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Jellyfish swarms, tourists, and the Christ-child

Mike N Dawson[1,2], Laura E. Martin[1,2] & Lolita K. Penland[2]
[1]*Department of Organismic Biology, Ecology, and Evolution, University of California, P.O. Box 951606, Los Angeles, CA 90095-1606, U.S.A.*
[2]*Coral Reef Research Foundation, Box 1765, Koror, PW 96940, Republic of Palau*
E-mail: mikend@ucla.edu

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Abstract

One of the most remarkable sights in the Western Pacific is a perennial swarm of 1.5 million golden medusae (*Mastigias* sp.) crowded into a land-locked marine lake in Palau, Micronesia. This 'Jellyfish Lake' became a popular off-gassing stopover for SCUBA divers and a destination in its own right for non-diving tourists in the mid-1980s. Since then, tourism in Palau has boomed, increasing 500% between 1986 and 1997. However, in December 1998, the golden-medusae disappeared. Apart from patchy occurrences between December 1998 and April 1999, the medusae have since been absent from the lake. Field measurements, including temperature and salinity depth profiles, *Mastigias* medusae population sizes, and the distribution of scyphistomae, in 'Jellyfish Lake' between 1979 and 1999 were integrated with laboratory-based experiments on the effects of salinity, temperature, sunscreen and zooxanthellae enrichment on *Mastigias* scyphistomae or medusae. These studies indicated that the disappearance of medusae was due to physical changes in lake structure, including a substantial increase in temperature, initiated by the 1997–98 El Niño. Here, we describe these studies, the changes in Jellyfish Lake and their probable influence on the *Mastigias*. We further elucidate the changes in Jellyfish Lake by reference to coincident changes in three other 'jellyfish lakes' in Palau: Big Jellyfish Lake, Clear Lake and Goby Lake.

Introduction

Several tropical marine lakes in Palau harbor immense perennial populations of two scyphozoan jellyfish: the golden-jellyfish, *Mastigias* sp., and the moon-jellyfish, *Aurelia* sp. (Hamner & Hauri, 1981; Hamner, 1982; Hamner et al., 1982). The golden medusae are behaviorally, morphologically and physiologically unique, the manifestations of many thousands of years of evolution in isolated ecosystems (Hamner & Hauri, 1981; Hamner, 1982; Hamner et al., 1982; Muscatine and Marian, 1982; Hamner & Hamner, 1998). A similar situation must be true for the moon-jellyfish although published data are lacking. These unique adaptations, most notably precise diurnal horizontal migrations by *Mastigias*, the high densities and perennial presences of both jellyfish species, and the closed nature of these ecosystems, in which the jellyfish are the top planktivores, make the marine lakes extremely attractive sites for a range of ecological and evolutionary investigations. These same features also make the lakes very attractive to tourists and the media.

Since the marine lakes were brought to the attention of the general public (Hamner, 1982), many nature and SCUBA magazines, radio and television shows, and even an IMAX production, 'The Living Sea', have featured the marine lakes in Palau. This publicity has established Jellyfish Lake, formally named 'Ongeim'l Tketau' (roughly 'fifth lake' in English), as one of the most popular snorkeling sites in the tropical Pacific (Hamner & Hamner, 1998; see also PVA, 1999). Between 1986, when Ongeim'l Tketau first was incorporated into dive tours (Etpison, 1997), and 1997, tourism in Palau increased 500% (PCS, 1999a). Almost 75 000 tourists visited Palau in 1997 and most likely between half and three-quarters of them visited Ongeim'l Tketau (Hamner, 1994; PCS, 1999a; pers. obs.). In recent years, tours have been expanded to incorporate other marine lakes that contain similar populations of *Mastigias*. These lakes, which include Goby Lake and Big Jellyfish Lake, have been host to several thousands of visitors (pers. obs.).

Tourists are attracted to the lakes by a strange mix of fact and fiction purveyed by tourist-oriented publications and other media. The most popular story is that *Mastigias* evolved into perennial sting-less farmers of an edible algal crop during millions of years of confinement in the lakes (e.g. Barbour, 1990). In reality, however, these *Mastigias* can sting humans mildly and kill microscopic prey, they are symbiotic with zooxanthellae but their feeding ecology is hardly agricultural (Muscatine et al., 1986), and they have been confined in the lakes probably for less than 20 000 years (Hamner et al., 1982). The perennial abundance of *Mastigias*, however, is a distinguishing feature of marine lake populations and has supported tourism year-round. Measurements made between 1979 and 1997 indicate that the lakes, and perhaps jellyfish populations, have been remarkably stable on time scales of months to millenia (Hamner et al., 1982; Hamner & Hamner, 1998). In the two decades following the first measurements, there has been only one report to the contrary: in 1987, many *Mastigias* medusae disappeared (Etpison, 1997). However, their disappearance was attributed to disturbance of the toxic monimolimnion by divers using SCUBA rather than to natural perturbations (Etpison, 1997).

This view of long-term ecosystem stability was altered catastrophically in fall, 1998, when the population of *Mastigias* medusae went into an unprecedented decline and disappeared. The disappearance was attributed variously to the 1997–98 El Niño (or translated, 'the Christ-child'), to stagnation of the lake because conduits that normally allowed tidal flux were somehow blocked, or to tourists who may have stolen or eaten the jellyfish, poisoned the medusae with sunscreen, or polluted the lake with urine.

During summer in 1999, we investigated a number of the hypotheses. Field observations and laboratory experiments indicated several factors quite likely contributed to the decline and disappearance of golden jellyfish from 'Jellyfish Lake' among which high water temperature may have been predominant. Ultimately, the disappearance probably can be traced to physical perturbations in lake structure that were initiated by the 1997–98 El Niño event.

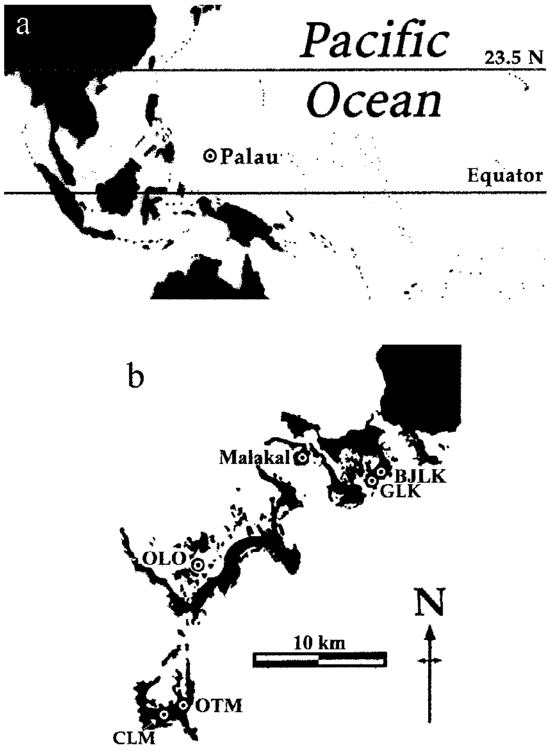

Figure 1. (a) Location of Palau in the western Pacific and (b) the marine lakes and other locations mentioned in the text. BJLK – Big Jellyfish Lake, Koror; GLK – Goby Lake, Koror; OLO – Ongael Lake, Ongael; CLM – Clear Lake, Mecherchar; OTM – Ongeim'l Tketau, Mecherchar (better known as "Jellyfish Lake", Hamner et al., 1982).

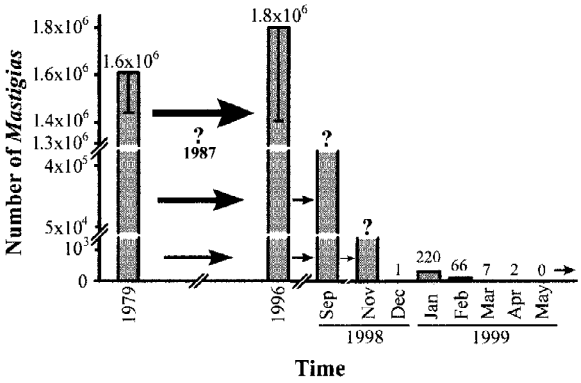

Figure 2. Estimates of *Mastigias* medusae population size in Ongeim'l Tketau between 1979 and 1999. Mean estimated population (± standard deviation) are shown for each quantitative sampling event. Qualitative observations were made in September and November, 1998 (L. J. Bell, M.N Dawson, L.E. Martin, B. Yates) for which population size is estimated from the size of aggregations, medusae size, and visual estimates of population size.

Materials and methods

Brief description of five marine lakes

The biological, chemical and physical characteristics of Ongeim'l Tketau, Big Jellyfish Lake, Clear Lake and Goby Lake (Figure 1) have been described by Hamner and colleagues (Hamner & Hauri, 1981; Hamner, 1982; Hamner et al., 1982; Hamner & Hamner, 1998). All four lakes are meromictic, or partly mixed, consisting of an upper mixolimnion floating above a lower monimolimnion. The salinity and temperature of the mixolimnion generally increase gradually with depth until a sharp increase in salinity and decrease in temperature establish a robust pycnocline marked by dense purple-sulfur bacteria (Hamner et al., 1982; Hamner & Hamner, 1998). Dissolved oxygen, in contrast, decreases from its maximum near the surface to zero at the pycnocline, the monimolimnetic waters below the pycnocline are highly reducing. However, these four lakes can be differentiated on the basis of surface area, depth of the mixolimnion, maximum depth, shape, orientation, surrounding topography and somewhat different faunas (Hamner & Hamner, 1998; pers. obs.). Ongael Lake (OLO) is a smaller and shallower lake whose holomictic waters are similar physically to those in the adjacent lagoon; its fauna is depauperate, but also lagoon-like. *Mastigias* inhabit all five lakes.

Field measurements and observations

From December, 1998, to December, 1999, 2 field-trips, approximately two weeks apart, were made to Ongeim'l Tketau (OTM) each month. During one trip, the lake was searched thoroughly, to depths of 6–8 m, for *Mastigias* sp. medusae by 3–4 snorkelers. All medusae found were measured. Medusae $>$10 mm were measured to the nearest one centimeter by flattening the exumbrella against a rule while in the lake; smaller medusae were measured under a dissecting microscope at the Coral Reef Research Foundation (CRRF), then preserved in DMSO+NaCl (Seutin et al., 1991; Dawson et al., 1998) for subsequent examination. During the second trip, 2 weeks later, the search for *Mastigias* medusae was repeated and vertical temperature, salinity and oxygen (TSO) profiles were measured using a YSI 85 meter (object, not distance). Additional trips to Ongeim'l Tketau using SCUBA were made during July–September, 1999, to search for the benthic scyphistoma stage of *Mastigias*. Scyphistomae were collected and taken to CRRF where they were examined under a microscope for zooxanthellae, planuloids and apparent health prior to use in experiments (see below). During the final trip on 9 September, 1999, we assessed the tidal range in Ongeim'l Tketau using synchronized half-hourly measurements of tidal height in the lake and the adjacent lagoon for one half tidal cycle (see Hamner & Hamner, 1998).

Monthly field-trips were made to Big Jellyfish Lake (BJLK) and Goby Lake (GLK) during which TSO profiles were measured and the size distributions of *Mastigias* sp. were estimated by visual censuses. Visual censuses were made by 3–4 snorkelers swimming multiple transects across the length and width of each lake. At the entrance into each lake, each snorkeler closed their eyes, finned 5 strokes (along different transects), then opened their eyes and caught the first medusa seen. The bell diameter of that medusa was measured as above. Each snorkeler then repeated the blind swim to find another medusa to measure; efforts were made to minimize the temptation to look for animals nearest the surface by varying the line of sight between cycles. The cycle was repeated until all transects were finished. In addition to the visual survey, in August 1999, the *Mastigias* sp. populations in these lakes also were surveyed using a 0.1095 m^2, 1 mm^2 mesh, net, hauled vertically from the lake bottom or below the chemocline, depending which was shallower. These same methods were used to measure jellyfish populations and water column structure in Clear Lake, Mercherchar, during trips in fall 1998 and summer 1999. Also reported here are observations from Clear Lake (CLM) that have particular relevance to this paper

Laboratory based experiments

Mastigias scyphistomae were collected by divers using SCUBA in OTM and GLK and by snorkelers in CLM. Aggregations of scyphistomae on their natural substrates were placed into rigid plastic 250–1000 ml jars full of lake water and transported to CRRF within 2 hours. At CRRF, the scyphistomae, still on their natural substrate, were transferred to 1 L plastic containers (diameter = height) of 1 μm filtered seawater adjusted to lake salinity and temperature. They were maintained this way for 24 h at which time they were examined under a dissecting microscope (magnification 7×–40×) and scored in five ways: on a four-point scale (0–3) for the zooxanthellae density in their tissues (see below), a Boolean (true/false) scale for strobilation and for the presence of planuloids, and simple counts of the numbers of planuloids and strobilae present.

Mastigias scyphistomae collected in OTM rarely contained visible zooxanthellae (cf. scyphistomae populations in other lakes which always had some zooxanthellae). Therefore, prior to experimentation, these scyphistomae were infected with zooxanthellae by feeding to them homogenized tissue from local *Mastigias papua* Lesson and leaving them in running seawater (∼29 °C, 34‰) and natural shade for up to several weeks. One batch of scyphistomae apparently was infected by zooxanthellae from anthozoans or *Tridacna* situated upstream.

Zooxanthellae density was assessed by examining scyphistomae under a dissecting microscope at 10×-40× magnification. The area of the calyx and oral disc pigmented by zooxanthellae and the intensity of that pigmentation were used to score all, n, scyphistomae in each replicate on a four-point (0–3, d) relative scale. These scores then were used to calculate an index, ZD, of the change in the mean zooxanthellae density in each replicate at time *t* relative to the mean density at the start of the experiment.

$$\mathrm{ZD}_t = \left(\sum_{i=1}^{n} d_{it}/n_t\right) / \left(\sum_{i=1}^{n} d_{i0}/n_0\right).$$

In the special case of an initial density equal to zero, i.e. when homogenized *M. papua* tissues were fed to OTM scyphistomae immediately preceding experimental manipulation, the change in mean zooxanthellae density was calculated as

$$\mathrm{ZD}_t = \left(\sum_{i=1}^{n} d_{it}/n_t\right) - \left(\sum_{i=1}^{n} d_{i0}/n_0\right).$$

Throughout all experiments, scyphistomae were scored by the five methods described above. Scyphistomae were illuminated by 'coral' aquarium lights but were not fed zooplankton because coloured food in the gastric cavity made it difficult to identify zooxanthellae and, therefore, compromised the assessment of zooxanthellae density. No animals were used for more than one experiment.

Effect of salinity on scyphistomae-zooxanthellae

OTM scyphistomae infected with zooxanthellae were divided equally into 10 separate vessels, duplicates were acclimated to five salinities ranging from 20‰ to 45‰ (original salinity, ∼32.5‰) over a period of 1 week and then maintained at target salinities for another 11 days. Seawater was adjusted to the appropriate salinity by dilution with rainwater or addition of aquarium salts in steps of about 1.5‰ per day. Seawater was replaced approximately every fourth day. Scyphistomae in all salinity treatments were kept at the same temperature (means 30.4–31.1 °C; s.d., 1.06–1.32 °C; ANOVA, df = 4,90, $p = 0.7866$). Scyphistomae were scored daily.

Effect of zooxanthellae enrichment on scyphistomae-zooxanthellae

Scyphistomae freshly collected from OTM were fed homogenized *M. papua* tissues and left in ambient conditions for several days. Control groups were treated similarly, except they were not fed homogenized *M. papua* tissues. Oneμm-filtered, 34‰ seawater was replaced every other day. The scyphistomae were scored on days 0 and 4.

Effect of temperature on scyphistomae-zooxanthellae

Ongeim'l Tketau scyphistomae infected with zooxanthellae were divided equally among 10 one-liter containers and acclimated to different temperature treatments. Eight of the ten containers were transferred from ambient (∼29 °C) to a 31 °C waterbath and then, at 2 h intervals, transferred sequentially, in pairs, to approximately 32 °C, 34 °C, and 35 °C waterbaths, until one pair of containers was at each of the five temperatures. The scyphistomae were maintained at these temperatures for 2 weeks. Polyps were scored daily and 34‰ surface seawater at the appropriate temperature was replaced every second day.

The experiment subsequently was repeated using freshly collected, azooxanthellate, scyphistomae which were fed *M. papua* tissues immediately before they were acclimated, stepwise, to the different temperature treatments. The scyphistomae were scored daily and 1 μm-filtered, 34‰ seawater was replaced every other day for two weeks.

In a third experiment, Goby Lake scyphistomae were divided equally between 10 one-liter containers of filtered, 27‰ seawater and placed into a 28 °C waterbath at CRRF. Filtered seawater prevented infection of scyphistomae with allochthanous sources of zooxanthellae. Two days later, the scyphistomae were acclimated to different temperature treatments and observed for 2 weeks. Scyphistomae were scored daily and seawater was replaced every second day for 2 weeks.

Effect of temperature on medusae

Medusae, ≤15 mm (bell diameter) were collected from BJLK and GLK in the same manner as polyps. Immediately on arrival at CRRF, medusae were distributed equally among 10 five-liter containers (9 medusae per container) and pairs of containers acclimated incrementally to five temperatures between 28 °C and 36 °C (as described for scyphistomae, above). Medusae were illuminated from 6 a.m. to 6 p.m. using household fluorescent lighting situated several meters from the aquaria. Except for monitoring periods, medusae were not illuminated between 6 p.m. and 6 a.m. Medusae were scored at 6-hour intervals, for up to 7 days, for the rate and strength of bell contractions and for their position in the water column. Medusae were considered terminally damaged when observed on two consecutive occasions pulsing very poorly on the container's bottom; these medusae did not recuperate if transferred to cooler temperatures.

Effect of sunscreen on medusae

Medusae collected as above were distributed evenly among four 3.5 L containers. Sunscreen (Coppertone 'Water Babies' UVA/UVB sunblock lotion, SPF 45, or BullFrog 'the QuickGel' SPF 36) was added to three containers in concentrations of 10^{-4}, 10^{-6}, and 10^{-9} (g ml^{-1}). Sunscreen was not added to the fourth, control, container. All four containers were kept in the open air at 26–28 °C under a canopy that afforded protection from rain and direct sunlight. The health of the medusae was assessed at 6-hour intervals for 5 days. This experiment was repeated three times, using 32 medusae from BJLK and OLO and 16 medusae from GLK.

Statistics

Statistical analyses were completed using SYSTAT v.6.0 for Windows 3.1.

Results

Field measurements and observations

In September, 1998, a large population of *Mastigias* medusae of all sizes was present in OTM although these medusae possibly were slightly fewer and, on average, larger than usual (Dawson & Martin, pers. obs.). By November, 1998, there were fewer large and many small medusae (L. J. Bell and B. Yates, pers. comm.). On 14th December, 1998, a thorough search throughout the lake revealed just one, 20 mm, *Mastigias* (Martin & Dawson, pers. obs.). Subsequently, medusae were encountered in small and declining numbers between January and April 1999 (Fig. 2). These medusae were all ≤1 cm, swimming normally and had a normal complement of zooxanthellae. There apparently was no strobilation of medusae after April 1999. Scyphistomae in OTM in summer 1999, found between approximately 6 and 14 m depth, were not strobilating and appeared azooxanthellate under the microscope (L. J. Bell, pers. comm. and Table 1).

Table 1. Zooxanthellae content and reproductive condition of *Mastigias* scyphistomae in three marine lakes, Summer 1999

Percentage of polyps that were		Ongeim'l Tketau[1]	Goby Lake[1]	Clear Lake[1]
Producing planuloids	%	7	1	9
Zooxanthellate	%	$\sim$2	89	45
	ZD	0.02	1.10	0.48
Strobilae	%	0	9	0

All counts were made on polyps kept in filtered seawater for 24 h after collection. Ongeim'l Tketau scyphistomae were collected on several different occasions between 26 Jul. and 4 Sep., 1999, n = 1,215.
Goby Lake polyps were collected on 12 Jan. 1999, *n* = 305.
Clear Lake polyps were collected on 26 Aug. 1999, *n* = 168.
ZD, zooxanthellae density index.

Other organisms in Ongeim'l Tketau also exhibited signs of stress during summer 1999. For example, more than 50% of the endemic anemones, *Entacmaea medusivora* (Fautin & Fitt, 1991), appeared flaccid, their tentacles largely hidden within invaginated oral discs, in contrast to their usual upright posture with tentacles extended. Many moon-jellyfish, *Aurelia* sp., were tattered and torn, inverted, or misshapen, although the population seemed no smaller than usual. Also, for the first time in four years, we saw a dead goby, *Acentrogobius janthinopterus* (Bleeker), floating at the surface of the lake.

The disappearance of *Mastigias* medusae in December, 1998, coincided with the presence of an abnormally hot and salty mixolimnion in Ongeim'l Tketau (Fig. 3a). The temperature of the mixolimnion continued to rise after December, 1998, peaking in April, 1999. It has remained high since. In contrast, the mean salinity of the mixolimnion has declined from its high in December 1998, although it is still above the mean of previous measurements. For most of 1999, a steep pycnocline at about 6 m depth maintained a hot and high salinity water mass at depth despite tidal flux involving shallower waters (Hamner et al., 1982; Hamner & Hamner, 1998). In September, 1999, the tidal pattern in the lake was normal, being damped to approximately 40% (0.69 m) and delayed by about 2.5 h compared with the lagoon (see Hamner & Hamner, 1998).

Other 'jellyfish lakes' also changed. The *Mastigias* population in Goby Lake in December 1998 was unusually small and consisted solely of animals less than 6 cm. However, strobilation by zooxanthellate *Mastigias* scyphistomae, located between approximately 4 and 6 m depth, and growth of medusae restored a normal population of medusae in Goby Lake by mid-1999 (Fig. 4; Table 1). The reduced populations of *Mastigias* medusae in Goby Lake in December 1998 coincided with an unusually hot and salty mixolimnion (Fig. 3b). The subsequent recovery of the populations coincided with the return of the mixolimnion towards its pre-1998 state.

In Clear Lake, the size distribution of *Mastigias* was heavily skewed towards large medusae in August 1999. Thousands of medusae $\geq$12 cm were present but we found only two medusae that were 2 cm and a few 6–8 cm bell diameter despite searching along transects, totaling approximately 2 km, throughout the lake. Although Clear Lake was not unusually hot, the mixolimnion was approximately 5‰ more saline than ever recorded previously. The shallowest scyphistomae that we found were at approximately 6 meters depth and these contained zooxanthellae but were not strobilating (Table 1).

Clear Lake also contained a large population of golden-*Mastigias* medusae in 1994, but typically (1979, 1995–97) has contained few or none of these medusae (Hamner et al., unpublished data). However, in May 1997, there was a small population ($<$1000 individuals) of white, apparently azooxanthellate, *Mastigias* medusae (Fig. 5), none larger than $\sim$35 mm and most less than $\sim$25 mm. Not one of $\sim$150 medusae observed *in situ* had any pigmentation and thorough microscopical analyses, including staining with Fluorescent Brightener 28 (Sigma Chemicals), found no remnants of zooxanthellae in 11 preserved medusae (Fig. 5). Three days later, the population was in decline, with a decrease in density of jellyfish and with only animals $\geq$10 mm showing no physical deterioration. We collected 40 medusae from this apparently senescent population and placed them in an aquarium where, despite the presence of an inoculum of zooxanthellae and successful feeding on *Artemia* nauplii, they died within 2 days.

Unlike the populations of medusae in Ongeim'l Tketau, Goby Lake, and Clear Lake, the population of *Mastigias* medusae in Big Jellyfish Lake was not affected obviously by changes in the mixolimnion during 1998–99 (Fig. 3c), nor were there any other obvious biotic changes. Both temperature and salinity have ameliorated since December 1998 although both still are above the means of pre-1998 measurements.

Laboratory based experiments

Effect of salinity on scyphistomae-zooxanthellae

A wide range of salinities and salinity changes, greater than any measured in Ongeim'l Tketau, allowed zooxanthellae increases of up to 160% (Fig. 6). Salinities below 25‰ generally caused the zooxanthellae density index to decrease (i.e. bleaching) whereas salinities as high as 45‰ permitted an increase in zooxanthellae density.

There was a weak positive but marginally non-significant correlation between salinity and survival of scyphistomae ($y = 0.0086x + 0.53$, $R^2 = 0.37$, $p = 0.062$). However, there was no correlation between survival and zooxanthellae density, indicating independence of these two effects.

Effect of zooxanthellae enrichment on scyphistomae-zooxanthellae

The zooxanthellae densities in OTM scyphistomae in the control and enriched treatments did not differ at the start of the experiment (*t*-test, df = 10, $p = 0.77$). However, 4 days later, zooxanthellae were significantly more dense in the enriched treatment than in the control (*t*-test, df = 10, $p = 0.05$; Fig. 7).

Effect of temperature on scyphistomae-zooxanthellae

Although there was some variation between experiments, the mean zooxanthellae density of infected scyphistomae, on average, remained stable in the 28.7 °C and 31.5 °C treatments. In contrast, in all experiments, mean zooxanthellae density decreased with each increment in temperature above 31.5 °C (Fig. 8a). Grouping the results from all experiments into 1 °C classes (beginning at 28.0 °C) and calculating their mean ranks indicated a significant negative effect of increased temperature on zooxanthellae density (Kruskal–Wallis Test, df = 4, $p = 0.04$).

A similar pattern was evident in scyphistomae infected with zooxanthellae immediately prior to temperature treatment. Greater increases in zooxanthellae density occurred at 28.7 °C and 31.5 °C than at 33.3

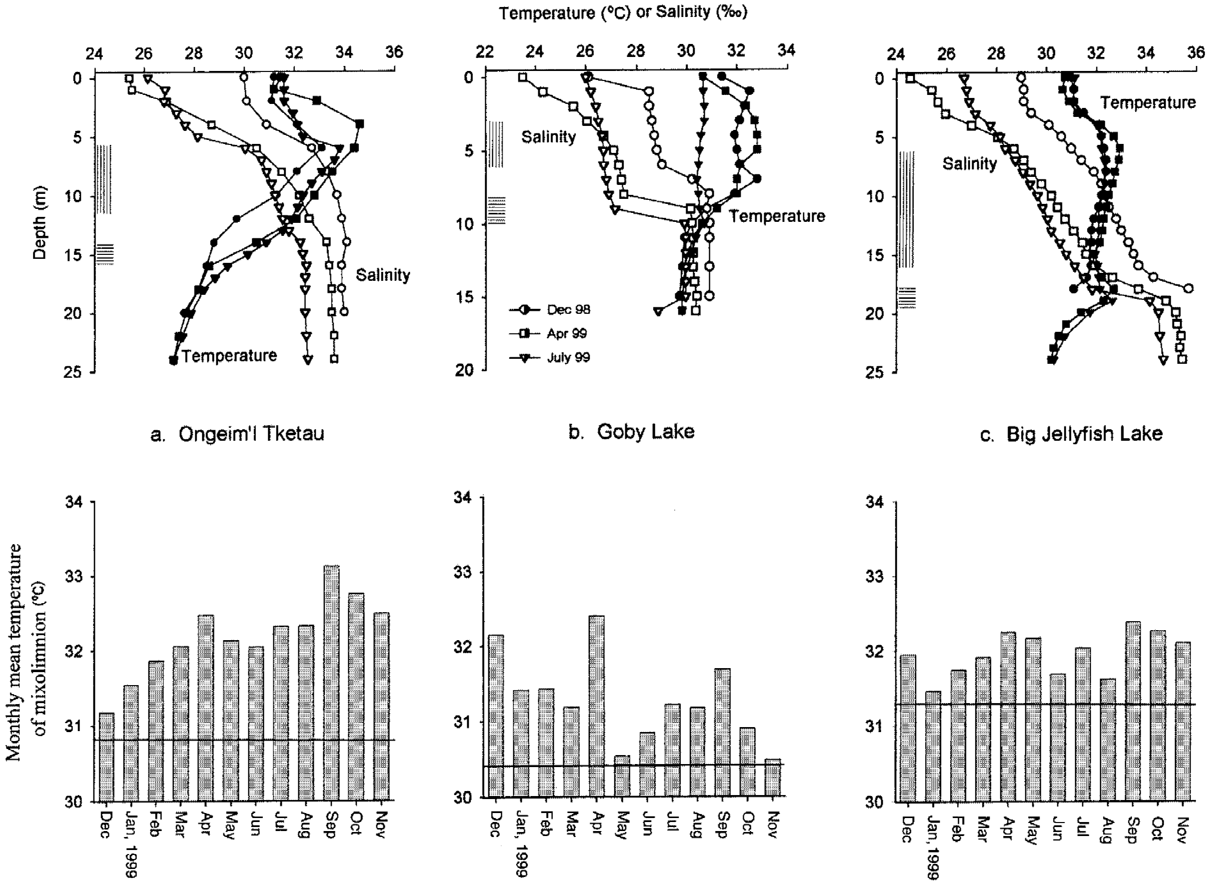

Figure 3. Physical structure of three meromictic marine lakes 1998–99. (a) Ongeim'l Tketau. (b) Goby Lake, Koror. (c) Big Jellyfish Lake, Koror. Top row: vertical profiles of the salinity and temperature of the lakes in December 1998 (circles), April 1999 (squares), and July 1999 (triangles). Vertical hatching against the left axis of each graph indicates the depth-range in which *Mastigias* polyps were found. Horizontal hatching against the left axes indicates the approximate depth of the chemocline separating the upper mixolimnion from the lower monimolimnion. Bottom row: monthly mean temperature of the mixolimnion (bars: average of monthly vertical temperature profiles excepting the upper 2 m which vary according to recent rainfall and tidal-cycles), compared to the mean of all such measurements made between 1978 and 1998 (line: Hamner et al., unpubl. data).

°C or 34.4 °C (Fig. 8b). However, this effect was not significant (Kruskal–Wallis Test, df = 3, $p = 0.8$).

Scyphistomae transferred subsequently from the 33.8 °C and 35.2 °C treatments to 28.7 °C began to show increases in zooxanthellae density after two weeks. Scyphistomae transferred in the opposite direction began bleaching within 3 days.

The survival of scyphistomae generally declined with increasing temperature (Fig. 9). Grouping the results from all experiments into 1 °C classes (beginning at 28.0 °C) and calculating their mean ranks indicated a marginally non-significant negative effect of increased temperature on survival (Kruskal–Wallis Test, df = 4, $p = 0.055$). There was no relationship between temperature and production of planuloids by scyphistomae (ANOVA, df = 7, 39, $p > 0.5$). The frequency of strobilation was greatest at 31.5 °C (12% of scyphopolyps), and less at both cooler (28.7 °C = 4%) and higher (33.3 °C = 5%; 34.4 °C = 4%) temperatures. Strobilation was not observed in either 33.8 °C or 35.2 °C treatments. No scyphopolyps were seen simultaneously strobilating and producing planuloids. Also, the frequency of strobilation and planuloid production in natural populations appeared to be inversely related (Table 1).

Effect of temperature on medusae

Increasing temperature significantly decreased the survivorship of small medusae from both Goby Lake and Big Jellyfish Lake (Fig. 10). This trend was exag-

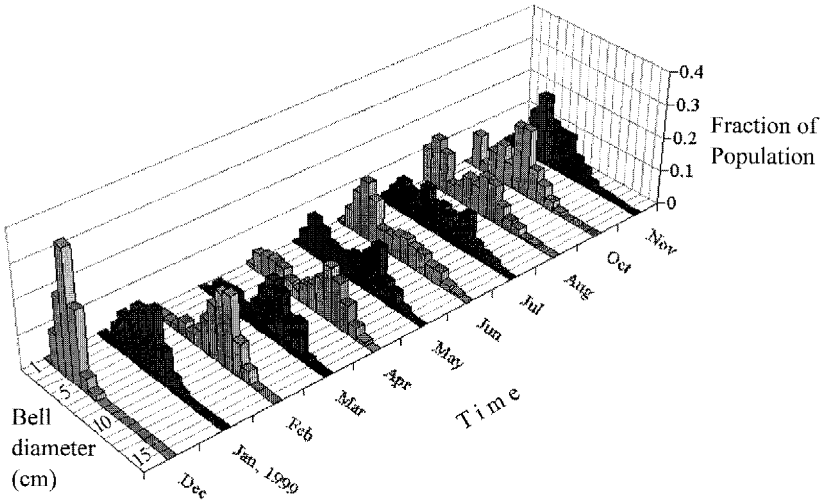

Figure 4. Size distribution of *Mastigias* medusae in Goby Lake, 1998–99. Compared to previous years, the mean size of *Mastigias* medusae in Goby Lake was unusually small in December 1998 (Hamner & Hauri, 1981; Dawson, pers. obs.). Strobilation and growth of medusae early in 1999 eradicated this discrepancy. Alternative months are shaded differently to distinguish adjacent months. Data were not collected in September 1999.

gerated at temperatures approaching and greater than 35 °C. Although this pattern is consistent between lakes, the magnitude of the effect is not. Medusae from Goby Lake died significantly more quickly than their Big Jellyfish Lake counterparts at all experimental temperatures (as demonstrated by 95% CI, Fig. 10), consistent with either container effects or other differences between these populations. Terminally damaged medusae did not appear bleached.

Effect of sunscreen on medusae

Coppertone sunscreen at concentrations of $\leq 10^{-6}$ had no discernible effect on the survival of medusae from BJLK and GLK within 5 days, but concentrations of 10^{-4} caused the death of all medusae within a few minutes (GLK) to several hours (BJLK). BullFrog was lethal to all OLO medusae within 30 min at a concentration of 10^{-4}, within 6 h at 10^{-5}, and within 30 h at 10^{-6}. Only one jellyfish died in one control experiment (BJLK).

Discussion

Jellyfish swarms and the Christ-child

The 1997–98 El Niño was, by some measures, the most severe on record (McPhaden, 1999; Wilkinson et al., 1999). In the western Pacific, dramatic changes in the prevailing winds, depth of the thermocline, drought, unusually high sea-levels, and elevated air and sea-surface temperatures (McPhaden, 1999, NOAA, 1999a) precipitated important biological changes (e.g. Chavez et al., 1999). In Palau, 'the Christ-child' brought a severe drought, which killed many large jungle trees and depleted Palau's only fresh-water lake, and caused exceptionally high tides, high sea surface temperatures, and widespread coral bleaching (PCS, 1999b; CRRF, unpubl. data). Coral bleaching – the perturbation of the coral-zooxanthellae symbiosis (e.g. Hoegh-Guldberg & Smith, 1989; Kleppel, 1989) – is an hallmark of the high sea surface temperatures associated with El Niño events (Brown et al., 1996; Jones et al., 1997; Winter et al., 1998) and, on a global scale, bleaching in 1997–98 was more extensive than any recorded previously (Wilkinson et al., 1999; Aronson et al., 2000). In Palau, at least 30% of all scleractinians and as many as 99% of some species died (PCS, 1999b).

The physical and biotic changes that occurred in the marine lakes in Palau during 1998 were of far greater magnitude than any fluctuations measured previously. Whether the perturbations were truly unprecedented, however, is unclear. Etpison (1997) reported that the medusa population in Ongeim'l Tketau was decimated in 1987 and, although she attributed the loss of medusae to scientific diving and SCUBA generated turbulence that disturbed the toxic monimolimnion, its coincidence with the El Niño of 1986–88 (Brown et al., 1996; NOAA, 1999b) now suggests a close link

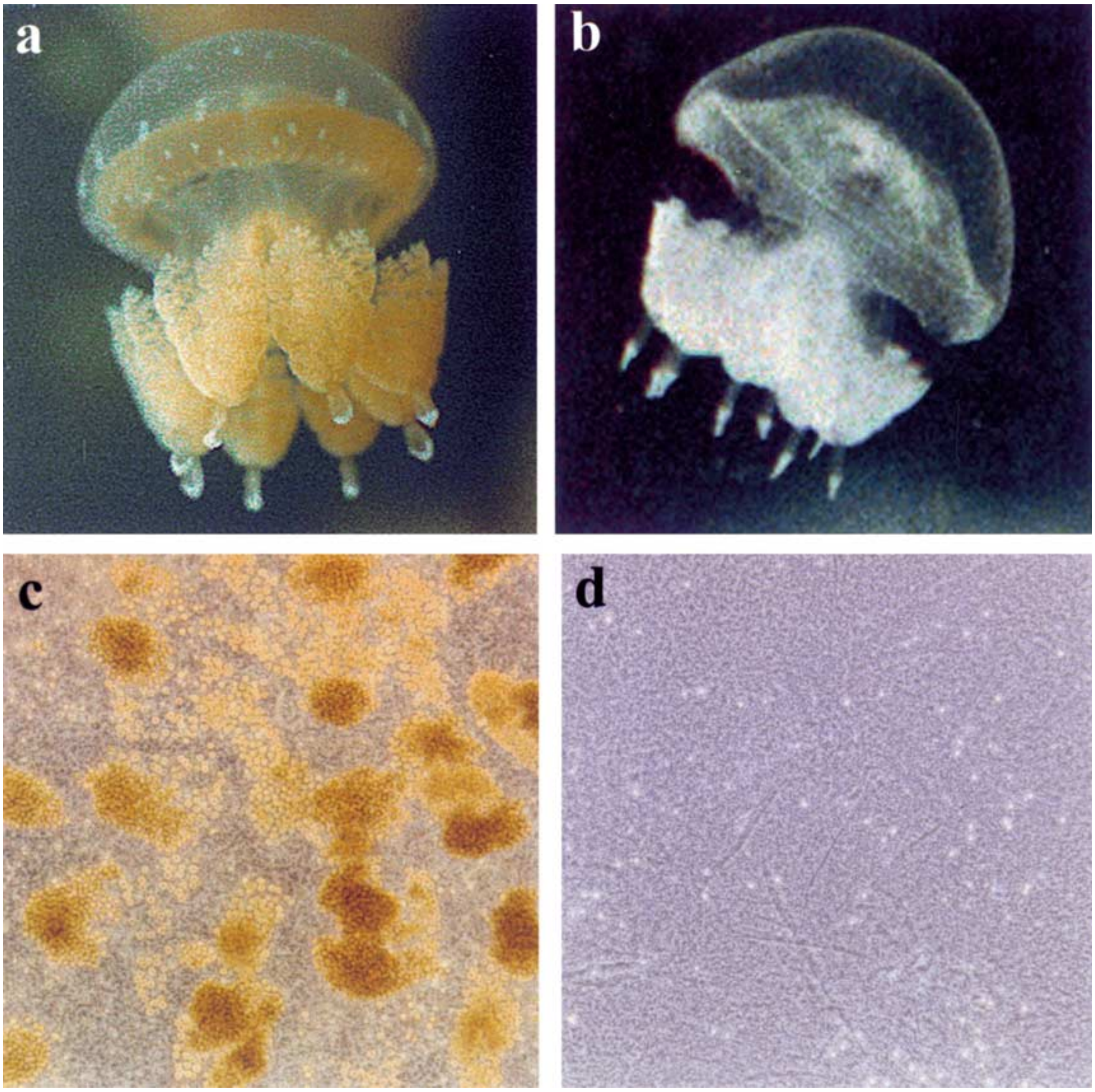

Figure 5. (a) A symbiotic golden-*Mastigias* medusa, approximately 30 mm bell diameter and (b) an azooxanthellate white-*Mastigias* of similar size. Under phase-contrast microscopy (magnification ×125), (c) tissue of golden-*Mastigias* is replete with clusters of heavily pigmented zooxanthellae (each zooxanthella is ~9 μm diameter [Muscatine et al., 1986]) while (d) zooxanthellae are conspicuously absent from tissue of white-*Mastigias*.

between climate change and marine lake ecosystem dynamics.

The most striking changes measured in the marine lakes in 1998–99 occurred in Ongeim'l Tketau where extremely high water temperatures and unusual stratification were associated with the disappearance of approximately 1.5 million *Mastigias* medusae. By contrast, *Mastigias* medusae in Goby, Clear, and Big Jellyfish lakes did not suffer the same fate. These lakes, which did not stratify to the same degree, never became as hot and generally were more variable physically than OTM. Their *Mastigias* populations either were not affected detrimentally or recovered relatively quickly. The coincidence of strong physical and biological changes in the lakes after two decades of apparent stability suggests they were related causally. Laboratory experiments support this interpretation – temperatures as high as those observed in Ongeim'l Tketau can have severe effects on *Mastigias*, including bleaching and increased mortality of scyphistomae

(Figs 8 and 9), inhibition of strobilation, and increased mortality of medusae (Fig. 10).

Ongeim'l Tketau

The disappearance of *Mastigias* medusae from Ongeim'l Tketau likely resulted from the coincidence of several unusual demographic events. Ongeim'l Tketau normally contains *Mastigias* medusae of all sizes indicating strobilation, growth, and mortality during all, or most, months of each year (Hamner et al., 1982). However, the medusa population in September, 1998, probably had a higher than normal proportion of large medusae because the production or recruitment of small and medium-sized medusae had been less frequent than usual during summer 1998. The large medusae present in September died before the end of November, 1998, leaving in the lake only uncharacteristically few and small medusae. It seems likely that the large, mature, medusae died as a natural consequence of reproductive senescence, as observed in other medusae (Arai, 1997:182–3). Mass mortality of large, presumably post-reproductive, *Mastigias* was observed previously in Ongeim'l Tketau in April, 1997, when hundreds to thousands of motionless medusae carpeted the lake bottom, underneath the previous afternoon's swarm (Dawson, pers. obs.). In contrast, the disappearance of all smaller medusae was anomalous.

The death of small and medium medusae from Ongeim'l Tektau in 1998 appears attributable more to high mortality of small medusae than to lack of strobilation. Between late-1998 and April, 1999, thousands of medusae were strobilated but none survived. Strobilation did not cease until May, 1999. There may be several reasons ephyrae and small medusae did not survive. One possibility is exposure to unusually high temperatures (Fig. 10), which may have occurred nightly when medusae migrated into deeper waters (Hamner et al., 1982). Alternatively, exposure to high temperatures may have been chronic if medusae became trapped behaviorally by and below the thermocline and halocline at 5–6 m (see Lance, 1962; Harder, 1968; Arai, 1973, 1976, 1992; Hamner et al., 1994; Dawson, 2000). Similarly, depending on the relationship between water column structure and the distributions of *Mastigias* medusae and their resources, the physical changes in OTM may have limited the availability of suitable prey (see also Uye, 1994) and access to light above the pycnocline or nutrients below it, at the chemocline. Notably, *Mastigias* medusae <40 mm rely heavily on zooplankton to meet their metabolic demands (McCloskey et al., 1994). However, the uninterrupted abundance of *Aurelia* in OTM throughout 1998–99 suggests prey were not scarce. Thus, the decline in *Mastigias* seems likely to be attributable to another factor, or factors, perhaps affecting their symbiosis with zooxanthellae.

Irrespective of the causes of their decline, medusae were present until April, 1999, after which strobilation ceased, probably inhibited principally by the unusually high temperature of the mixolimnion (but see also Purcell et al., 1999; Condon et al., 2001; Lucas, 2001; Watanabe & Ishii, 2001). High temperatures likely caused scyphistomae to bleach (Fig. 8), thus removing or reducing the zooxanthellae presumably required for strobilation (Sugiura, 1964, 1965; but see below). In addition, high temperatures may have reduced strobilation by increasing the mortality rate of scyphistomae (Fig. 9), although the loss of polyps may have been mitigated by the production of planuloids (Table 1). Finally, after April, 1999, water temperatures in Ongeim'l Tketau fluctuated little, relative to those in other jellyfish lakes, perhaps depriving scyphistomae of the temperature changes presumably needed to stimulate strobilation (Sugiura, 1964, 1965; see also Figs 3 and 4). Thus, on the basis of laboratory experiments and field measurements, relative to other jellyfish lakes, there should have been few, if any, zooxanthellate or strobilating scyphistomae in Ongeim'l Tketau after April, 1999, and field collections in summer 1999 demonstrated that this was the case (Table 1).

Goby, Clear and Big Jellyfish lakes

The small body size and number of *Mastigias* medusae in Goby Lake in December, 1998 (Fig. 4), suggests the recent dynamics of the golden-jellyfish population may have been similar to those in Ongeim'l Tketau. However, the cohort of small medusae in Goby Lake in December, 1998, grew successfully. By August 1999, the golden-jellyfish population had returned to approximately its pre-1998 condition and there were many zooxanthellate strobilae in the lake (Table 1).

By contrast, Clear Lake, in August 1999, contained almost exclusively *Mastigias* medusae $\geq$12 cm and the scyphistomae collected were only moderately infected with zooxanthellae and not strobilating. The dearth of small medusae and strobilation in CLM may have been attributable to low levels of zooxanthellae (Table 1) which are important for strobilation (Sugiura, 1964, 1965; Arai, 1997). However, other factors also are implicated (e.g. Purcell et al., 1999; Con-

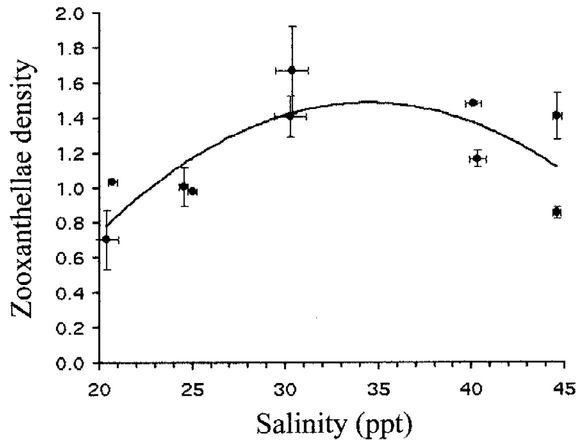

Figure 6. The effect of salinity on the zooxanthellae density index for *Mastigias* scyphistomae collected in Ongeim'l Tketau. Scyphistomae were collected from salinities of 31–32‰ and acclimated to 34‰ during the 3 weeks prior to the experiment. Subsequently, the scyphistomae were acclimated to the experimental salinities at which they were held for 11 days. Fitted curve: $y = -0.0032x^2 + 0.222x - 2.4623$, $R^2 = 0.5488$. 95% Confidence Interval (CI) error bars are shown.

don et al., 2001; Lucas, 2001; Watanabe & Ishii, 2001) because zooxanthellae are not absolutely necessary for strobilation – the white *Mastigias* of 1997 more likely were strobilated aposymbiotically (e.g. Rahat & Adar, 1980) than bleached post-strobilation because bleached animals typically retain some remnants of zooxanthellae (Glynn & D'Croz, 1990; Hayes & Bush, 1990; Kuroki & van Woesik, 1999; but see Fig. 5). Irrespective of the reason for the dearth of small and medium *Mastigias* medusae, CLM in August 1999 may have resembled OTM in Fall 1998, just prior to the disappearance of the *Mastigias* population.

Alone among the four lakes reported here, Big Jellyfish Lake experienced no obvious changes in its biota. Possibly this was because temperature extremes in Big Jellyfish Lake were more modest than in other lakes (Fig. 3). However, it also is possible that BJLK *Mastigias* are adapted better to temperature extremes than *Mastigias* in other lakes (Fig. 10). Such local adaptation might explain the demographic differences observed between lake populations in 1998–99 and is consistent with previous evidence of lake-specific adaptations in marine lake *Mastigias* (Hamner & Hauri, 1981; Muscatine & Marian, 1982; McCloskey et al., 1994) and co-adaptation of zooxanthellae and hosts (Rowan & Knowlton, 1995; see also Fig. 8a). Moreover, the events of 1998-99 suggest that natural selection and adaptation may be ongoing in at least some populations of *Mastigias*.

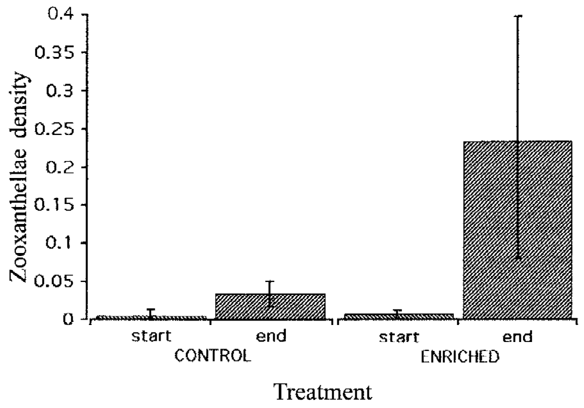

Figure 7. The effect of zooxanthellae enrichment on the zooxanthellae density index for scyphistomae from Ongeim'l Tketau. Homogenized mouth-arm tissues of *Mastigias papua* were added to 'enriched' treatments but not to controls. Student's *t*-test showed a significantly greater ($p = 0.05$) increase in the density of zooxanthellae in 'enriched' over 'control' treatments after 4 days. 95% CI error bars.

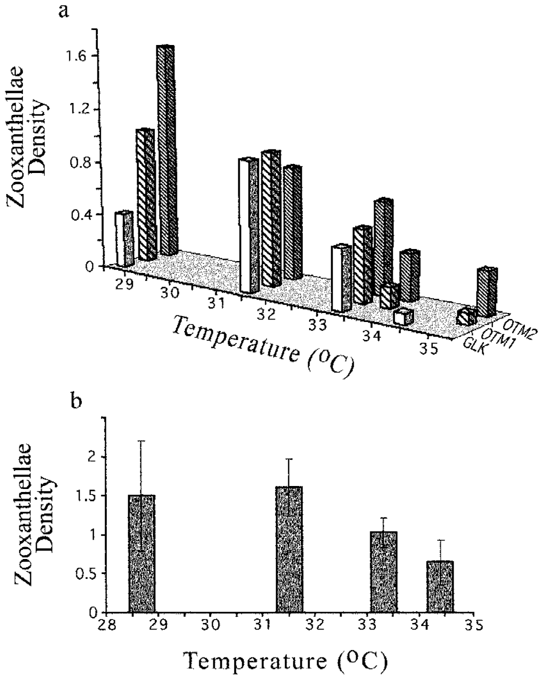

Figure 8. The effect of temperature on the zooxanthellae density index for *Mastigias* scyphistomae. (a) Change in zooxanthellae density in scyphistomae containing established populations of zooxanthellae. GLK, Goby Lake, Koror; OTM1, Ongeim'l Tketau, Mecherchar, infected with non-*Mastigias* zooxanthellae. OTM2, Ongeim'l Tketau, Mecherchar, enriched with zooxanthellae from *Mastigias papua*. (b) The increase in zooxanthellae density (± 95% CI) in scyphistomae that were inoculated with *M. papua* zooxanthellae immediately prior to the experiment. Center of bar indicates temperature treatment.

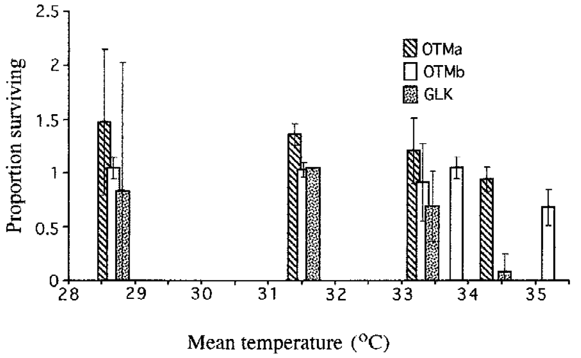

Figure 9. The effect of temperature on mean survival (± 95% CI) of *Mastigias* scyphistomae inoculated with *M. papua* zooxanthellae immediately prior to the experiment (OTMa) and those with established populations of zooxanthellae (OTMb, GLK). Center of white bar indicates temperature treatment.

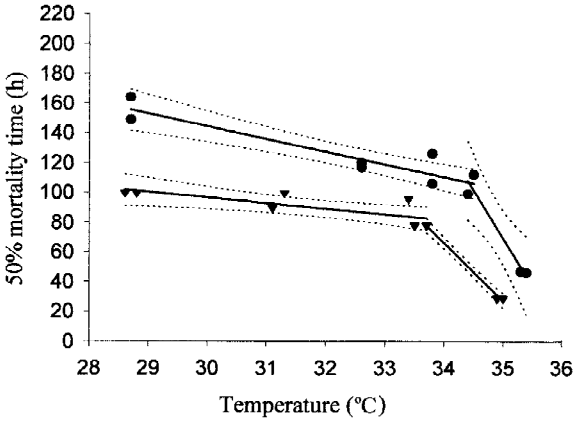

Figure 10. Effect of temperature on the 50%-mortality time of *Mastigias* medusae from BJLK (circles) and GLK (triangles). Increasing temperature decreases survivorship (i.e. regressions are significantly different from zero, see below), an effect that is particularly severe at the highest temperatures studied. The linear regressions fitted to BJLK data are, $y = -8.552x + 401.11$, $R^2 = 0.859$, $p = 0.001$, and $y = -64.024x + 2310.45$, $R^2 = 0.943$, $p = 0.029$. The regressions fitted to GLK data are, $y = -3.781x + 210.087$, $R^2 = 0.6075$, $p = 0.023$, and $y = -39.07x + 1394.75$, $R^2 = 0.997$, $p = 0.002$. Dotted lines show 95% confidence intervals on the regressions.

Tourists and other factors

Tourists probably played little role in the disappearance of *Mastigias* medusae. Populations of *Mastigias* medusae declined almost synchronously in Ongeim'l Tketau and Goby Lake although few tourists visited Goby Lake, and it simply was not logistically feasible that tourists ate, stole or otherwise killed all one-and-a-half million medusae in Ongeim'l Tketau. Moreover, *Mastigias* medusae had not been affected deleteriously by many previous years of sometimes higher tourism. In addition, although sunblock can kill golden-medusae, it is highly unlikely that acutely lethal concentrations, which turn seawater milky, ever have been present in Ongeim'l Tketau. Whether there are detrimental effects due to chronic exposure of *Mastigias* to sunscreen, however, is yet to be investigated experimentally.

The disappearance of *Mastigias* medusae also was not attributable to stagnation of the lake caused by reduced tidal exchange, because the conduits connecting the lake and lagoon were not blocked. The extreme stratification and over-heating of the mixolimnion of Ongeim'l Tketau most likely were induced by El Niño weather patterns. High salinity also is an unlikely explanation for the disappearance because, although salinity was high in December 1998, *Mastigias* did not disappear entirely until April 1999, when salinity profiles already had returned to normal (Fig. 2; Hamner & Hamner, 1998). Moreover, *Mastigias* medusae frequently migrate vertically between waters differing by 3‰ (Hamner et al., 1982) and experimental salinity changes of 10‰ in 7 days generally are somewhat deleterious, but not lethal, to *Mastigias* scyphistomae (Fig. 6; also see Weiler & Black, 1991). Thus, at this time, there is little evidence to implicate factors other than temperature in the disappearance of *Mastigias* medusae from Ongeim'l Tketau.

Closing remarks

In January, 2000, *Mastigias* medusae were observed in OTM for the first time since April 1999. A small strobilation event occurred after the lake had cooled, by December 1999, to its lowest temperature (max. 32.8 °C) since January 1999. This cohort of medusae matured and grew successfully to as large as 19 cm. Since then, three additional strobilation events have produced mature medusae up to 23 cm. The *Mastigias* population in OTM has increased gradually in size but, as of May 2000, remains probably less than 10^4 strong.

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