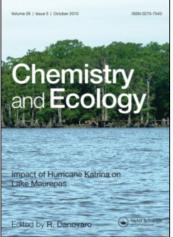
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Chemistry and Ecology

Publication details, including instructions for authors and subscription information: http://www.informaworld.com/smpp/title~content=t713455114

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To cite this Article Cerrano, C. , Azzini, F. , Bavestrello, G. , Calcinai, B. , Pansini, M. , Sarti, M. and Thung, D.(2006) 'Marine lakes of karst islands in Ha Long Bay (Vietnam)', Chemistry and Ecology, 22: 6, 489 – 500 **To link to this Article: DOI:** 10.1080/02757540601024835 **URL:** http://dx.doi.org/10.1080/02757540601024835

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Marine lakes of karst islands in Ha Long Bay (Vietnam)

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(Received 1 August 2006; in final form 11 September 2006)

Ha Long Bay in North Vietnam is characterized by karst towers and bigger islands totalling more than 3000 isles. Karst processes carved hundreds of caves out of the limestone and contributed to the formation of many enclosed and semi-enclosed saltwater lakes. Here, we report the results of a general survey of several lakes and the first data on the Hang Du I lake, a small basin devoid of any apparent communication with the surrounding sea. Hang Du I is characterized by the presence of Rhizostomeae, genus Mastigias, suggesting strong similarities with the famous lakes described from the archipelago of Palau. Among the benthic organisms sponges are the most important group. Temperature and abundance of the monsoon rains are the main factors influencing remarkable seasonal variations in physical-chemical parameters and the community structure of the lake. A thermal crisis with water temperatures up to 36 °C was recorded in September 2003. In this period, usually abundant medusae and sea anemones totally disappeared. Sponge populations showed fast growth rates in winter and spring and a partial degeneration to face the harsh conditions of the summer season. When isolated from the surrounding marine environment, the saltwater lakes share the condition of oceanic islands, representing spots of habitats surrounded by a completely different environment. The Ha Long Bay marine lakes are not easy to access, being surrounded by tropical forest, but local people usually exploit them for both fishery and oyster harvesting. There is an urgent need to develop measures of protection for these endangered and unique environments, natural laboratories that facilitate the study of evolution of marine organisms, where biodiversity has been until now totally unexplored.

Keywords: Stratified lakes; Tower karst; Life cycle; Porifera; Tonkin Gulf

1. Introduction

Ha Long Bay is one of the most extensive and best-developed areas of tower karst in the world. The eastern Adriatic, Greek, and Aegean coasts of Turkey provide other outstanding examples of tower karst although not of drowned tower karst, which is a style of karst landscape found mainly in the tropics and subtropics. Ha Long Bay is not unique in SE Asia for being a drowned tower karst; other sites where such a phenomenon occurs include the Mergui archipelago off the Andaman coast of Burma and other localities in northern Malaysia, Indonesia, and Thailand.

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However, the great extent of the Ha Long Bay tower karst and the richness of its forms (both current and 'fossil' forms) set it apart from all comparable areas of drowned tower karst in SE Asia [1].

The Ha Long Bay towers date back to the middle of the Tertiary Period (over 35 mya) when subsidence of the massive Pacific plate led to the uplift of millions of years of oceanic deposition and to the exposure to a tropical climate [2]. The monsoon regime causes abundant rains (up to 2000 mm yr⁻¹) during the summer, from May to October, with possible typhoons from June to September. The cold and dry north-east winter-time monsoons last from November to April. The mean annual temperature in Ha Long Bay is 25 °C. In these conditions, karst processes have carved many pockets out of the limestone leading to the formation of saltwater lakes when the area was flooded by the rising sea level following the last glacial maximum (*c*. 18 000 yr BP) [2]. In the area, about 3000 islands are present, ranging from small towers to large, topographically complex, islands. Two of these larger islands, Cat Ba and Dao Cai Bau, contain about 40 saltwater lakes; six occur in Dau Be Island [1]. The highest calcareous islands are as high as 400 m, and the deepest bathymetry between peaks can reach 25 m depth.

The saltwater lakes of Ha Long Bay differ remarkably from one another, but they are all more or less isolated from the sea; therefore, they may be considered as small marine 'habitat

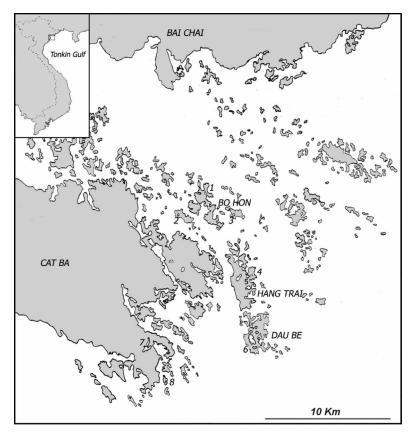


Figure 1. Map of the western part of Ha Long Bay (North Vietnam). Numbers indicate the rough position of the studied lakes within the four marked island groups: Bo Hon, Cat Ba, Hang Trai and Dau Be. 1: Hang Luong Lake; 2: Me Cung Lake; 3: Bui Xam Lake; 4: Hang Du I Lake; 5: Hang Du II Lake; 6: Dau Be Lake; 7: Cat Ba Lake; 8: Hang Tham Lake.

| | 1. Hang Luong | 2. Me Cung | 3. Bui Xam | 4. Hang Du I | 5. Hang Du II | 6. Dau Be | 7. Cat Ba | 8. Hang Tham |
|--------------------------------------|---------------|----------------|--------------|--------------|---------------------------|----------------|----------------|-------------------------|
| Island | Bo Hon | Bo Hon | Bo Hon | Hang Trai | Hang Trai | Dau Be | Cat Ba | Cat Ba |
| Estimated area (ha) | 3 | 1.5 | 0.8 | 0.8 | 3.1 | 0.06 | 140 | 0.8 |
| Minimum distance from the sea (m) | 20 | 80 | 100 | 50 | 20 | 5 | 20 | 10 |
| Type of communication | Large tunnels | Small conduits | Undetectable | Undetectable | Large tunnels | Small conduits | Small conduits | Large tunnels |
| Human | | | | | | | | |
| impact | Unknown | Unknown | Unknown | Unknown | Exploited for aquaculture | Unknown | Unknown | Exploited for aquacultu |

Table 1. General features of the surveyed lakes and of their communication with the sea.

islands' surrounded by land. Their communication with the sea-evident in many cases and hidden in others – is an environmental hindrance that marine organisms need to overcome to enter the lake. Such a situation, in the marine environment, is reminiscent of the concept of insularity that has been so useful for understanding the community structure and evolution of terrestrial ecosystems [3–6].

The best known comparable habitats are meromictic marine lakes in Palau [7], in which the column water is more or less permanently stratified. In Palau, at least four meromictic lakes are inhabited by large populations of mildly stinging jellyfishes [8–10] that have attracted the attention of media and tourism [11]. These medusae, belonging to the genus *Mastigias* (Scyphozoa, Rhizostomeae), show circadian horizontal and vertical migration behaviours [8] and, in two lakes, are preyed upon by *Entacmea medusivora* Fautin & Fitt, 1991, a jellyfisheating sea anemone.

This first study, in the framework of a project on the marine biodiversity of the coasts of Vietnam, attempts a screening of several Ha Long Bay lakes showing different levels of isolation with respect to the neighbouring sea, aiming to describe their general characteristics and fauna, with special attention for sponges.

2. Methods

Three periods of fieldwork were performed in North Vietnam–April 2003, September 2003, and April 2004–in collaboration with a team from the Hai Phong Institute of Oceanology (HIO). Eight lakes, chosen because they differed in size, general characteristics, and communication with the sea, were preliminarily surveyed in the small islands of Ha Long Bay and in Cat Ba Island (figure 1, table 1).

Exploration and sampling were conducted by diving, whenever it was possible to carry all the gear through the steep paths leading to the lakes, in other cases only by snorkelling (lakes 7 and 8).

Special attention was paid to the apparently most enclosed lakes, particularly to Hang Du I, the most isolated basin and the only one where *Mastigias* has been observed. Physical–chemical characteristics of Hang Du I were recorded by the HIO team. To perform a general description of the fauna, qualitative samples of sponges, cnidarians, and other invertebrates were photographed and collected. The distribution and abundance of sponges along the south-eastern coast of the lake were preliminarily estimated in September 2003 and April 2004, by a single horizontal transect 20 m long and 1 m wide at 1.5 m of depth.

3. Results

3.1 Physical environment

All the lakes are relatively shallow (less than 10 m deep), and most have rather turbid waters due to the abundance of fine sediment and decaying vegetable debris on the bottom. Physical–chemical measurements in four lakes during September 2003 showed considerable inter-lake variation (table 2).

Hang Du I Lake (figure 2a), visited three times, is located in the Hang Trai Island, among steep, overhanging cliffs that shelter it from the wind. It has a rounded shape with a diameter of about 80 m and a maximum depth of 8 m. The water is still and clear, unlike that of the other lakes, but the fine sediment covering the shores and the bottom is very easily resuspended. Tidal excursion, and therefore communication with the open sea, is indicated by a belt, about

| Locations | Temperature (°C) | pH | $DO (mg l^{-1})$ | Salinity (S, ‰) |
|--------------|------------------|------|------------------|-----------------|
| 1. Hang Luon | 30.5 | 7.77 | 5.85 | 21.5 |
| 2. Me Cung | 29.8 | 8.52 | 8.10 | 25.0 |
| 3. Bui Xam | 31.9 | 7.57 | 7.38 | 25.0 |
| 4. Hang Du I | 29.1 | 8.08 | 6.56 | 7.0 |

Table 2. Physical-chemical surface conditions of some marine lakes of the Ha Long Bay recorded by the HIOstaff in September 2003.

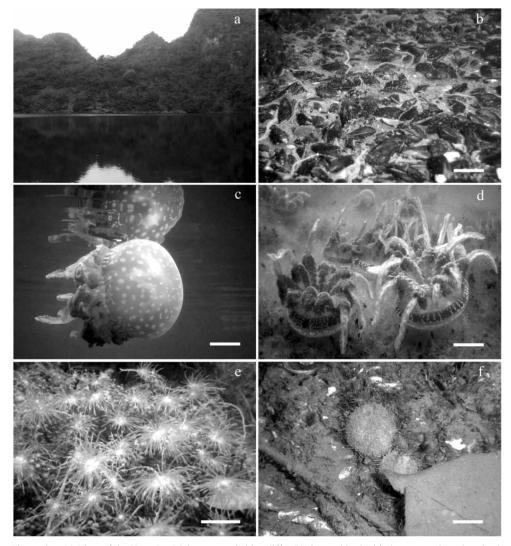


Figure 2. (a) View of the Hang Du I lake surrounded by cliffs; (b) the muddy-detritic bottom at about 3 m depth covered by algae and bivalves; (c) *Mastigias* sp. jellyfishes swimming rhythmically close to the surface; (d) *Mastigias* sp. specimens resting upside down on the bottom, at 2-3 m depth; (e) dense population of sea anemones, settled on algae and mussels, which thrive in springtime from the surface to a depth of about 4 m; (f) specimens of the demosponge *Tethya seychellensis*, covered by buds, occupying shadowed positions on the rocky part of the bottom. Scale bars: b, 1 cm; c, 1.5 cm; d, 2 cm; e, 1 cm; f, 1.5 cm.

| | April 2003 | September 2003 | April 2004 |
|---|------------|----------------|------------|
| Thickness of the superficial rainwater layer (cm) | 50 | 150 | 10 |
| Surface temperature (°C) | 27 | 30 | 24 |
| Bottom temperature (°C) | 30 | 36 | 26 |

Table 3. Variations of physical conditions of Hang Du Lake I, recorded in situ by diving computer.

1 m thick, of bivalves (mostly *Ostrea echinata* Quoy & Gaimard, 1832) thriving on the rocky intertidal part of the shores. This basin displays large environmental variations including the abundance and the thickness of the rain-water layer (table 3).

During the survey of April 2003, there was a freshwater surface layer about 0.5 m thick that became three times thicker in September, following the monsoon. The bottom sediment of the lake, in this last period, was rich in a decomposing organic debris of decaying algae, bivalve shells, and sponges. It hosted a huge number of polychaetes (more than 1000 specimens per 400 cm²) feeding on organic matter. In the following spring (April 2004), the freshwater layer was both thinner and colder than the year before.

3.2 Biological environment

Hang Du I lake was visited three times. The other lakes were visited twice or only once. The centre of the lake, where the likely maximum depth could be recorded, was not always reached. For this reason, it is possible to give only a short and partial description of all the visited lakes. For Hang Du I Lake, more information is available, and for three lakes, a list of sponge species is given.

Hang Luong Lake (figure 1) is a wide cove that communicates with the open sea through a tunnel 20 m long and 5 m wide; the tunnel is subject to strong tidal currents. Benthic fauna (mainly sponges and octocorals) is more abundant in the tunnel than in the lake.

Me Cung Lake (figure 1) can be almost reached by walking on a path, 10 m long, through the forest. On the muddy bottom, many free sponge specimens were recorded. The maximum depth of the lake is about 8 m.

Bui Xam Lake (figure 1) is very shallow (4 m maximum depth) and characterized by a belt of massive corals partially covered by at least two species of *Caulerpa*. The bivalves *Ostrea echinata* and, below, *Isognomon* isognomon are very common. Below 1 m, the bottom is completely buried by soft sediments.

Hang Du II Lake (figure 1 (L., 1758)) communicates with the open sea through an artificial opening. The lake can be reached both by diving and by walking. The underwater passage hosts many sponges, preyed upon by cowrie molluscs, and octocorals. The rocky shores of the lake are colonized by *Isognomon* isognomon and are partially covered by a belt of corals, occasionally damaged by trampling.

Dau Be Lake (figure 1) is small, with soft sediments burying many benthic organisms. There are at least two species of *Caulerpa* and several sponge species that are well adapted to live buried into the sediment.

Cat Ba Lake (figure 1) is the widest lake among those here reported (table 1). It is separated from the open sea by a few metres of rock, but a small communication allows tidally mediated water exchange. This lake is less muddy than the others and hosts the same sea anemones found in Hang Du I Lake.

Hang Tham Lake (figure 1) has an artificial opening that, allowing communication with the open sea, keeps water clear. There are massive corals and *Isognomon* isognomon.

The more fully studied Hang Du I Lake (figure 1) is about 30 m from the open sea. There is no true path to the lake, but the access is free from trees. A small mangrove patch (*Rizophora* cf. *stylosa*) grows on the south-eastern shore of the lake, where the shore is less steep. The bottom profile is bowl-shaped and shows a very simple zonation. A belt of *Ostrea echinata* is evident in the intertidal. From approximately 0 to 2 m depth (relative to the low-water mark), there are rocks of variable size with algae (at least two species of *Caulerpa*) and epiphytic small mussels (Mytilidae) (figure 2b); from about 2 to 4 m depth, the same taxa grow on a muddy detritic bottom; from about 4 to 8 m depth, the bottom is present (i.e. rocks, algae, mytilids, leaves, and wood debris on the muddy bottom), the population of sea anemones shows 100% cover (figure 2e). The main macro-invertebrate taxa are sponges, sea anemones (*Mastigias* sp.; figure 2c), polychaetes, molluscs, and tunicates. No corals were found in Hang Du I.

The macro-invertebrate populations, like the physical environment, showed remarkable variations in the different seasons. The *Mastigias* were present only in spring (both 2003 and 2004) but absent in September 2003. Many specimens rest on the bottom upside down (figure 2d), as *Cassiopea* jellyfishes do.

Sea anemones (about 1 cm across) which, like the jellyfishes, were observed only in spring, were then extremely numerous (figure 2e). They host zooxanthellae and had never been noted to feed on jellyfishes. They grow everywhere in the lake: on any kind of hard substrate and epiphytic on algae and mangrove roots. They appear to have an ability to divide very rapidly into fragments, when disturbed, and regenerate quickly.

In Hang Du I, a few sponge species occupy sheltered niches under overhanging superficial rocks (especially *Tethya seychellensis* (Wright, 1881); figure 2f) or under the mangrove canopy (*Haliclona* spp.). Due to the water stillness, even relatively soft species (devoid of a stout skeleton) may reach an unusual height of 30–40 cm. Three sponges (*Suberites* sp. (figure 3a and b), *Protosuberites* sp. (figure 3c and d), and Dictyonella sp.) are very common: they thrive in the rocky and detritic part of the bottom and show a very rapid growth in fall and winter, the relatively cold season (figure 3a and c). The late spring and summer thermal crisis greatly affects these sponges, causing a partial degeneration of the massive specimens, which survive as minute or encrusting aestivating forms (figure 3b and d).

Six sponge species were detected in the superficial transect performed in the Hang Du I lake (table 4). They were all present both during September 2003 and in April 2004.

Their distribution looks rather uniform, taking into account that the excavating species (*Cliona aurivilli* (Lindgren, 1897) and *Cliona celata* (Grant, 1826)) are bound to the presence of a rocky bottom, and *Tethya seychellensis*, which requires shadowed positions, may sometimes be absent. *Suberites* sp. and *Protosuberites* sp., which are not disturbed by the algal covering and thrive in full light, are the most abundant species. The transects did not allow an estimation of the volume decrease in the massive specimens in late summer, because sponges are still present on the substrate.

Periodical environmental variations of the Hang Du I lake affect all the main invertebrate taxa, whose abundance is provisionally evaluated in table 5. Jellyfishes, sea anemones, and ascidians were not detected in September 2003, while demosponges decrease, and polychaetes bloom in the same period. In the following spring, all the taxa are present again.

Sponges were present in all the other lakes we studied, but our work focused mainly on three of the more isolated lakes. We recorded approximately 27 taxa, not all identified to species level (table 6). The diversity of the demosponges was higher in Me Cung lake (18 species) than in Hang Du I and Bui Xam (nine species in each). No species was common to the three lakes, and only *Protosuberites* sp. and *Suberites* sp. were never recorded in the surrounding sea.

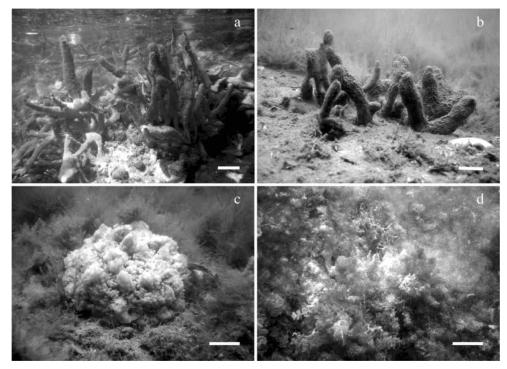


Figure 3. Erect and massive sponge species such as (a) *Suberites* sp. and (c) *Protosuberites* sp. These thrive in spring and withstand the summer thermal crisis through a partial degeneration of their bodies (b, d, respectively). Scale bars: a, 3 cm; b, 1.5 cm; c, 3.5 cm; d, 2 cm.

| Distance (m) | Cliona aurivilli | Suberites sp. | Dictyonella sp. | Protosuberites Suberites sp. | Cliona celata | Tethya seychellensis |
|---------------|---------------------|---------------|-----------------|---------------------------------|---------------|-------------------------|
| September 200 | 3 | | | | | |
| 0–5 | 0 | 2 | 0 | 0 | 3 | 0 |
| 5-10 | 1 | 8 | 1 | 4 | 0 | 1 |
| 10-15 | 0 | 4 | 2 | 7 | 4 | 2 |
| 15-20 | 2 | 3 | 1 | 8 | 3 | 1 |
| Total | 3 | 17 | 4 | 19 | 10 | 4 |
| April 2004 | | | | | | |
| 0-5 | 2 | 8 | 1 | 4 | 2 | 1 |
| 5-10 | 1 | 1 | 3 | 8 | 2 | 3 |
| 10-15 | 1 | 4 | 0 | 2 | 1 | 0 |
| 15-20 | 5 | 5 | 0 | 4 | 6 | 0 |
| Total | 9 | 18 | 4 | 18 | 11 | 4 |

Table 4. Hang Du I Lake: Distribution and abundance (specimens per 5 m²) of six sponge species along a
horizontal transect on the south-eastern coast.

Table 5. Rough abundance of the commonest taxa occurring in the lake of Hang Du I during the three surveys.

| | April 2003 | September 2003 | April 2004 |
|-----------------------------|------------|----------------|------------|
| Jellyfishes (Mastigias sp.) | +++ | _ | ++ |
| Sea anemones | +++ | _ | ++ |
| Polychaetes | + | +++ | + |
| Tunicates | + | _ | ++ |
| Demosponges | +++ | + | +++ |

Note: -, absent; +, present; ++, common; +++, abundant.

| | Lakes | | | |
|--|-----------|---------|-----------|--|
| Species | Hang Du I | Bui Xam | Me Cung I | |
| Aka mucosa Bergquist, 1965 | | Х | | |
| Cliona aurivilli (Lindgren, 1897) | X | | | |
| Cliona orientalis Thiele, 1900 | | Х | | |
| Cliona celata Grant, 1826 | Х | | | |
| Cliothosa hancocki (Topsent, 1888) | | | Х | |
| Pione carpenteri Hancock, 1867 | Х | Х | | |
| Spirastrella decumbens Ridley, 1884 | | Х | | |
| Sphaeciospongia tentorioides (Dendy, 1905) | | Х | Х | |
| Chondrilla australiensis (Carter, 1873) | | Х | Х | |
| Desmanthus cf. incrustans (Topsent, 1889) | | Х | | |
| Dysidea cf. fragilis (Montagu, 1818) | | Х | | |
| Dysidea cinerea Keller, 1889 | | | Х | |
| Gellius sp. | | Х | | |
| Haliclona spp. HL 33, HL 35 | Х | | | |
| Haliclona spp. HL 94, 99 | | Х | | |
| Haliclona sp. HL 13 | | | Х | |
| Haliclona sp. HL 95 | | Х | Х | |
| Dictyonella sp. | Х | | | |
| Ircinia sp. HL 85 | | Х | Х | |
| Mycale parishii (Bowerbank, 1875) | | | Х | |
| Petrosia nigricans Lindgren, 1897 | | Х | | |
| Suberites sp. | Х | X | | |
| Protosuberites sp. | X | X | | |
| Spongia cf. officinalis Linnaeus, 1759 | | X | Х | |
| Tethya seychellensis (Wright, 1881) | Х | X | | |

Table 6. Demosponges recorded in the three enclosed lakes studied at Ha Long Bay.

Note: The species belonging to the genera Aka, Cliona, Cliothosa, Pione, and Spirastrella are boring sponges.

4. Discussion

For about two decades, several studies have focused on meromictic lakes, mainly in tropical areas, for their peculiar faunas adapted to long-term stability in the physical–chemical parameters [7]. Generally, these lakes are characterized by their isolation from the surrounding sea and by the unusual presence of jellyfishes belonging to the genus *Mastigias*. In this work, we have preliminarily described a complex system of marine lakes in Ha Long Bay having different degrees of isolation. Moreover, we have focused our work on the dynamics of one of these lakes and on the biodiversity of sponges, a group scarcely considered in the faunistic studies of marine lakes published until now [12, 13].

4.1 Variation among lakes

Three types of lake categories have been tentatively defined according to water exchange with the sea: (1) lakes with large tunnels (when an opening or canal allow a continuous exchange); (2) lakes with small conduits (when small canals or water percolating through rocks are detectable); (3) enclosed lakes (when any surface communication is undetectable, and saltwater enters the lakes through the underground karst system).

One of the lakes, Hang Du I, is completely enclosed and characterized by the presence of *Mastigias* sp., of an unidentified species of sea anemone, and of several massive and boring sponges. This anemone does not feed on jellyfishes, unlike *Entacmaea medusivora* so common in the lakes of Palau [14]. Two other enclosed lakes were recorded but were completely devoid of jellyfishes: this may be attributed to the absence in these lakes of mangroves that

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were considered crucial for larval metamorphosis during the life cycle of the species of the genus [15].

There is evidence that variations in the weather conditions, and especially of the quantity of rain, directly affect the lake environment and organism's life cycle. Also, the degree of isolation of a lake, as indicated by its size, distance from the sea, and the presence or absence of a surface connection with the sea, may influence temporal variations.

4.2 Variation between sampling events in Hang Du I (physical and biological)

The sheltered position of Hang Du I limits water mixing due to wind and enhances stratification, resulting in the formation of a surface lens of fresh, cooler water overlaying a deeper layer of more saline, warmer water. Thus, we recorded striking seasonal variations of salinity and temperature in 2003, and a remarkably different situation in the following spring 2004 (table 2).

The Hang Du I lake evidenced marked changes in the abundance of different groups: in the warm season, jellyfishes and sea anemones completely disappeared, and sponges and tunicates strongly decreased. On the contrary, in the same period, bottom polychaetes showed a strong density increase, likely related to the rain of organic matter coming from the degeneration of benthic organism of the upper layers, as suggested by the presence on the bottom of many decomposing sponge fragments.

Sponge populations in the lakes are able to withstand conditions much harsher than in the neighbouring sea. The rough abundance of demosponges shown in table 5 seems not to correspond with the total number of sponges reported in table 4 that is very similar between the two sampling periods (September 2003 and April 2004).

These data highlight that sponges maintain their position during bad environmental conditions, but strongly reducing their dimensions. The drastic response they show is known in freshwater sponges [16] but is scarcely explored in marine sponges [17]. Seasonal variations leading to the disappearance of a *Halichondria panicea* (Pallas, 1766) population have been observed in coastal saltwater lakes [18], while the periodical reorganization of sponge specimens was recorded also in marine habitats [19, 20].

In spite of the functional and structural importance of Porifera, from polar [21] to tropical latitudes [22–24], few studies are available on the dynamics of sponges, possibly because of their relatively slow growth in marine environments. On the other hand, the autumn and winter after the summer crisis at Hang Du I is characterised by a regeneration process of damaged sponge tissue, which is known to be much faster than the normal growth rate [25]. The very unusual population dynamics, observed in Hang Du I lake for three species at least, is an adaptation to these particular environments where sponges: (1) require the possibility of surviving to adverse conditions by a reorganization of their body or by the production of resting stages and (2) should be able to produce biomass in a very short time, in order to commence sexual reproduction before the next adverse period.

Recent findings in Porifera evidence that the cADPR/ADP-ribosyl cyclase system, a potent and universal intracellular calcium mobilizer, mediates temperature sensing [26] and temperature-induced functional effects [27]. In particular, high temperature can negatively affect this biochemical pathway, increasing the concentration of intracellular calcium until apoptotic phenomena are induced [27]. These biochemical processes could partially explain the ever-more frequent mass mortality events linked to climate change, events that are compromising world biodiversity and that invoke the finding of biodiversity hot spots useful for conservation management [28, 29].

4.3 Usefulness of marine lakes for ecological and evolutionary research

The study of the life cycles of marine organisms in these small, enclosed systems, due to extreme environmental variations, offers the possibility to explore several intriguing aspects of marine ecology that are still debatable, such as the blooms of gelatinous plankton [30]. The absence of an apparent, surface communication with the neighboring sea may be an important isolating factor for the selection of endemic species: the demosponges *Suberites* sp., and *Prosuberites* sp., in fact, were just recorded in the Hang Du I and Bui Xam lakes and never detected outside.

In the lakes, the sudden disappearance of species such as jellyfishes and sea anemones, and the drastic reduction in other taxa such as sponges, polychaetes, and ascidians, may lead in a short time to complex feedback that can modulate the community structure, modifying its stability and productivity [31]. In the case of the lake of Hang Du I, in the span of one year we found three different assemblages (table 5), due to a mass mortality event (between April and September) and a subsequent bloom. The North Vietnam climate is influenced by the winds of Central Asia, which give rise to pronounced winter and summer seasons. Owing to their small dimensions, lakes can be quickly influenced by the yearly variations of the weather conditions that mainly affect their temperature and salinity. Therefore, they offer the possibility to explore, in a more or less simplified system, several general ecological problems especially regarding the resilience of the marine communities, on a timescale shorter than in open sea, and avoiding the limitations of simulated laboratory experiments.

Acknowledgements

The authors wish to thank the National Park Authority of Ha Long Bay and the staff of the Hai Phong Institute of Oceanology for supporting the fieldwork and Michael N. Dawson (Section of Evolution and Ecology Division of Biological Sciences, University of California) for his help and improvement of the manuscript.

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