ M PO_4^{-3} .

We have chosen the hermatypic coral *Stylophora pistillata* (Esper) as the object of study for various reasons. This coral species is ecologically flexible, and grows throughout Indo-Pacific reefs, occupying various ecological niches. *S. pistillata* has a wide light range from 100 to 0.5% of subsurface photosynthetically active radiation (PAR₀) (Falkowski and Dubinsky, 1981; Titlyanov et al., 1981; Dubinsky et al., 1984; Titlyanov and Latypov, 1991). It was found both in the highly eutrophic waters of the Gulf of Siam (Titlyanov and Latypov, 1991) and in the oligotrophic waters of the Phantom Bank in the Timor Sea (Titlyanov et al., 1983). Among 16 species of scleractinian corals studied by Sorokin (1990) at Heron Island, *S. pistillata* ranked 5th in its autotrophic function activity and 1st for predation (Sorokin, 1990).

Collection and incubation of corals

Separate exterior branches of *S. pistillata* colonies, from shallow (2 m), exposed and shaded bottom sites, and also from the depths of 20 and 40 m, were collected by scuba diving. Within 15–30 min they were brought in a plastic bucket to the laboratory, where they were placed in aquaria filled with natural or nitrogen enriched seawater, according to treatment. The system consisted of three (1, 2 and 3) five-chamber aquaria. In the separate 15 chambers, water was constantly circulated through filter (sand, pebbles, cockleshells) at the bottom of each chamber by airlift. Illumination in the three aquaria was adjusted by means of neutral density light filters (fine plastic net) to levels closely resembling that found in three different natural habitats from where the corals were collected (90, 20 and 5% PAR₀). Temperature in the aquaria was 24–25°C during the day and 22–23°C at night.

Incubation with water, nutrients and Artemia

Some branches from the aquaria with seawater and close-to-natural illumination were analysed on the day of collection or the following day for determination of initial biomass parameters and photosynthesis and respiration rates. A second series of samples was analyzed 2 days later for determination of predation activity, and third part was kept in aquaria for 14–17 days to allow adaptation to different combinations of illumination, nutrient concentration and zooplankton feeding. In aquaria 1, 2 and 3, we maintained the illumination at 90–80%, 20–30% and 5–1% of PAR₀, respectively. In separate chambers of the three aquaria, different feeding conditions were maintained: seawater; seawater enriched with 20 μ M (NH₄)₂SO₄; and with *Artemia salina*

Table 1. Production characteristics of zooxanthellae and coral branches of *Stylophora* pistillata from different light habitats. Values are means and standard deviations of 5 measurements (branches) of photosynthesis, respiration and chlorophyll contents, zooxanthellae volume of 1000 cells in each measurement and frequency of cell division of 1500 cells in ones.

Parameters	Depth 2 m 90% PAR ₀	Depth 20 m 20% PAR ₀	Depth 40 m 5% PAR ₀	P value**
Means volume of zooxanthellae, µm ³	465±70	464±42	679±57	0.034
Frequency of dividing zooxanthellae, %	2.5±0.1	2.1±1.4	0.56±0.2	0.008
Chl a+c2*, µg per 10 ⁶ zooxanthellae	5.0±1.3	8.6±0.6	10.1±0.7	0.012
Zooxanthellae 10 ³ per polyp	14.6±4.3	19.7±5.1	24.3±4.0	0.031
P _{gross} , μMO2 per 10 ³ polyp per h	54.5±5.6	51.5±8.8	25.4±6.0	0.024
Rd, µMO2 per 10 ³ polyp per h	25.9±3.8	25.4±6.0	18.2±4.6	0.027

^{*}Chl a+c2 sum of chlorophylls a and c2; P_{gross} , = maximum gross photosynthesis; R_d = dark respiration of coral branches; ** One-way ANOVA factorial design.

nauplii in concentration 5 nauplii per 1 ml of seawater. Every morning from 08:00 to 9:00 h the aquaria with experimental corals were washed by running seawater and the above additions replaced.

Analytical procedures

Rates of net photosynthesis and dark respiration of coral branches were determined in a thermostated 680 ml plexiglass chamber using a Clark type electrode YSI 5331 Model according to Leleltkin et al. (1996). The number of polyps in a coral branch was calculated by direct observation under a stereoscopic microscope. The surface area of the skeleton was determined by subdividing it into small pieces, measuring the projected area of the pieces on a leaf-area image-analyzer (Delta Devices), and assuming the pieces to have a subcylindrical shape (Falkowski and Dubinsky, 1981). The living tissue was

removed by Water-Pik (Johannes and Wiebe, 1970), and the volume of the resulting homogenate was recorded. Samples were taken for determination of zooxanthellae number (by hemocytometer), frequency of dividing zooxanthellae and chlorophylls α and c_2 (Jeffrey and Humphrey, 1975). Diameters of zooxanthellae were measured by an ocular-micrometer, and their sizes were calculated by the formula of a sphere volume. Dividing cells were determined from appearance of initial cell wall in mother cells to forming of own cell envelope in the daughter cells. In each light variant 5 branches were separately analyzed. Means and standard deviation calculated on the basis n=5 (see Table 1).

Predation activity of coral polyps was determined in the experiment with *Artemia salina* nauplii. Coral branches were removed from the chambers, put in 200 ml glass vessels containing seawater to which nauplii were added in concentration of 10 to 20 ml⁻¹ according to Sorokin (1990). During the feeding experiments the temperature in the vessels was equal to in the sea (23–25°C), gentle mixing was provided by an air pump, and illumination was the same as in the aquaria from which the samples were taken. Corals were fed for 2 hours. After feeding the coral branches were carefully rinsed to assure collection of all killed but not ingested nauplii, and subsequently returned to their respective chambers. The number of live and dead nauplii in the water within the feeding vessels was counted in micropipette (1 ml) under a stereomicroscope. Rates of killing and ingestion of nauplii were calculated by the following formulae:

$$V_k$$
 (killing rate) = $\frac{a_0 \cdot v_0 - a_1 \cdot v_1}{t \cdot n}$ (1)

$$V_i \text{ (ingestion rate)} = \frac{(a_0 \cdot v_0) - (a_1 \cdot v_1 + a_2 \cdot v_1)}{t \cdot n}$$
 (2)

Where v_0 = initial volume of seawater with nauplii, v_1 = volume of seawater with nauplii after the experiment, a_0 = initial concentration of live nauplii, a_1 = a concentration of live nauplii after the experiment, a_2 = concentration of dead nauplii, t = duration of the experiment, n = polyp number in a coral branch. The feeding efficiency was calculated as:

$$E_f = V_i/V_k$$

In each variant of the experiment on influence of light conditions on feeding of corals with zooplankton (Figs. 1 and 2) three coral branches were used, means and standard deviation calculated on the basis of n=3. Differences between means with p<0.05 were considered significant. In each variant on daily

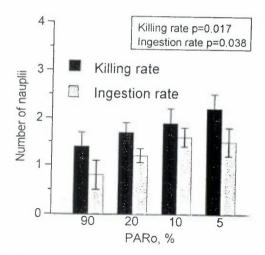


Figure 1. Killing and ingestion rates of *Artemia salina* nauplii (per polyp, per hour) by exterior branches of *Stylophora pistillata* colonies from habitats with different light intensities. P values are from one-way ANOVAs.

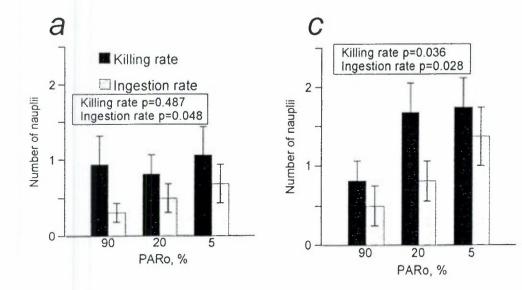
dynamics of feeding process (Figs. 3–5) only in one branch was used. Three analogous experiments on daily dynamics of feeding process at different days were performed. Means and standard deviations were calculated on the basis of data of these three experiments (n=3).

The influence of feeding and light conditions on activity of killing and ingestion of nauplii by corals estimated by an analysis of variance (one-way ANOVA), after examination of potential heteroscedasticity via Fmax-test. If the effect was significant (at significance level of 5%), a "Student's t-test" was used to evaluate differences between results of some experiments. All calculations were made using Statistics Proc (realise 5.1) Stat Soft. Inc.

3. Results

Physiological state of coral colonies from different light habitats

Results of measurements of production characteristics of S. pistillata coral branches from 2, 20 and 40 m depths are given in Table 1. The one-way ANOVA showed significant effect of light intensity on polyp's physiological characteristics: With a decrease in illumination from 90 to 20% of PAR₀ values of such characteristics as size of zooxanthellae cells, frequency of dividing zooxanthellae, rates of gross maximal photosynthesis and dark respiration remained practically unchanged. Chlorophyll (a + c₂) concentration in



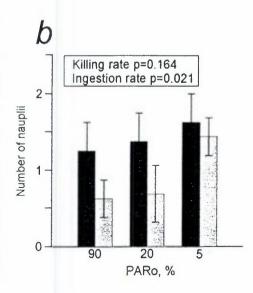
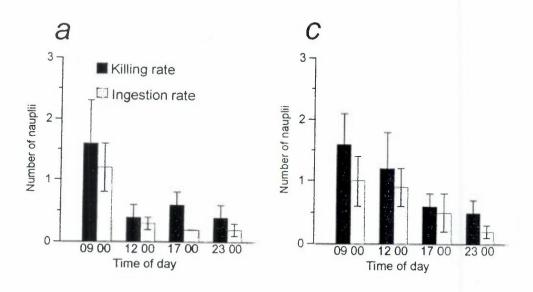


Figure 2. Killing and ingestion rates of *A. salina* nauplii (per polyp, per h) by external branches of *S. pistillata* colonies adapted to different light regimes and different feeding conditions: a – seawater; b – seawater with 20 µM (NH4)2SO4; c – seawater with added *Artemia salina* nauplii. P values are from one-way ANOVAs.



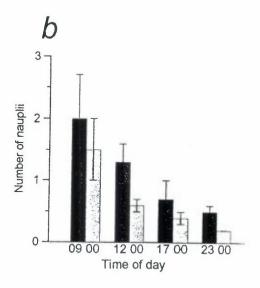
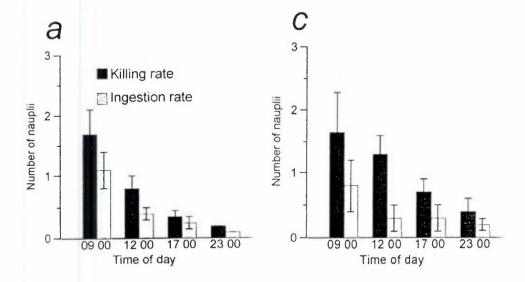


Figure 3. Killing and ingestion rates of *A. salina* nauplii (per polyp, per h) by exterior branches of *S. pistillata* colonies during the day adapted to 90% PAR0: a – seawater; b – seawater with 20 μ M (NH4)2SO4; c – seawater with added *Artemia salina* nauplii.



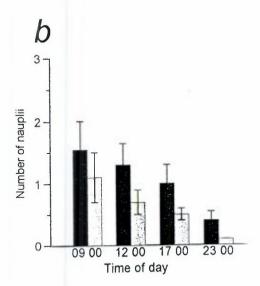
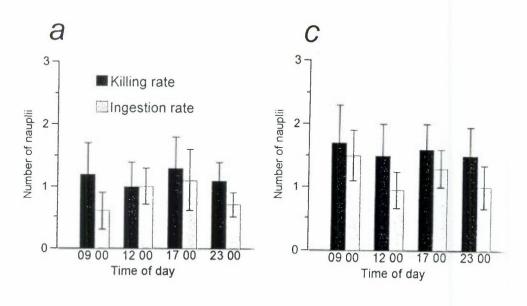


Figure 4. Killing and ingestion rates of *A. salina* nauplii (per polyp, per h) by exterior branches of *S. pistillata* colonies during the day adapted to 20% PAR₀: a – seawater; b – seawater with 20 μM (NH₄)₂SO₄; c – seawater with added *Artemia salina* nauplii.



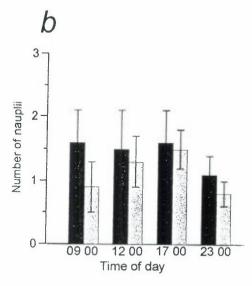


Figure 5. Killing and ingestion rates of A. salina nauplii (per polyp, per h) by exterior branches of S. pistillata colonies during the day adapted to 5% PAR₀: a – seawater; b – seawater with 20 μ M (NH₄)₂SO₄; c – seawater with added Artemia salina nauplii.

zooxanthellae cells increased by 72%, zooxanthellae number in a polyp increased by 35%. At 40 m depth (5% PAR₀) all measured characteristics, except the rate of maximal gross photosynthesis, changed in comparison with that from depth 2 m (90% PAR₀). Mean size of zooxanthellae increased by 46%, absolute values of frequency of dividing zooxanthellae dropped from 2.5 to 0.56%, chlorophyll (a + c₂) concentration in zooxanthellae increased 2.1 times; zooxanthellae concentration in a polyp increased by 66%, respiration rate dropped by more than 30%. With respect to the drop of dark respiration level, the ratio $P_{\rm gross}$ to $R_{\rm d}$ increased from 2.1 to 2.6.

Activity of Artemia killing and feeding by corals inhabiting different light conditions

We determined the potential activity of *Artemia* nauplii ingestion (feeding) and the rate of their killing by corals taken from 2, 20 and 40 m depths and from grottoes with illumination 10% PAR $_0$ (Fig. 1). The one-way ANOVA showed that polyp's nauplii killing and ingestion depended upon light intensity in the habitat of the colonies (p<0.05 for both reactions). At the same time the greatest rates of killing nauplii by polyps (about 2 nauplii by one polyp per hour) and ingestion (about 1.5 nauplii) were found in variants with low light (5 and 10% PAR $_0$). The least rates of killing (about 1.5 nauplii) and ingestion (about 0.7 nauplii) were found in bright light (90% PAR $_0$) (Fig. 1). It was shown that at illumination decrease from 90% (2 m) to 20% (20 m) of PAR $_0$, potential activity of nauplii feeding increased by 50–60%, and the ratio of fed to killed nauplii increased as well. A further decrease of illumination approximately down to 10% of PAR $_0$ kept stimulating activity of nauplii eating and increasing of E $_f$. The extreme low light (5% PAR $_0$) also stimulated killing as eating of nauplii, although E $_f$ was equal to that of variant under 90% PAR $_0$ (Fig. 1).

Activity of Artemia killing and feeding by corals adapted to different light and feeding conditions in aquaria

Coral branches acclimated for two weeks in aquaria to 90, 20 and 5% of PAR_0 and to different feeding conditions, were fed with *Artemia salina* nauplii in morning hours from 9:00 to 11:00. In all feeding conditions in seawater (Fig. 2a), with nitrogen enrichment (Fig. 2b) and with animal food feeding (Fig. 2c), coral branches adapted to low light (5% of PAR_0), ate nauplii 1.2–2.8 times more actively than corals adapted to high light (90% PAR_0). Stimulating effect of low light on activity of nauplii feeding displayed more distinctly in chambers with nitrogen enrichment and with nauplii feeding.

Reliable differences in the rates of nauplii killing under different light

intensities were observed only in variants with animal feeding, where under light 20 and 5% PAR_0 the rates of killing were more than two times higher, than under 90% PAR_0 (Fig. 2c). The coefficient E_f significantly increased with reducing light intensity from 20 to 5% PAR_0 only in variants with mineral and animal additions (P<0.05).

One-way ANOVA showed that after two weeks in aquarium the killing rate of nauplii by polyps depended upon light regime both under natural seawater conditions and under ammonium enrichment (Figs. 2a, b).

Daily fluctuations of feeding activity of corals in experimental conditions

Daily dynamics of rates of nauplii killing was investigated at all three above-mentioned light regimes in chambers with seawater, seawater enriched with nitrogen and seawater with constant nauplii additions (Figs. 3–5). ANOVA showed significant daily dynamics of killing and ingestion activity of corals from high light and moderate light incubation (P value in this experiment was not more than 0.02). In light conditions of 90 and 20% of PAR $_0$ (Figs. 3 and 4) the highest activity of feeding was displayed by corals in early morning hours, and towards the afternoon it lowered approximately twice (in some cases 5–6 times) and it kept dropping in the evening. Killing rate in these light variants also dropped from morning to night, but not so rapidly as feeding rate, therefore, the ratio $\rm V_i/\rm V_k$ dropped towards night. In all feeding conditions, daily dynamics of feeding was approximately the same at high and moderate illumination.

At low light (5% of PAR₀) we have not observed reliable changes of activities of nauplii killing and feeding in aquaria from 9:00 to 23:00 h in three variants of feeding (Fig. 5). Daily fluctuations in the rates of killing and eating of nauplii in all variants of the experiment amounted from 1.6 to 1.3 and from 1.4 to 0.8 nauplii per polyp per hour, respectively (P value from one-way ANOVAs was more than 0.41).

4. Discussion

Exterior branches of the coral colonies of *Stylophora pistillata*, taken from the Gulf of Eilat in November from the depths of 2, 20 and 40 m, considerably differed by their physiological state. These differences depended upon light conditions in habitats of the corals where light intensities were about 90, 20 and 5% PAR₀, respectively. Branches of *S. pistillata* dwelled in dim (20% PAR₀) and low (5% PAR₀) light, exhibited higher zooxanthella densities in polyp tissues and the zooxanthellae had higher concentrations of chlorophylls. The differences in zooxanthella densities and chlorophyll

content indicates that the coral branches were adapted to light in their habitats. Both adaptive reactions: the accumulation of photosynthetic pigments in zooxanthellae and increase in zooxanthella population density in polyps are common for hermatypic coral. Colonies under shade have increased light absorbence (Titlyanov et al., 1980; Falkowski and Dubinsky, 1981; Porter et al., 1984; Titlyanov, 1991a). Branches of S. vistillata, taken from the depth of 40 m exposed to extreme low light, differed from the others by low level of respiration and high ratio of Pgross to Rd, and its zooxanthellae showed larger sizes and very low indices of dividing cell frequency. The level of primary production (autotrophic function) for colonies of S. pistillata from the Gulf of Eilat (at depths from 2 to 20 m) was approximately equal and dropped five times at depth about 40 m (Porter et al., 1984). Low level of respiration of corals adapted to low light have been reported earlier for S. pistillata (Porter et al., 1984; Leletkin et al., 1996), as for other species of hermatypic corals (Chalker et al., 1983; Titlyanov, 1991b). That it is probably one of the responses of the corals to low light, which allows them to use rationally photosynthates under conditions of its deficiency. Nevertheless, at evident light deficiency at 40 m depth, S. pistillata did not lose its autotrophic potentialities and was capable of their complete realization at high light. At that time, under extreme low light zooxanthella population was presented mostly by large, rarely dividing cells and, in all probability, by old zooxanthellae. Furthermore, it is quite possible that large zooxanthellae from extremely shaded colonies of S. pistillata has another genetically determined type of zooxanthellae (Rowan, 1998; Titlyanov et al., in press).

In our analyses the reduce in light intensity, in the field as in aquaria (from 90 to 20% PAR₀) stimulated one kind of heterotrophic feeding – predation, more than 1.5 times. At further illumination drop down to 10% of PAR₀, predation capacities kept growing, but extremely low illumination did not cause further increase of predation activity. The level of predation activity depended on feeding conditions, corals displayed maximal activity when they were maintained in water with ammonium additions and at regular feeding with *Artemia* nauplii.

It is known that *S. pistillata* coral is related to the ecological group of animals which are capable of predation over 24 h with the maximum being in night hours (Sorokin, 1990). During our aquaria experiments, corals dwelling at high and moderate light increased predation activity in the morning and after that it dropped toward the middle of night. At the same time, corals from extremely low light conditions hunted approximately with similar activity from 09:00 to 23:00 hrs.

Predation of S. pistillata coral was evaluated by the rate of Artemia nauplii killing and the rate of their feeding. The ratio of these values (E_f) ranged in the experiments has very considerable limits from 0.9 to 0.1. All revealed

predation regularities can be equally related both to killing and feeding of nauplii, but the change of the rate ratio in different experimental conditions showed that coral utilized prey more efficiently (ate it more actively) at shading, in the morning and under conditions of sufficient mineral feeding.

Thus, it was shown for the first time that with the drop of light intensity in a habitat of *S. pistillata*, coral activation of potential capacities of one way of its heterotrophic feeding – predation – took place, and more effective utilization of prey as well. High activity of predation was provided by sufficient feeding with ammonium and zooplankton.

A question arises about internal mechanisms of predation stimulation. One of the adaptive reactions of predation stimulation of coral to the drop of autotrophic level is probably the change of daily dynamics in this way of feeding. Shaded colonies hunt actively all day, whereas illuminated ones – in the morning. Based on well-studied predation mechanism of corals (Yonge, 1940; Goreau et al., 1971; Porter, 1974; Sorokin, 1990) one can suppose that one of the adaptive reactions of predation to the drop in autotrophic level of coral may be activation of food reaction, hence its manifestations as greater hemoreceptive sensitivity to zooplankton (Johannes et al., 1969; Mariscal, 1971), greater activity of tentacles and nematocysts (Porter, 1974) and greater secretion of mucus binding prey (Sorokin, 1990). These suggestions are only a product of speculation, but after proving that coral predation is stimulated by a drop in light intensity, interest arises as to the nature and reactions of adaptation.

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