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Biology of small juveniles of the tropical holothurian *Actinopyga echinites*: growth, mortality, and habitat preferences

Abstract Several morphological, physiological and ecological experiments on the general biology of small juveniles (drained body weight=0.09 to 17.34 g) of *Actinopyga echinites* (Jäger 1833) (Echinodermata, Holothuroidea) were conducted between August 1991 and July 1992 at Bise reef flat, Okinawa, southern Japan. Supplementary experiments were carried out at the laboratory. The experiments were designed with a view to potential stock enhancement projects of *A. echinites* and other commercially exploited tropical sea cucumbers of the coral reef zone. During the enclosure experiments, the average percentage of drained body weight to fresh body weight of the juveniles was 48.3%. The specimens displayed a growth rate of 1500% during the 11-mo period. Their drained body weight increased from 0.87 to 12.82 g. The juveniles' internal and skeletal morphology differed considerably from the morphology of adult *A. echinites*. Two new types of skeletal spicules were discovered. Individual growth of all spicule types monitored differed notably, and shrinkage was observed for the two newly discovered types. Relative frequency of the spicule types within the skeletons changed with increasing body weights of the individuals. The juveniles of *A. echinites* displayed a strong habitat preference for plate-like substrate types such as eroded limestone or dead coral plates. Skeletons of *Acropora spp.* were accepted at a much lower rate. Weight-frequency distributions of the specimens on varying substrate types and between various times of the day showed significant differences. Cryptic behaviour of the juveniles was observed at all times of the day. Natural mortality of the holothurians, excluding predation and minor dislodgement effects, was low at 0.6% mo^{-1}. When predation effects were introduced to the experiments, mortality reached a rate of 0.3% mo^{-1}. The average percentage of predation effects within the natural mortality total was 76.8%. Juvenile *A. echinites* exhibited a maximum short-distance migration speed of 9 cm h^{-1}. This was two orders of magnitude slower than the speed observed in adults (900 cm h^{-1}) when differences in total body length were taken into consideration. The holothurians had two activity peaks during the 4-h periods monitored, around sunrise and sunset, respectively.

Introduction

Within the tropical Pacific region, there is an acute need for adequate management and stock enhancement projects for commercially exploited sea cucumber species. Catch statistics of the most valuable species have already indicated a decline, and fishery efforts are steadily forced to shift to holothurians of comparatively lower quality and market value (Conand and Sloan 1989). The estimated unsaturated capacity of the world market was 300000 tons in 1988 (Conand 1989). The holothurians enter the market predominantly as bêche-de-mer. This boiled and dried product is widely accepted as food in China and in most nations influenced by Chinese culture. In some countries, it is believed to have an aphrodisiacal character.

Scientific information on the ecology of tropical holothurians is still inadequate. Standard methods of ecological analysis do not apply to the taxon. Due to the fact that sea cucumbers lack growth rings within their already limited skeletons, assessments of the individual age of a specimen or the determination of the age-frequency distribution within a population are not possible. Recent tagging experiments conducted for several species were of limited success because the tegument structure of the holothurians enabled them to shed even penetrating floy tags (Conand 1983).

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A consequential problem with respect to tropical holothurian biology is the lack of any comprehensive information on the life history of the small juvenile stages. Under normal circumstances, it is next to impossible to detect small juveniles of any tropical holothurian species in the field. This significant gap in the overall knowledge of the ecology of holothurians prevails because laboratory rearing of this group has not yet been perfected. As a consequence of this lack of basic biological information, no conclusive research on community structures and population dynamics of sea cucumbers is available at this time. The implementation of stock enhancement programmes in areas where holothurian populations are already overfished is still unfeasible. Intended strengthening of recruitment through the potential release of juveniles to reef areas is not workable as long as essential biological aspects of certain life stages have not been established.

It was the objective of the project described here to acquire basic biological information on the small juvenile life stages of *Actinopyga echinites*. Several autonomous as well as dependent biological variables of juvenile *A. echinites* were evaluated during an overall experimental period of 1 yr. *A. echinites* may be a welcome model species for commercially exploited tropical holothurians inhabiting the outer reef flat.

Fig. 1 Design of a modified polypropylene box used during the field experiments on growth and mortality rates of juvenile *Actinopyga echinites*. Box with closed lid secured by four concrete blocks (12 kg each) and eight steel anchors (bottom left). Elevation of the box design shows three removable trays, a styrofoam shield to create a shadow zone, and a floating mesh frame encircling the inner rim of the box (top left). Design of a removable tray containing varying substrate types during the experiments (bottom right). Close-up of the floating mesh frame installed to prevent emigration (top right)

Materials and methods

Actinopyga echinites (Jäger 1833), Holothuriidae, Aspidochirotida, is a sea cucumber species with a wide distribution range in the tropical and subtropical Indo-Pacific region (Panning 1944; Cherbonnier 1955; Rowe 1969; Clark and Rowe 1971). The species is abundant, but not particularly dominant at any locality. The popular name of *A. echinites* is "deep-water red fish" or "Hung-Hur" (in Chinese). These holothurians have a dorsally arched subcylindrical body which is ventrally flattened. There are 20 peltate yellowish oral tentacles present in adult specimens. The body colour is variable from grayish to dark brown. The identification of the juvenile *A. echinites* in this report is based on Clark and Rowe (1971), Rowe and Doty (1977) and Reyes-Leonardo (1984) who established identification criteria for adult specimens. The morphological parameters of the juveniles differed slightly differences from adult *A. echinites*. Tissue samples were deposited at the Institute of Marine Sciences, University of Kiel, Germany. A comprehensive description of the general biology and ecology of tropical holothurians is given by Bakus (1973) and should be referred to for any additional details on the taxon not given in this article.

A total of 628 juvenile specimens analyzed in the present study were collected south of Eefu Beach on the west coast of Kume Island, 75 km east of Okinawa Island on 28 July 1991. The range of drained body weight within the cohort was 0.09 to 1.20 g at this time. The *Actinopyga echinites* individuals had been washed to the upper reef zone by a strong typhoon that hit Kume Island on 27–28 July 1991 (max. speed 150 km h⁻¹). The field experiments were conducted on the reef flat (fringing reef) at Bise Village (127°52′ 5″E, 26°42′ 10″N) on the northwestern coast of Motobu Peninsula, Okinawa, Japan, from August 1991 to July 1992. This particular site was chosen for the experiments because the area displayed the highest density of adult *A. echinites* on Okinawa.

Specimens of *Actinopyga echinites* were analyzed for morphology and for morphometric parameters based on the studies of Clark and Rowe (1971), Doty (1977), Massin (1979), Feral and Massin (1982), Tan Tiu (1981), and Cannon and Silver (1986). A dissection and a light microscope were used. Sketches of the outer body mor-
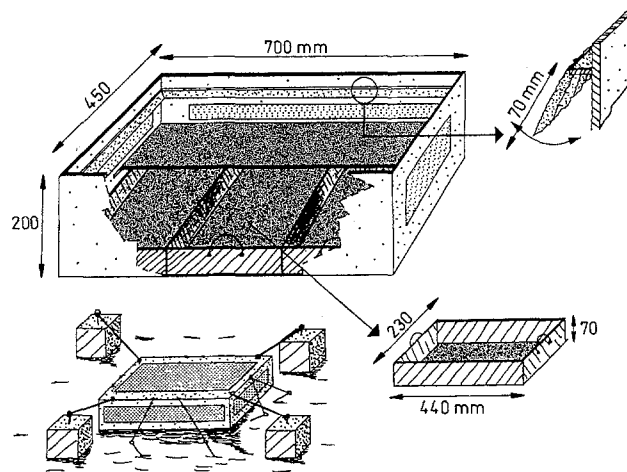
phology and particular body regions of interest for systematical classification were prepared. Additionally, the dimensions of the skeletal spicules (types) were determined and their structures were sketched. During the entire experimental period, spicule size and frequency of particular spicule types within the skeleton were monitored monthly in order to analyze potential weight dependent changes of these formations. Two juveniles with a body weight close to the monthly determined average body weight were analyzed each month. The whole individuals were dissolved (weak KOH-solution) to determine relative frequencies of spicule types within the body tissues of the specimens. The obtained suspensions were filtered (150 μm) and randomized subsamples were analyzed to determine spicule quantities.

The growth parameters of the juveniles evaluated in the present study were compared to estimations of theoretical growth in adult *Actinopyga echinites* from Conand (1989). Conand's original data set, which consisted of only theoretical fresh weights, was converted to drained weights using the conversion factor established in the present study. Conand (1989) was not able to specify the age of the holothurians at the beginning of her observation period. In order to permit a direct comparison with the present study, the starting age in Conand's study was defined as $t=365$ d. The youngest specimens in her theoretical study were 1 yr old. This specification was feasible with respect to the average weights of *A. echinites* observed during the present study.

Three progressive enclosure experiments, methodically based on each other, were conducted in the field in order to determine substrate preferences, light-zone preferences, growth and mortality of the juveniles. Natural mortality was analyzed weekly or monthly, both including and excluding predation effects and potential minor dislodgement effects. Tagging as well as releasing and recovery of the holothurians in the field was out of the question due to their small size. Instead, the specimens were kept in three modified polypropylene boxes (length/width/height: 700×450×200 mm), each contributing a parallel set of data (Fig. 1). The boxes were closed with removable lids during the first and second field experiments. During the third experiment the lids were removed. The lids and walls of the boxes had windows covered with a 2-mm polyethylene mesh. The boxes were modified in order to provide space for three replaceable

trays which could contain three matching or varying substrate types. The trays were arranged parallel to each other (Fig. 1) and had no contact with the box wall in order to avoid side effects from the box. A certain percentage of the area of each tray could be darkened by adding a horizontal styrofoam shield to create zones of higher and lower light intensity for each substrate type (tray) monitored. The area covered was 50% shadow on all substrate types during the first and second experiments and 25% shadow during the third field experiment. In order to prevent the juveniles of *Actinopyga echinites* from escaping after removal of the lids, floating mesh frames were installed encircling the inner walls of the boxes (Fig. 1). The effectiveness of this design was tested during a laboratory experiment prior to initiation of the field trials.

The boxes were submerged at Bise Reef flat at a depth of 1 m below mean low water spring tide. A distance of 10 m separated each box. The wider sides of the boxes faced the tidal currents, thereby enhancing water exchange. The narrow sides faced the direction where the impact of strong wave actions (during typhoons) would probably occur. The boxes were securely fastened to the sea floor using four concrete blocks (12 kg each) and eight steel anchors (length=300 mm) for each box. The windows of the boxes were cleaned at maximum intervals of 2 wk. The trays were removed from the boxes for each observation because the evaluation of the morphometric and behavioural parameters, by counting, had to be conducted on land. As a closed unit containing both the individual substrate and the attached specimens, the trays were separately placed into transparent plastic bags and immediately transported out of the water. On land, the holothurians on each artificial habitat type were counted and individual weights were taken as fresh weights (g) excluding cloacal water.

In addition to the experiment boxes, two similar boxes, which functioned as back-up stocks and at the same time as a control group during the experiments on predation effects (third field experiment), were submerged at a distance of 10 m. The design of these back-up boxes and the substrate types they contained were progressively adjusted according to the three experimental boxes monitored. These boxes were held closed during the entire experimental period. The *Actinopyga echinites* individuals within the back-up boxes were used to replace missing individuals inside the experimental boxes after each observation, in order to eliminate density-dependent environmental effects. Thus, density of the specimens within the experimental boxes was adjusted at a definite level (n=120 ind). However, the number of individuals available was not sufficient for the entire experimental period.

First field experiment: habitat preference (rough scale)

The first field experiment was designed in order to determine gross habitat preferences of juvenile of *Actinopyga echinites*. The experiment was conducted over a period of 5 wk from 1 August 1991 to 9 September 1991. A total of 360 individuals was randomized and 120 individuals were placed into each of the three boxes. At the start of each period, the holothurians were divided into two groups of 60 individuals and were placed on the borderlines between the three substrate types and the two illumination (light/shadow) zones (Fig. 1). The six habitat types monitored during the experiment were: A. Coarse sand of 0.5 to 5.0 mm grain diameter (light/shadow). B. Branches of dead *Acropora spp.* (light/shadow). C. Dead coral plates and limestone (light/shadow).

Every week, the distribution patterns of the holothurians within the boxes were determined and individual weight was evaluated for each specimen in the manner described below. Relative mortality was calculated for each experimental period, and dead individuals were replaced with individuals from the back-up boxes. All data were collected between 11:00 and 14:00 hrs on any sampling date. Two additional experiments were carried out during the nights of 15 and 17 August 1991 because it was possible that distribution patterns might have been different between night and daytime.

Second field experiment: habitat preference (fine scale)

The second field experiment was conducted from 17 September to 24 October 1991 and had the same design as the first experiment. The sampling frequency was again weekly. Unlike the first field experiment, the following six habitat types were provided: A. 75% coarse sand/25% plates (light/shadow). B. 50% coarse sand/50% plates (light/shadow), C. 25% coarse sand/75% plates (light/shadow).

Third field experiment: growth, natural mortality and predation effects

The general design of the third field experiment was similar to the first and second one except that the lids covering the experimental boxes were removed. This allowed the access of potential predators such as *Tonna perdix* (Gastropoda, Mollusca), scorpion- and lionfish, groupers, lizardfish, triggerfish, and pufferfish. Potential dislodgement of the specimens was minimized by the distinctive design of the boxes (high walls and floating mesh frame), by location of the boxes within an area of minor wave impact and through the practice of closing the boxes during periods of strong wave action (typhoons). The experiment was conducted from 2 November to 27 July 1992. Growth and mortality of the specimens were determined every month. Only one habitat type was supplied: mixture of 25% coarse sand/75% dead coral plates or eroded limestone. Different light zones were created (25% light/75% shadow zone each) but not analyzed individually.

Laboratory experiment: short-distance migration behaviour

The experimental methodologies in the field were supplemented by a laboratory experiment. Linked to the aspect of habitat preferences, this experiment was initiated in order to analyze the average migration speed of undisturbed juvenile *Actinopyga echinites* of the size range 0.19 to 3.49 g (fresh weight). It was conducted on 11 January 1992.

A total of 50 individuals was taken from the back-up boxes in the field and was monitored in an aquarium tank after an acclimatization period of 1 wk. Over a period of 4 h under four different daytime conditions (e.g. under varying light intensities) distances migrated were recorded. The distances were measured using coloured metal pins attached to a polyethylene grid (5 mm grid-width) that was suspended above the specimens. The migration speed was calculated as cm h^{-1}. The bottom substrate consisted of a combination of dead coral/limestone plates and coarse sand from the experimental site. The experimental periods were set as: (1) 02:00 to 06:00 hrs; (2) 10:00 to 14:00 hrs; (3) 19:00 to 23:00 hrs; (4) 23:00 to 03:00 hrs.

In addition to the aquarium experiment of the juveniles, 50 adult *Actinopyga echinites* were analyzed for locomotive speed in the field. Steel pins were used to mark starting points, and the distance travelled was measured after periods of 10 min.

Weight determination

The term "fresh weight" (g) used in the present study was defined as the total body weight of a live specimen excluding cloacal water. The exclusion of the water content of the cloaca, the posterior part of the intestine, was important to eliminate the possibility of experimental bias. The cloacal water typically constitutes a considerable part of the body weight of sea cucumbers (Choe 1963; Conand 1981). Usually, it is not possible to tell whether an individual has or has not already discharged this water volume prior to determination of weight. In order to ensure that the discharge had taken place, the holothurians were kept out of the water for 15 min, which forced them to open their anal sphincter. This timespan was established through preliminary experiments.

The term "drained weight" (g) used in the present study was defined as total body weight of an individual excluding cloacal and coelom water. A determination of the drained weight was possible only through dissection of the specimens. The evaluation of drained weight was an important aspect to consider because it enabled comparisons between the final results of this study and previous results on the growth parameters of adult holothurians. A determination of dry weights and, in particular, ash-free dry weights was not made because these parameters are not commonly used for adult holothurians.

The number of individuals monitored in the present study was already very limited and could not be jeopardized in any way. In view of this situation the relationship between fresh and drained weight was determined only after all experiments were finished. In random order, a total of 120 *Actinopyga echinites* were analyzed for fresh and drained weight during three different daytime intervals on 28 July 1992. In doing so, the potential inconsistency of the relationship between the average fresh and drained weight of the specimens was evaluated. The observation periods were defined as: (1) 08:00 to 10:00 hrs; (2) 11:00 to 13:00 hrs; (3) 16:00 to 18:00 hrs.

A conversion factor from drained weight to fresh weight was defined as the smallest difference between these two parameters observed during any daytime period, the rationale being that this minimum factor was closest to the true relationship between these two parameters. The application of the daily averages would have led to overestimations of drained weights.

— Anal tooth
— Sphincter
— Anal orifice
— Outer anal rim

25 μm

Fig. 2 *Actinopyga echinites*. General morphology of a juvenile *A. echinites*. **a** External morphology of a specimen of 17 mm length, maximum diameter 9 mm. **b** Pelate tentacle. **c** Anal opening: anal sphincter and anal teeth are dark brownish colour. *1* to *5* Observed types of skeletal spicules found in body tissue of *A. echinites*. *1* Asymmetrically branched solid rods. *2* Symmetrically branched solid rods. *3* Dichotomously branched thin rods. *4* Unbranched linear solid rods. *5* Branched spade-shaped rods. Type 1, 2 and 3 spicules compare to Clark and Rowe (1971) for adult *A. echinites*. Type 4 and 5 are newly discovered types for juvenile *A. echinites*.

Results

The average drained weights as percentages of fresh weights of the juvenile *Actinopyga echinites* were significantly different from each other and 48.3% during the period 08:00 to 10:00 hrs, 54.3% during the period 11:00 to 13:00 hrs and 51.9% from 16:00 to 18:00 hrs. The smallest average conversion factor f=0.4825 was thus observed during the period from 08:00 to 10:00 hrs. This factor was applied to all calculations of drained weights from fresh weights whenever appropriate.

General morphology and morphometry

The monitored specimens of *Actinopyga echinites* displayed a weight range (average drained weights) of 0.09 to 1.20 g at the initiation of the first experiment and 7.29 to 17.34 g at termination of the last experiment after 11 mo. The average length of the specimens, although constituting a highly vacillating morphometric parameter, was initially 15 and 71 mm at termination of the experiments.

The coloration of the holothurians varied between dark beige and dark brown. The outer tegument was covered with numerous papillae (Fig. 2). The body wall of the specimens was thick and stiff. It was 2 mm thick in small (8 g drained body weight) individuals and 4.5 mm thick in large (16 g drained body weight) individuals. The anal orifices were guarded by five short truncate teeth and closed by a black coloured sphincter (Fig. 2). Twenty peltate whitish tentacles were arranged in a circle around the ventrally located mouth (Fig. 2). Cuvierian tubules were present but low in number and of a white colour instead of light pink, which was reported for adult *Actinopyga echinites* (Conand 1986). Evisceration was never observed during the present study. It was not possible to detect rudimental gonads in any of the dissected individuals. The digestive tracts of the holothurians were short. The relation of the length of the digestive tract to body length was 110 to 120%. Unlike in adult *A. echinites*, the intestines did not consist of numerous loops. The *lacuna intestinalis* and the *vena transversalis* showed a low number of ramifications.
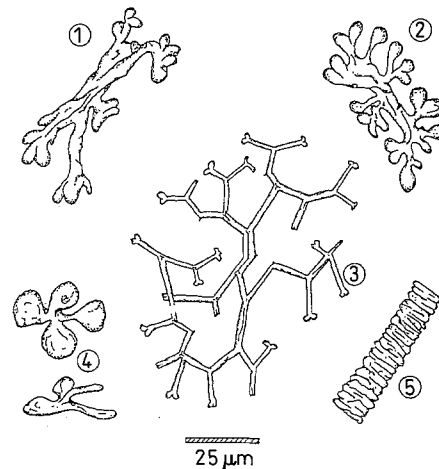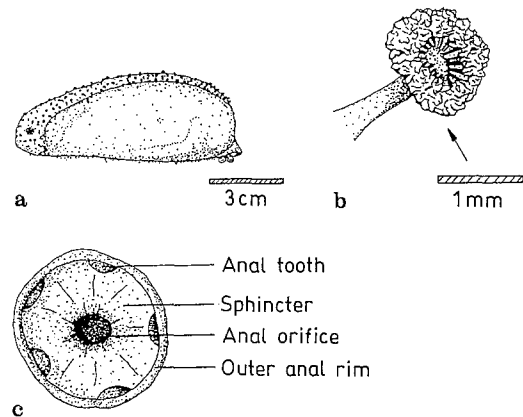
Structure, size and frequency of skeletal spicules

In addition to the calcareous oesophagal ring (Fig. 3), the skeleton of the juvenile *Actinopyga echinites* consisted of five types of minute spicules (Table 1, Fig. 2), namely, disk-shaped types: Type 1 asymmetrically branched solid rods, Type 2 symmetrically branched solid rods, Type 3 dichotomously branched thin rods; and other types: Type 4 unbranched linear solid rods, Type 5 branched spade-shaped solid rods.

The percentage of spicules of Type 4 and 5 was very low. Type 4 spicules were limited to the tube feet, the tentacles and the inner organs of the holothurians. Type 5 was exclusively found within the ventral tegument. The other three types were apparent in all body teguments. All types of spicules, except Types 4 and 5, showed lateral growth during the analyzed period of 12 mo (Fig. 4). During the
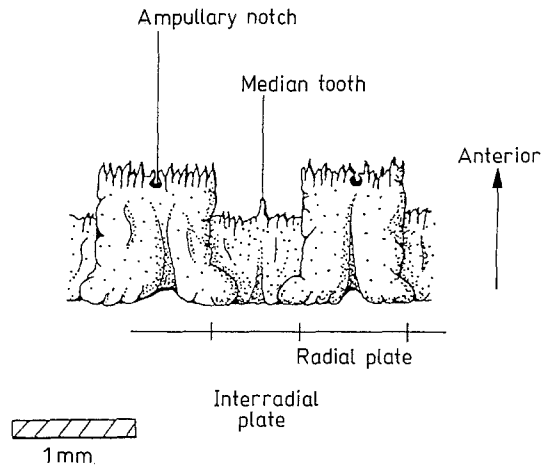
Fig. 3 *Actinopyga echinites.* Morphology of the calcareous oesophagal ring. The calcareous ring consists of ten segments (five radial and five interradial segments). The ring was dissected from a specimen of 8.2 mm body length and had a diameter of 2.5 mm
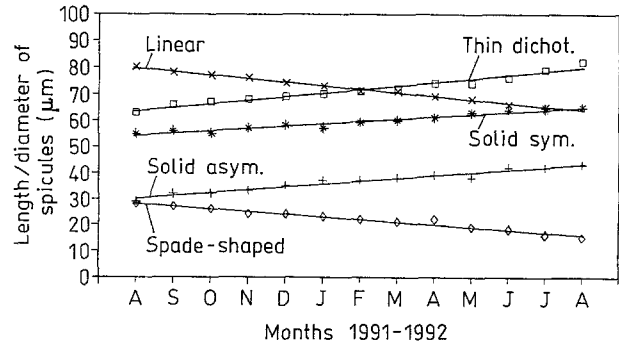

Fig. 4 *Actinopyga echinites.* Development of average size of calcareous skeletal spicules of *A. echinites* kept under natural conditions from August 1991 to August 1992. Dimension (μm) is length for the unbranched linear rods and maximum diameter for all other spicule types. Standard deviations, ranging from 2.2 to 4.4, showed no particular trends or oscillations and are thus not included in the figure. Each month, twenty spicules from two specimens were randomly analyzed after holothurians had been dissolved in weak KOH-solution for 3 d. This small monthly sample size was selected because of the genuinely limited total number of juveniles during the ecological experiments. Size was measured using a light microscope. During the same period, average drained body weight of the juveniles exponentially increased from 0.87 to 12.82 g

Table 1 *Actinopyga echinites.* Types, average dimension and frequency of skeletal spicules found in juvenile *A. echinites.* Body tissue types not further specified. Dimensions and frequencies determined from intact spicules only. Observation period: August 1991 to July 1992. Number of individuals analyzed: 2 mo^{-1}. Total number of individuals observed: 24

Spicule type	Average length (l) or max. diameter (d) (μm)	Average frequency for entire ind (%)	Tissue type
Asymmetrically branched solid rods	36.0±12.3 (d)	60.0±6.4	All body tissues
Symetrically branched thin rods	59.5±17.5 (d)	18.0±2.3	All body tissues
Dichotomously branched thin rods	71.5±11.0 (d)	16.5±2.1	All body tissues
Unbranched linear solid rods	75.0±21.4 (l)	3.5±1.2	Tube feet, tentacles, inner organs
Branched spade-shaped solid rods	25.0±13.1 (d)	2.0±0.8	Ventral body wall

same period, the average drained body weight of the juveniles increased from 0.87 to 12.82 g. The disk-shaped rods showed an increase in diameter of 20 to 25% yr^{-1}. The solid unbranched linear rods and the spade-shaped rods exhibited shrinkage (20 and 13 μm yr^{-1}, respectively). Growth or shrinkage of all spicule types was linear during the entire experimental period.

The probable age of the specimens where the disappearance of Type 4 and 5 spicules would be complete, if shrinkage continues to be linear, was extrapolated as t=5 1/4 yr for Type 4 and t=3 yr for Type 5. Frequency of the different spicules types changed with increasing body weight of *Actinopyga echinites.* The highest frequency within the

skeleton (Table 1) was observed for Type 1 (54 to 66%), Type 2 (13 to 25%) and Type 3 (13 to 17%). The number of Type 2, 4 and 5 spicules decreased with increasing body weight. Frequency of the asymmetrically branched solid spicules and the thin dichotomously branched spicules increased at the same time. In addition, the latter two types displayed increased numbers of ramifications within their structures.

Habitat preference

During the first field experiment, the juvenile *Actinopyga echinites* displayed a strong preference (69.3%) for the plate substrate consisting of limestone and dead coralline material (Fig. 5). The sandy substrate was accepted to a lower degree (26.1%), and dead *Acropora spp.* branches were almost completely avoided (4.6%). The holothurians inhabiting the sandy substrate showed a higher average weight of 1.55 g (Figs. 7, 8) than those on the plate substrate (1.42 g). Weight-frequency distributions were significantly different (t-test, $p<0.05$) between these two groups (Fig. 6). There were no significant differences (t-test, $p<0.05$) between the weight distributions of holothurians on *Acropora spp.* branches and those on sand or coral plates.

During the second field experiment, the holothurians strongly (71.8%) preferred the substrate mixture of 75% limestone/coral plates and 25% coarse sand (Fig. 5). The remaining individuals were almost all equally divided among the 50/50% and the 25/75% substrate combinations (12.1 and 16.2%, respectively). There was no significant difference in average weights (Figs. 7, 8) or weight distributions of the juveniles among the particular substrate types (t-test, $p<0.05$).
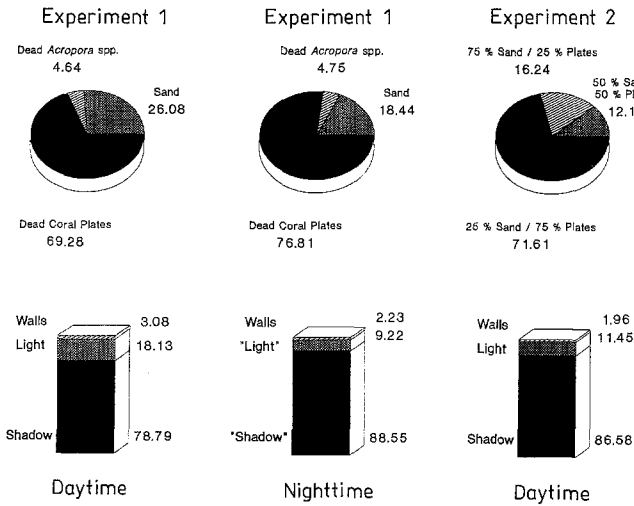
Experiment 1 — Dead *Acropora* spp. 4.64 / Sand 26.08 / Dead Coral Plates 69.28

Experiment 1 — Dead *Acropora* spp. 4.75 / Sand 18.44 / Dead Coral Plates 76.81

Experiment 2 — 75 % Sand / 25 % Plates 16.24 / 50 % Sand / 50 % Plates 12.15 / 25 % Sand / 75 % Plates 71.61

Daytime: Walls 3.08 / Light 18.13 / Shadow 78.79

Nighttime: Walls 2.23 / "Light" 9.22 / "Shadow" 88.55

Daytime: Walls 1.96 / Light 11.45 / Shadow 86.58

Fig. 5 *Actinopyga echinites.* Substrate and light-zone preferences of small juvenile *A. echinites* (*n*=360 ind) during two enclosure experiments (modified polypropylene boxes). During Expt 1, distributions were analyzed both during the day and at nighttime. Expt 2 was limited to daytime observations. Substrate types (light zones) during first experimental period (5 wk) were: coarse sand of 0.5 to 5.0 mm grain diameter (light/shadow); branches of dead Acropora spp. (light/shadow); dead coral plates and limestone (light/shadow). Substrate types (light zones) during second experimental period (5 wk) were: (1) 75% coarse sand/25% plates (light/shadow); (2) 50% coarse sand/50% plates (light/shadow); (3) 25% coarse sand/75% plates (light/shadow). Pie charts show distributions on substrate types excluding individuals attached to the box walls. Bar charts show distributions of juvenile *A. echinites* in light zones (and on substrates) as well as percentages of individuals including individuals attached to the box walls
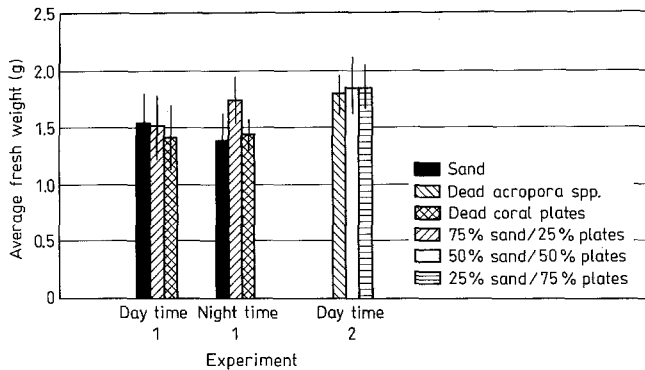

Fig. 6 *Actinopyga echinites.* Average fresh body weight (g) of small juvenile *A. echinites* on separate substrate types during two consecutive enclosure experiments at Bise Reef, Okinawa, Japan (August to October 1991). Expt 1 was conducted during the day as well as during the night. Expt 2 was conducted during the daytime only. Illumination effects are removed for clarification of substrate-type induced effects. Total number of individuals examined wk^{-1} was *n*=360. Error bars indicate SD

Fig. 7 *Actinopyga echinites.* Average fresh body weight (g) of small juvenile *A. echinites* in two illumination zones (light/shadow) during two consecutive enclosure experiments at Bise Reef, Okinawa, Japan (August to October 1991). Expt 1 was condicted during the day as well as during the night. Expt 2 was condicted during the daytime only. Substrate effects are removed for clarification of light-induced effects. Total number of individuals examined wk^{-1} was *n*=360.

Fig. 8 *Actinopyga echinites.* Comparison of distributions of (fresh) body weights of small juvenile *A. echinites* on **A** different substrate types on sandy substrate and **B** during the day and nighttime during an enclosure experiment (August 1992) at Bise Reef, Okinawa, Japan

The individuals examined exhibited a stronger adhesion to the plate substrate than to the *Acropora spp.* branches. This was observed when trying to remove undisturbed specimens within the experimental boxes. The individuals on the branches demonstrated more active movement, whereas the individuals on the plate substrate appeared to
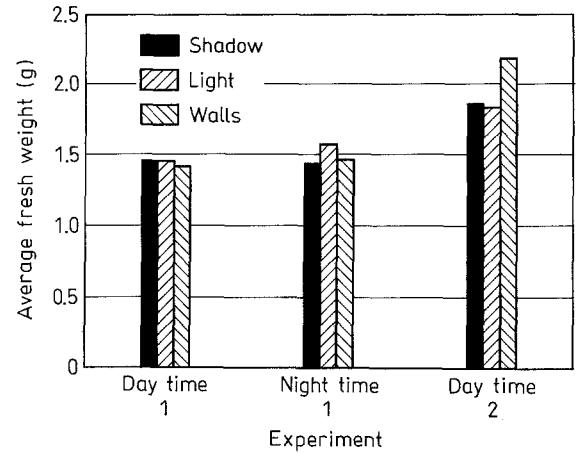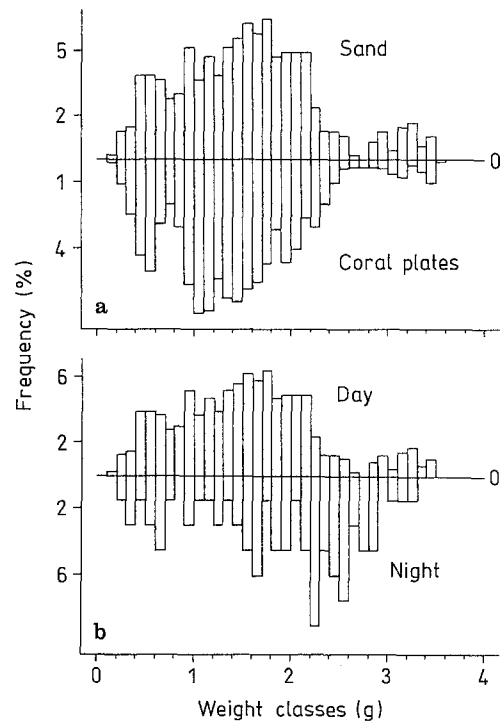
be stationary. The juveniles on the sandy substrate type were partly burrowed and had all their ventral tentacles attached to sand grains. The juveniles showed a strong preference for darkened substrate types during the first and second field experiment (Fig. 5). Light zone preferences were more evident on the optimized substrate types used during

the second experiment (86.6%) than on the 100%-plate substrate during the first experiment (78.8%). Only 2 to 3% of the specimens were attached to the tray or box walls. This finding, in addition to the established enclosing effect of the floating mesh frames, implied that escape effects were not to be anticipated during the subsequent third experiment. No significant differences were found for any of the parallel samples (boxes) between the three experimental boxes regarding weight distributions between light and shadow zones (t-test, $p < 0.05$). Frequency distributions in light and shadow zones on particular substrate types did not differ significantly between parallel boxes either (t-test, $p < 0.05$).

During nighttime, the distribution of the holothurians (Fig. 5) shifted slightly in favour of the plate substrate (76.8%) compared to daytime distributions during the first experiment (69.3%). While percentages of individuals on the *Acropora spp.* substrate were almost similar to those during the daytime (4.8 and 4.6%, respectively), there was significantly less preference (t-test, $p > 0.05$) for the sandy substrate during the nighttime (18.4% Expt 1; 26.1% Expt 2). Compared to distributions between the shadow and the light zones during the daytime, the "light" zones were avoided to a higher degree at night (9.2% at night / 18.1% during the daytime; t-test, $p > 0.05$). The average drained body weight showed no significant differences (t-test, $p < 0.05$) between daytime and nighttime during the first experiment (Figs. 7, 8). On all substrates, the holothurians were less firmly attached to the surface during the nighttime. The activity of the juveniles was higher at night. More individuals were observed feeding on the sediments covering the substrates at night than during daytime sampling. A U-test conducted between weight frequency distributions of the individuals on the sandy substrate during the day or nighttime revealed a significant ($p < 0.05$) statistical difference (Fig. 8). This indicated that diurnal migration had taken place.

Mortality

The natural mortality of the juveniles was almost constant between 0.4 and 0.8% (average=0.6%) mo^{-1} during Expts 1 and 2 (Fig. 9). It was not possible to establish the cause of this mortality. Three dead individuals which were recovered from the boxes showed no signs of external damage, but their body walls were soft and in the process of disintegration or decomposition. Missing specimens were also classified as disintegrated, because this process has been reported to occur comparatively fast in holothurians (Bakus 1973; Takahashi 1974). The invasion of predators into the boxes or the escape of juveniles from the boxes was not possible.

After the removal of the box lids and the invasion of potential predators, natural mortality rates increased to an average value of 3.3% of the individuals per month (Fig. 9). An increase of almost 500% during the first month of predator access was observed on several occasions (0.4 to 1.85%). No predation effects were observed for the con-
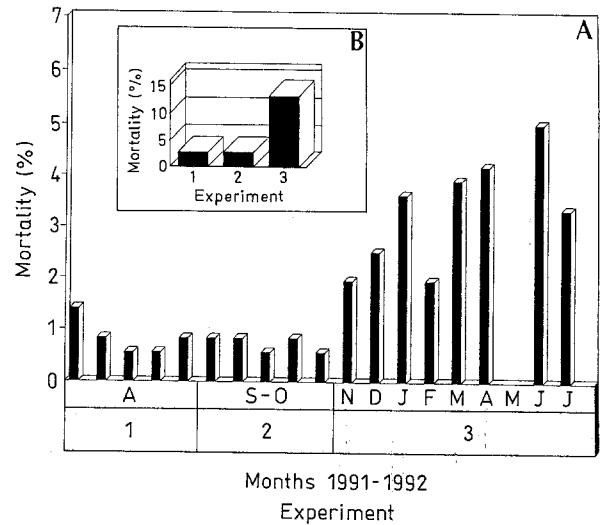

Fig. 9 *Actinopyga echinites.* Natural mortality rates of small juvenile *A. echinites* during three consecutive enclosure experiments from August 1991 to July 1992, at Bise Reef, Okinawa, Japan. Expts 1 and 2 (5 wk) excluded predation effects (box lids closed). Expt 3 (9 mo) included predation and minor dislodgement effects (box lids opened). **A** average mortality rates during 1-mo periods. **B** Average mortality rates during 4-mo periods (extrapolated for Expts 1 and 2). All results presented as missing percentages of $n=360$ ind applied to triplicate boxes at the start of each observation period. Sampling was weekly during Expts 1 and 2, monthly during Expt 3
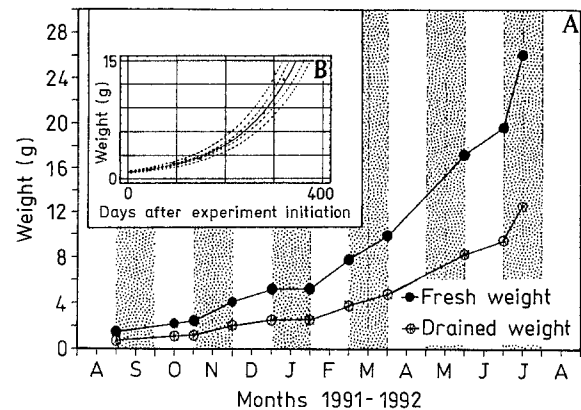

Fig. 10 *Actinopyga echinites.* Development of average body weight (g) of small juvenile *A. echinites* during 11 mo (August 1991 to July 1992) in three consecutive enclosure experiments at Bise Reef, Okinawa, Japan. **A** Average fresh weights and calculated drained weights. **B** Exponential regression fitting of drained body weights observed. Due to progressive mortality, the total number of individuals analyzed per month decreased from initial 360 individuals from August 1991 to May 1992 (monthly reinstallment of $n=360$ from back-up box) to 265 individuals in July 1992

trol group (back-up box). Predation pressure as part of the natural mortality rate of *Actinopyga echinites* juveniles intensified with increasing average body weight of the individuals (1.31 to 12.82 g) from 72.3% in November 1991 to 88.1% in July 1992. The average percentage of predation effects was 76.8%. This may have included minor dislodgement effects. Predation-free natural mortality was independent from increasing average weights of *A. echinites.*
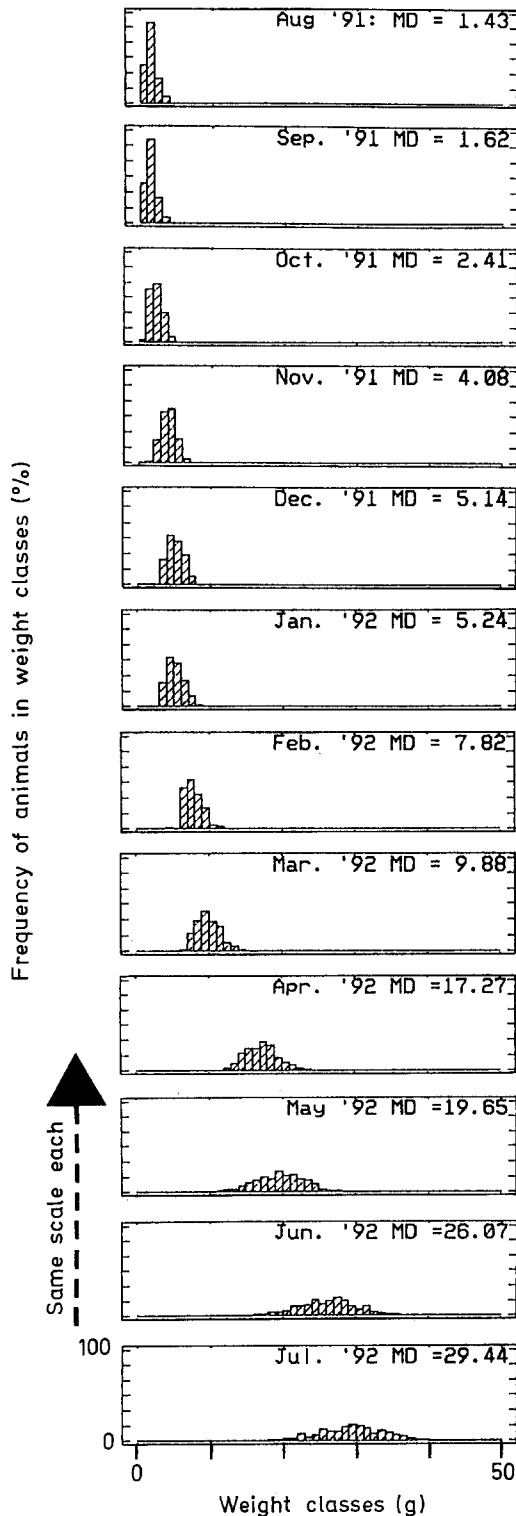
Potential predators which were observed in the vicinity of, as well as inside, the experimental boxes were *Tonna perdix* (Gastropoda, Mollusca) and fish of several families: Scorpaenidae (scorpion- and lionfish), small Serranidae (groupers), Synodontidae (lizardfish), Balistidae (triggerfish), Tetraodontidae (pufferfish).

Growth

The average growth of *Actinopyga echinites* drained body weight versus time (Fig. 10) can be described by the equation:

$$weight = e^{[-0.244+(t—t_0)0.00855]}$$

Dimension of t is in days. The regression coefficient (Fig. 10 B) is $r=0.9905$.

The fresh, as well as drained weights of the holothurians increased continuously during the complete run of the field experiments. The initial average drained body weight was 0.87 g. After 11 mo, it had increased by a factor of 15 to 12.82 g. Weight increase diminished during the period from December 1991 to February 1992, which is the winter season on Okinawa. The average monthly water temperature at the study site was at a minimum (20.7°C) during this three-month period. Weight frequencies showed a typical progression of normal distributions during the entire experimental period (Fig. 11).

It was feasible to visually connect the growth curves of the juvenile and adult *Actinopyga echinites* (Fig. 12). The 99% confidence interval of the theoretical study embodies a substantial portion of the growth curve in the present study. This regression performed by Conand (1989) shows a linear increase of weight because she calculated the theoretical growth using the von Bertalanffy growth equation, which has to be considered an approximation. Juvenile
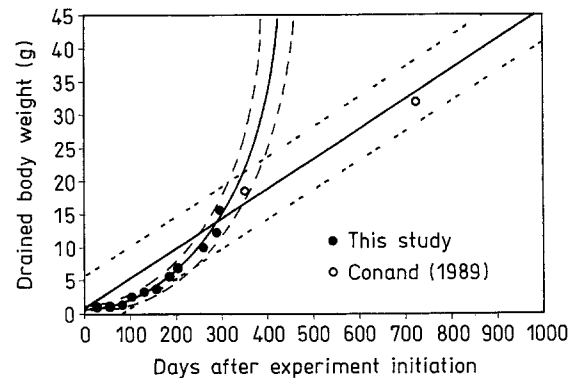

Fig. 11 *Actinopyga echinites*. Weight frequency distributions (g) of small juvenile *A. echinites* in weight classes during three consecutive enclosure experiments at Bise Reef, Okinawa, Japan, from August 1991 to July 1992. Continuous lines are fitted normal distributions. Total number of individuals analyzed was $n=360$ ind from August 1991 to February 1992, $n=289$ ind in June 1992, and $n=265$ ind in July 1992

Fig. 12 *Actinopyga echinites*. Growth of juvenile *A. echinites* during three consecutive enclosure experiments at Bise Reef, Okinawa, Japan (August 1991 to July 1992). Growth presented as increment of the average individual drained body weight (g). Filled circles represent results from the current study. An exponential regression is fitted to the data. Open circles represent results from Conand (1989). A linear regression is fitted to these data. Conand (1989) analyzed growth of adult *A. echinites*. Thus, the remaining data points lay outside the range of the figure but are involved during regression fitting. Dotted lines are 99% confidence intervals
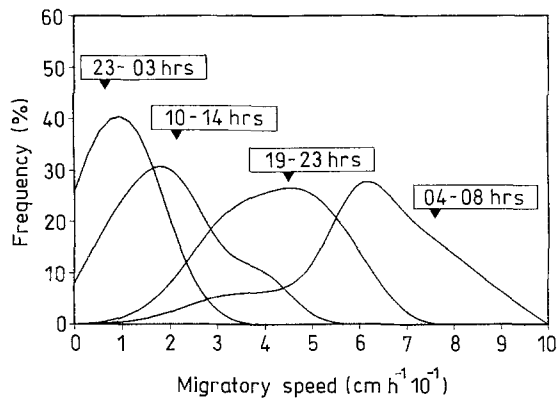
Fig. 13 *Actinopyga echinites*. Average migratory speed (cm⁻ʰ) of undisturbed juvenile *A. echinites* at four daytime periods during an aquarium experiment. Observation periods were 4 h each. Distances were determined every hour using a mesh frame suspended above the specimens. The daily light cycle was adjusted to natural conditions. Natural seawater and substrate from sites of high abundance of adult *A. echinites* (Bise Reef) were used. Consistency and structure of the substrate was homogeneous. No shadow zones were offered. Total number of individuals observed was $n=50$

growth observed during the experiments was faster than the theoretical growth of the adult *A. echinites* in the study by Conand (1989).

Migration behaviour

In the aquarium tank, 50 juvenile *Actinopyga echinites* taken from the back-up boxes showed distinct levels of migration activity during each of the four periods monitored (Fig. 13). A certain rate of migration was observed during all periods. The maximum speed was determined as 9 cm h^{-1} during the second nocturnal period from 02:00 to 06:00 hrs. This speed was reached by only 6% of the juveniles at this time. The juvenile holothurians reached a second peak of activity during the period from 19:00 to 23:00 hrs. Lowest activity was observed during the first nocturnal observation period from 23:00 to 03:00 hrs. A statistical comparison of the distributions of activity levels showed significant differences of the migration behaviour between all periods (U-tests: $p < 0.05$).

The fifty adult specimens of *Actinopyga echinites* analyzed for migratory speed in the field showed a maximum locomotive speed of 15 cm min^{-1} ($=900$ cm h^{-1}). Maximum activity occurred at night, but no distinct peaks were apparent.

Discussion

Weight determination

The average percentage of drained weight as a part of fresh weight (48.3%) was considerably lower than that reported by Conand (1986) for adult *Actinopyga echinites* (75.3%).

In part, this dissimilarity between the age groups may be the result of thinner teguments and the lack of reproductive organs in the small juvenile specimens examined in the present study. The juvenile *Actinopyga echinites* displayed varying fresh and drained body weight proportions at different times of the day (48.25 to 54.25 g). This physiological strategy could be reflective of their specific daily feeding behaviour which should require osmoregulatory changes. In order to digest the nutrients assimilated, the holothurians might have to increase water exchange during the early morning hours and, as a result, elevate oxygen levels within their coelom. Additionally, osmoregulatory aspects may be of importance.

Morphology

All of the distinctive morphological features of the adult *Actinopyga echinites* specimens were already recognizable in the juveniles. Colour, morphometric proportions and typical shape of the holothurians had already been developed (Fig. 2). The final number of tentacles ($n=20$) had been established. The anal teeth, which are an important characteristic of the genus *Actinopyga*, were still truncate, but nevertheless detectable. If these decisive patterns prove to exist for other coral reef zone holothurians as well, the general identification of juvenile sea cucumbers in the field may be possible in the future.

There was some indication that a number of differences in the inner organs exist between the juvenile and adult morphology of *Actinopyga echinites*. It was not possible to detect even rudimentary reproductive organs. The colour of the Cuvierian tubules was whitish instead of pink, which was reported for adult *A. echinites* by Conand (1986). In relation to total body length, the digestive tract of the juveniles was shorter than in the adults. Additionally, the *lacuna intestinalis* and the *vena transversalis* showed fewer ramifications. These results indicate that, in juvenile *A. echinites*, the assimilation process of nutrients from the intestinal cavity into the haemal system is more dependent on digestive speed and the amount of ingested material per time than in adults (Massin 1979), because the chemical contact area is more limited.

The skeletal morphology of the small juveniles also differed considerably from that of adult *Actinopyga echinites* (Figs. 2, 3). Two new types of spicules were observed in the juveniles: solid unbranched linear rods and solid spade-shaped rods (Fig. 2). Nevertheless, shrinkage (Fig. 4) and decrease in frequency (Table 1) related to age, exclusively observed in these two types, indicate that few if any of these spicules occur in adult *A. echinites*. This conclusion is supported by the extrapolations of the shrinkage process beyond the experimental period. If shrinkage of these two spicule types continues to be linear, adults, 3 yr of age, may have lost all their linear rods. The same development is likely to occur with respect to the spade-shaped rods of individuals, 5 1/4 yr of age. The absence of these particular types of spicules, which has been reported in all morphological studies conducted on adult *A. echinites* to date

(Rowe and Doty 1977; Reyes-Leonardo 1984), substantiates this conclusion.

All other types of spicules displayed linear growth during the monitored experimental period. However, it is unlikely that an increase in diameter or length will continue to be linear with age because the observed dimensions of the spicules in the present study had already reached 65 to 80% of the dimensions reported for adult *Actinopyga echinites* (Clark and Rowe 1971). The morphology, physiology and behavioural ecology of small juvenile tropical holothurians may be considerably different from the biology of adult tropical sea cucumbers. Although the outer appearance of the juveniles can be quite similar to the adult morphology, specific identification of the juveniles, based on morphological keys established for adult sea cucumbers, may not be possible. The likelihood that varying combinations of dissimilar types of skeletal spicules are present within the body tissues of juvenile and adult holothurians of the same species is highly probable.

Habitat preference and migration behaviour

Juvenile *Actinopyga echinites* had a strong preference for solid substrate types such as eroded limestone plates or the skeletons of dead table corals (Fig. 5). The avoidance of the substrate type which consisted of dead branches of acroporids may have been caused by low sedimentation rates due to hydrographic effects around these cylindrical structures. Sandy substrates were the least preferred. The preference for solid but structured substrate types may be related to the small size of the individuals. The holothurians attempted to attach themselves to the substrate with as many tube feet as possible. This is an adaptation in order to survive within the frontal zone of fringing reefs where wave action is comparatively stronger than inside back reefs (Graus and Macintyre 1989). The weight distributions of *A. echinites* on separate substrate types and in different light zones on the substrates (Figs. 6, 7, 8) reflect a weight-dependent trend of settlement on the sandy substrates. With increasing size, the holothurians appear more capable of stabilizing themselves on this mobile sediment.

The comparatively thicker surface layer of material rich in organic content, such as bacteria covers or detritus (Kemp 1987), may be a factor determining the juveniles' preference for solid types of substrates. Here, the nutrient-rich parts of the sediments are more readily accessible for epibenthic deposit-feeders than they are within sandy substrates (Rhoads and Young 1970). On hard substrate, it is not critical that the holothurians ingest whole large inorganic particles for the purpose of obtaining attached organic matter. This aspect may be particularly important for juvenile holothurians because they are, due to the small diameter of their oesophagus, not able to ingest larger particles (Massin 1982).

The holothurians examined selectively occupied the darkened areas of substrates. Cryptic behaviour has been reported for adults of almost all known tropical holothurians (Baker 1929; Pawson 1974; Sloan 1979; Harriott

1984). Most adult tropical holothurians do not exhibit frequent cryptic behaviour during the daylight period and leave their resting places for feeding. However, as observed during the two additional surveys of adult daily activity patterns in the present study, this age group of *Actinopyga echinites* does not exhibit cryptic behaviour during any time of the day. In contrast, juveniles showed cryptic behaviour at all times during a 24-hour period. This behavioural strategy may be primarily influenced by predation pressure, by the low migratory speed of the holothurians, by the sufficient supply of nutrient-rich sediments and by the risk of becoming dislocated from underlying substrates.

The migratory behaviour and locomotive speed of several holothurian species has been previously investigated (Parker 1921; Yamanouti 1939; Fankboner 1978; Izumi 1991). Most studies were conducted for the purpose of examining aspects of the muscle physiology of the taxon (Takahashi 1974). Da Silva et al. (1986) studied the movement and the orientation behaviour of adult *Parastichopus californicus* (Aspidochirotidae) on a daily basis and reported an average locomotive speed of 3.9 m d^{-1}. Unfortunately, Da Silva et al. (1986) did not specify the average size of the specimens monitored in their study and, thus, their results can not be compared to any later surveys. Hammond (1982), as well, does not point out the body sizes of *Holothuria thomasi*, *H. mexicana* and *Isostichopus badionotus* he analyzed in his study, but he provides temporal differences of migration behaviour during a 24-h period. Hammond reports a maximum speed of 25 cm min^{-1} and nocturnal peaks of migration and feeding activity. The species in his study exhibited a minimal peak activity level during the first hours of the night.

Primarily, the migrational distance of the juveniles of *Actinopyga echinites* may be a consequence of their need to detect spots of high nutrient concentrations within the sediment. The juveniles displayed higher activity levels during the night with a peak during the last hours of darkness (Fig. 13). This activity pattern has a strong correlation to the feeding behaviour and sediment ingestion rates of adult tropical holothurians (Wiedemeyer 1993). However, no differences existed in the average drained body weights of individuals on different substrates between sampling during the day and during the night. Thus, the sampling strategy applied during the experiments was representative of the complete daily cycle.

Stationary behaviour was very prominent in juvenile *Actinopyga echinites* compared to the adult holothurians of the species. The purpose of the high speed which was observed in adult *A. echinites* is not immediately obvious. Effective feeding does not seem very likely at a high velocity of 15 cm min^{-1}. Migration speed of the adults was two orders of magnitude faster than the maximum speed observed for the juveniles, when differences in body length were taken into consideration. It may constitute a behavioural strategy on the part of the adult holothurians used in order to locate areas of higher food concentration as quickly as possible. The oral tentacles keep loose contact with the substrate while the individuals are moving. Although the exact size of the specimens analyzed by Da Silva

et al. (1986) and by Hammond (1982) is not known, it is obvious from the results of the present study that the relative speed of the individuals monitored did not replicate their findings.

The newly observed small spicules and the presence of fewer ramifications among the types of spicules already known enables an increased body flexibility of juvenile compared to adult *Actinopyga echinites*. As a result, the juveniles are capable of hiding in the narrow crevices of hard substrates and show a tendency to do so. Continuous cryptic behaviour, very limited short-distance migrations and firm adhesion to the substrate enable juvenile *A. echinites* to inhabit the frontal zone of the coral reefs. The tendency to migrate to more exposed substrate types with increasing weight reveals a slow transition to less cryptic adult behaviour. Avoidance of substrates having cylindrical structures such as skeletons of branching corals and the attraction to plate-like substrate types suggests a distinct settlement strategy of the juveniles. A correlation could exist between the presence of nutrient rich surface sediment layers and this strategy.

Natural mortality and predation effects

The juveniles of *Actinopyga echinites* showed relatively lower rates of natural mortality compared to the predation rates reported for other tropical holothurian species (adults), even when exposed to predation effects. The average ratio between natural mortality of treatments including and excluding predation (1:3.34=23.3%) was well below the range reported for other benthic invertebrates (Underwood and Denley 1984). This result is even strengthened by the fact that predation effects monitored during the experiments include unavoidable minor dislodgement effects. Bonham and Held (1963), Kropp (1982) and Conand (1989) reported low predation effects on the adults of several tropical holothurian species. Here, predation was induced by large molluscs such as *Tonna perdix* and by several fish species (Tetraodontidae, *Caranx spp.*, *Sebastes spp.*). Rutherford (1973), however, described a very high predation rate induced by *Pycnopodia helianthoides* (Echinodermata) on *Cucumaria pseudocurata* and an overall natural mortality of this small sea cucumber species of 96 to 97% during the first year of its life cycle. Bakus (1974) drew the conclusion that a strong relationship should exist between low predation rates and toxicity in adult holothurians. The present report does not monitor this aspect separately, but low predation rates, despite a relatively high density of potential predators and their comparatively easy access to the substrates within the experimental boxes, support this finding for small juvenile holothurians as well.

During the experiments, natural mortality of *Actinopyga echinites*, excluding predation, was lower than was reported for juvenile *Stichopus japonicus* (Izumi 1991). This may have been caused by general differences between the ecology in the tropical and the temperate (*S. japonicus*) marine environments. Additionally, it should be noted that the impact of occasional typhoon events and sea level fluctuations was excluded during the experiments. These factors may amplify natural mortality rates (Yamaguchi 1975).

It was surprising that mortality rates of the juveniles increased with size, which is quite unusual for most marine invertebrates (Paine 1984). The cause for this increase was detected solely in the increase of predation (and possibly dislodgement) effects during growth of the individuals. This finding does not lead to low predation rates observed in adults (Bonham and Held 1963; Kropp 1982; Conand 1989). The reason for this incongruity may, to a certain degree, be a time-dependent acclimation of predators to the introduced structure of the polypropylene boxes during the experiment. Nevertheless, the acclimation period of more than 2 mo prior to initiation of the experiments is considered satisfactory. It is possible that predation effects were slightly underestimated during the initial monitoring period. A plausible cause for the increase of predation effects is the change in cryptic behaviour of *Actinopyga echinites* during the experimental period of 12 mo. As the holothurians grew, they displayed a progressive tendency to leave the protected locations of the substrates (crevices in platesubstrates). During the experiments, a preference to feed on more exposed sandy substrates developed.

Natural mortality of juvenile *Actinopyga echinites* was comparatively low, even when predation effects were included. Nevertheless, it should be kept in mind that dislodgement effects were not entirely excluded during the experiments. They may considerably increase the rate of natural mortality particularly in areas of strong wave impact. With respect to potential stock enhancement, an exponential growth rate and low mortality rate during the early life stage of the juveniles suggest that, for the holothurians to reach maturity, it is advisable to release the juveniles from the outdoor tanks to the field as early as possible. As predation makes up to 77% of natural mortality of the juveniles, the survival rate in the field may decrease considerably while the individuals' body weight increases because larger juveniles of *A. echinites* tend to inhabit more exposed substrate types.

Growth

Growth of holothurians is the least established biological parameter of the taxon. Several authors have studied the average growth of adults from population subsamples (Doty 1977; Ebert 1978; Shelley 1981, 1985). Rutherford (1973) observed increases to be up to 30 times the initial weight during the first year of the life cycle of *Cucumaria pseudocurata*, a small dendrochirote sea cucumber species. In the present study, *Actinopyga echinites* showed a lower but comparable weight increase of approximately 15 times (0.87 to 12.82 g) during 1 yr. The juveniles exhibited a typical development of their normally distributed weight frequency (Fig. 11) with age (chi-square test). This confirms that the holothurians analyzed initially originated from one cohort of *A. echinites*.

The age group (t yr) examined in the present study has not yet been empirically studied because the individuals are not detectable in the field. The juveniles of *Actinopyga echinites* monitored were discovered by chance. There was no option to select an economically more important target species or one which was more representative of the general biology of tropical holothurians. In combination with the experiments discussed here, the entire life cycle of *A. echinites* has now been investigated. Chen et al. (1991) have studied larval development and growth of *A. echinites* in the laboratory. Conand (1989) presented theoretical growth data of several tropical holothurian species including *A. echinites*. Her results, which were based on tagging experiments, constitute the only data set which is derived from direct observations of individuals. Unfortunately, there was considerable bias in the tagging procedures due to variable tag losses. Nevertheless, the combination of these three reports constitutes the first comprehensive scientific coverage of the ecology of the entire life-cycle of a tropical holothurian species.

Growth of the juveniles of *Actinopyga echinites* can be approximated by an exponential equation. This does not contradict Conand's approximation of the adults' growth to the von Bertalanffy growth equation (Conand 1989). The juveniles displayed exponential growth during the period monitored (Fig. 10 B). A secondary seasonal effect was observed with the growth rate slowing down during winter. A direct comparison with the growth curve from Conand (1989) (Fig. 12) indicates that the calculations of the present study correspond with her theoretical results. Exponential growth of the juveniles has to slow down with increasing weight and must approximate a saturation curve below the regression established by Conand (1989).

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