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Article abstract

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Hexactinellid Sponge Reefs on the Canadian Continental Shelf: A Unique "Living Fossil"

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SUMMARY
Globally unique hexactinellid (siliceous) sponge reefs, found in deep (200 m), glacially scoured troughs of the western Canadian continental shelf, have been explored by a manned submersible. Submersible observations and geophysical data allow examination of the physical and biological processes that have shaped the sponge reefs, which began to form about 9 thousand years (k.y.) ago. The mounds (bioherms) and sheet-like accumulations (biostromes) cover a low-angle, non-depositional, iceberg-scoured seafloor, relict since the deglaciation of the region. Biohermal structures are up to 19 m in height, and are covered with hexactinosan sponges up to 1.5 m tall, creating a benthic habitat that discontinously covers roughly 700 km^2. Similar to extinct siliceous sponge reefs, mud mounds, and reef mounds that were widespread during the Mesozoic, the modern reefs are like a "living fossil" and provide a unique modern analogue. Fishing activities, especially trawling or bottom dragging, have damaged the slow-growing reefs in some areas.

RÉSUMÉ
Uniques au monde, les récifs d'éponges d'hexactinellides (siliceux) qui se trouvent à 200 m de profondeur dans des fosses d'abrasion glaciaires du plateau continental de l'Ouest du Canada, ont été explorés à partir de sous-marins habités. Les observations sous-marines et les données de géophysique permettent d'étudier les mécanismes physiques et biologiques qui ont présidé à l'édification des récifs d'éponges qui ont commencé à se former aux environs de 9 ka BP. Ces édifices récifaux en amas (biohermes), et en couches (biostromes) recouvrent un fond marin légèrement incliné par l'abrasion d'icebergs post-glaciaires. Ces biohermes ont jusqu'à 19 m de hauteur et sont recouverts d'une couche de 1,5 m de hauteur d'éponges hexactinellidiennes, forment un habitat couvrant de manière discontinue une surface de 700 km^2. Semblables à ces récifs d'éponges très répandus au Mésozoïques, amas boueux et amas récifaux, les récifs modernes sont de véritables fossiles vivants, et sont à ce titre forts utiles pour la compréhension de leurs contreparties fossiles. Par endroits, les activités de pêche industrielle, particulièrement le chalutage ou le dragage de fond ont endommagé ces édifices récifales à croissantes lentes.

INTRODUCTION
Hexactinellid sponges are known to have existed since the Late Proterozoic (Gehling and Rigby 1996), and the Hexactinellida are the earliest known metazoans that can be related to an extant animal group. The first representatives of the Subclass Hexactinosa appeared in the Devonian, and during the Mesozoic these sponges became important reef-building organisms in deeper water due to their fused rigid siliceous skeleton. The first hexactinosan sponge reefs are recorded in the Middle Triassic of Poland (Bodzioch, 1991). These are locally very restricted and are of decimetre scale. Late Triassic siliceous sponge reefs are known from China (Wendt *et al.*, 1989). These are the first known larger siliceous sponge reefs (up to 10 m) and are, with respect to their shape, internal architecture, and faunal association, quite similar to those of the Jurassic. The distribution of the sponge reef facies culminated in the Late Jurassic. On the northern shelf of the Tethys and the adjacent North Atlantic basins, siliceous sponges formed a discontinous deeper water reef belt extending over more than 7000 km. Outcrops are known from the Caucasus Mountains, from Romania, Poland, Germany, Switzerland, France, Spain, Portugal, off Newfoundland, and Oklahoma (among others: Jansa *et al.*, 1982; Leinfelder *et al.*, 1993; Werner *et al.*, 1994; Krautter 1995, 1997; Gaillard 1983; Oppliger 1926; Schrammen 1936; Flügel and Steiger 1981; Pisera 1997; Trammer 1982, 1989; Herrmann 1996). This sponge reef belt was the largest bioconstruction ever built on Earth.

In Cretaceous times, the distribution of siliceous sponge reefs was more or less restricted to western Europe (Defretin-Lefranc, 1958; Hinde, 1880; Termier and Termier, 1985) and sponge reef facies was of lesser importance than coral and rudist reefs of this age. After Cretaceous time there was a remarkable decline in the distribution of these reefs and today they appear to have completely disappeared, worldwide, with one known exception, found on the British Columbia continental shelf. The sponge reefs found off the west coast of Canada are the only known hexactinosan sponge reefs in the world. These reefs were discovered by the Geological Survey of Canada (GSC) in 1987-1988 during regional geophysical surveys (Conway *et al.*, 1991). In order to further study these reefs, a joint project between the GSC and the University of Stuttgart was undertaken in 1999. The first direct human observation of a reef type that was widespread during the Age of Dinosaurs was made in July 1999.

GEOLOGICAL SETTING
The sponge reef complexes occupy the east-central portions of the three major troughs that cross the northwestern Canadian continental shelf (Fig. 1). The troughs, which are up to 500 m deep, were repeatedly glacially scoured during the Quaternary (Luternauer and Murray, 1983), and they are separated by banks that reach to within 30 m of sea level. The seafloor geology of the shelf reflects the intensive regional late Wisconsinan glaciation, which occurred between 21 k.y. and 14 k.y. ago. During the glaciation, thick tills and glaciomarine sediments were deposited in the troughs, and ice advanced to the shelf edge (Luternauer *et*

al., 1989a; Barrie and Bornhold, 1989; Barrie *et al.*, 1991; Barrie and Conway, 1999). Subsequent to the nearly complete covering of the shelf by ice, sea level changes accompanied deglaciation, resulting in sea levels up to 150 m below present day between 13.5 k.y. and 10 k.y. ago over much of the shelf (Luternauer *et al.*, 1989b; Josenhans *et. al*, 1995 and 1997; Barrie and Conway, 1999). The resultant surficial sediment distribution reflects this glacial and sea level history, with banks covered by sands and gravels, and troughs floored by finer sediments. On the outer shelf, the troughs are mantled by reworked glacial sands and muds dating from the late Wisconsin lowstand of sea level. Inshore of these deposits, on the mid- to inner-shelf, is a relict, iceberg-furrowed seafloor that has been the site of extensive sponge reef development during most of Holocene time (Conway *et al.*, 1991).

OCEANOGRAPHIC SETTING

Oceanographic currents are dominated by a prevailing northward flow along the eastern side of Hecate Strait and a southward return flow along the southwestern side of Hecate Strait and Queen Charlotte Sound (Crawford and Thomson, 1991). Tidal currents are clockwise rotary in Queen Charlotte Sound and rectilinear in Hecate Strait, due to bathymetric constraints (Thomson, 1981). Combined wave-induced oscillatory flow and mean bottom currents are capable of transporting fine sand at least 10% of the time at depths of 100 m in the region (Barrie *et al.*, 1988). In the troughs, where the sponge reefs have developed, bottom currents are, in general, aligned roughly parallel to the trough axes and can exceed 0.45 m·sec^{-1} (Huggett *et al.*, 1981; Conway *et al.*, 1991).

METHODS

Cruise PGC9901 (using Canadian Coast Guard Ship *John P. Tully*) collected data at previously identified sponge reef sites during a research cruise from 9-25 July 1999. The cruise was a multi-parameter survey using different geological, geophysical, and oceanographic methods to examine the sponge reefs and their physical and oceanographic environment. Underway geophysical surveying was accomplished using a Simrad dual-frequency sidescan sonar system collecting digital data at frequencies of 120 kHz and 330 kHz . Two areas of seafloor in Hecate Strait were surveyed with a close line spacing to allow the construction of sidescan sonar mosaics. Huntec Deep-Tow seismic data were collected simultaneously to provide acoustic penetration of the sponge sediments, thus allowing determination of their thickness.

The submersible Delta, a commercially operated two-person scientific submersible, was used for direct observation, sampling, videotaping, and still photography of the reefs. Eighteen dive transects of 1-3 hours duration were completed across reef areas selected from acoustic data. Data reduction of video and still photography included the transfer of observations of biota and environmental data to an ArcInfo GIS format.

Piston cores, which penetrated up to 6 m into the seabed, were collected at two sites, and Shipek grab samples were recovered from six stations. Cores were split and described and subsampled for analyses of micropaleontology and chemical analyses, including organic carbon, carbonate carbon, nitrogen, and opaline silica. Grain size analysis was completed on core subsamples using a Micromeritics 5000D for the mud fractions and an automated settling tube for sands. Radiocarbon samples were dated at Lawrence Livermore Laboratory. Drift camera transects were run at seven sites using a still camera equipped with a bottom contact switch, and a large bucket type sampler (IKU Sampler) was used in order to recover large-volume (0.75 m^3) samples of the reef surface and subsurface. Foraminifera and clay mineralogy subsamples were collected from core and grab samples and from submersible slurp gun samples. In addition, six oceanographic water-sampling stations were occupied

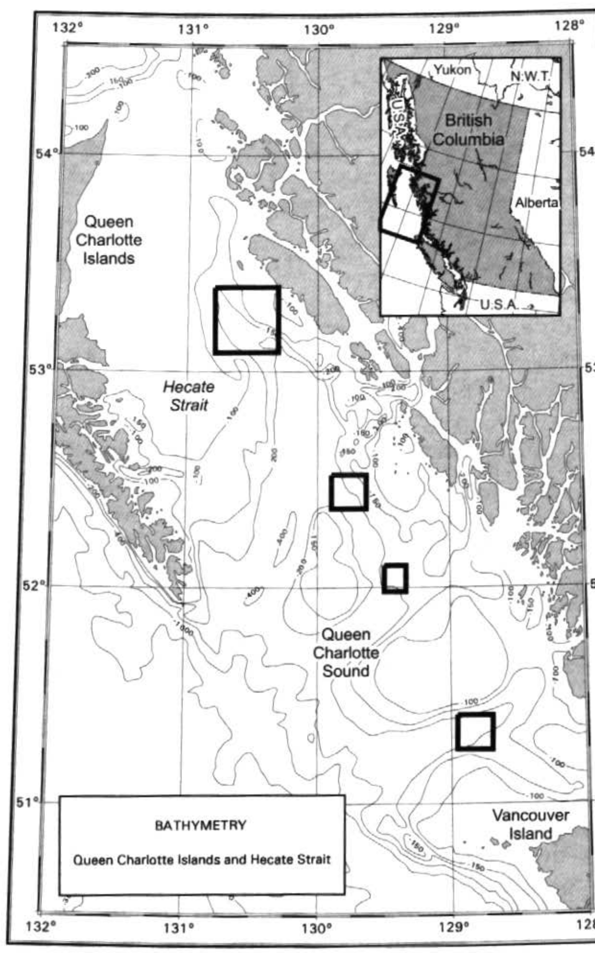


Figure 1 Bathymetry of the western Canadian shelf. Sponge reef areas surveyed during cruise PGC9901 are indicated within black rectangles. Depth contours in metres.

adjacent to reef areas. Nutrient and density measurements have been completed on these water samples.

RESULTS

Figure 1 shows the areas where geophysical surveying and submersible diving were done during cruise PGC9901. Dive tracks provided groundtruth for geophysical surveys and confirmed that in all cases the areas identified acoustically as being sponge reefs did, in fact, support sponge reefs at the seafloor. Mapping of the distribution of the reefs is readily done with sidescan sonar and high-resolution seismic data (Fig. 2). The acoustic anomaly associated with the reefs is distinctive (Conway *et al.,* 1991), especially when sidescan sonar and seismic profiling are used in tandem.

Reef Surface

Submersible dives and surface grab samples indicate that the sponge reef surfaces are covered with three species of Hexactinosan sponge, the main reef builders (Fig. 3). These species include *Heterochone calyx*, *Aphrocallistes vastus,* and *Farrea occa*, all members of the Order Hexactinosa. Abundant hexactinellid sponges of the Order Lyssacinosa, including *Rhabdocalyptus dawsoni*, *Acanthascus platei*, *Acanthasus cactus*, and *Staurocalyptus dowlingi* are also present on the reef. Compiled dive results indicate that living sponge distribution over reef sites is variable, with some areas being very densely populated while others support only sparse, living sponge populations. Submersible observations indicate that species of crab, shrimp, prawns, euphausids, and rockfish use the irregular shapes of the individual sponges and reef structure as refugia and seafloor habitat. Seafloor areas immediately adjacent to the sponge reefs, composed of glaciomarine, ice-scoured sediments, host a different epifauna, characterized by sea whips, large solitary sponges, and sparse soft corals. Differences in fish and invertebrate species and abundances between reef and non-reef areas are apparent, and burrows were more often observed in adjacent areas than on the reefs. The known distribution of the sponge reefs (Fig. 4) was compiled by examination of all archived high-resolution geophysical data from northern shelf regions held by GSC-Pacific (Barrie *et al.,* 1991), as well as data collected during the present study.

Reef Sediments and Subsurface

High levels of organic carbon, opaline silica, and carbonate characterize the reef sediments compared to the underlying glaciomarine sediments and "background" Holocene muds. Core TUL99-A09 (Fig. 5) recovered a typical sequence of sediment at a reef site in Hecate Strait. Abundant foraminifera and sparse bivalves are found within the core. Radiocarbon chronology for this core indicates a mid-to-late Holocene age for the sponge reef sequence at this site (Fig. 5, Lithology). This chronology is consistent with the development of the reefs in the early Holocene on top of an iceberg-furrowed, relict surface, and expansion of the reefs throughout the Holocene. Generalized thickness of the sponge reef complex in northern Hecate Strait was measured by compiling an isopach map (Fig. 6), which shows that the maximum thickness of the sponge mounds is 19 m, with an average thickness in the Hecate Strait complex of 6-8 m. The orientation of the major mound and ridge structures within the complex is confirmed by sidescan sonar data collected simultaneously and compiled as a mosaic. The isopach map shows the nature of large structures oriented generally parallel to the trough axis.

Attachment of Hexactinosan sponges to skeletons of dead sponges was observed in hand samples taken from

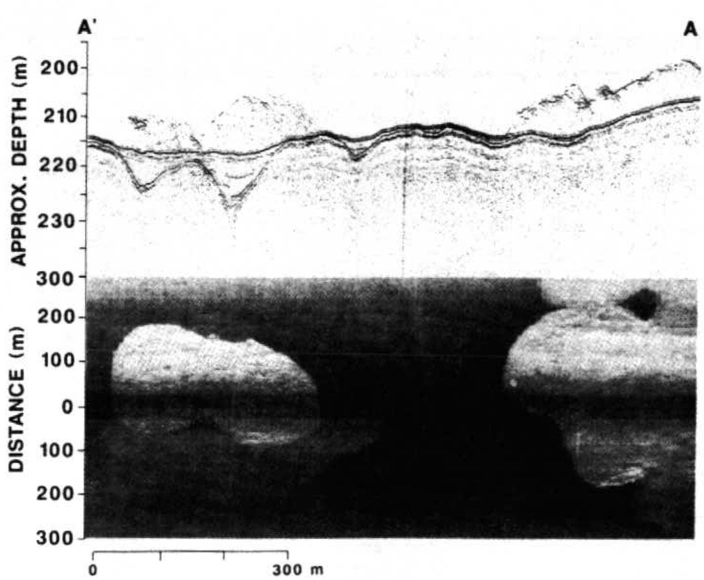


Figure 2 Acoustic character of sponge reefs showing seismic profile (above) and sidescan sonogram (below) of sponge reefs in Queen Charlotte Sound. Sponge reefs are clay rich so non-reflective (white) while sandy, gravelly glacial sediments are reflective (dark). Note thickness to 10 m of biohermal mounds on the left and the horizontal scale of the biostromal accumulation at lower left.

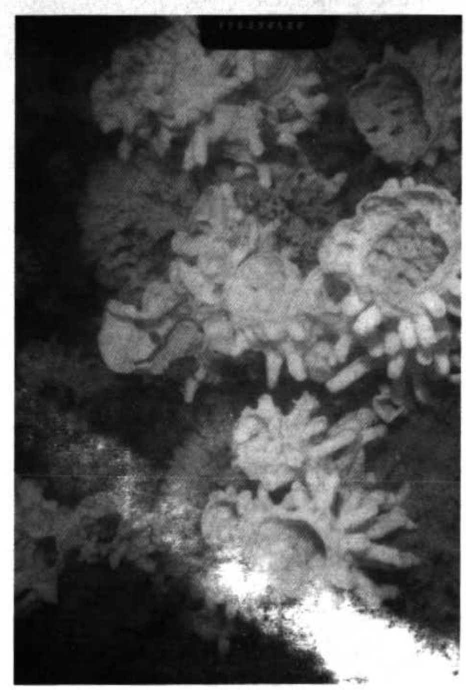


Figure 3 Surface of healthy sponge reef in Hecate Strait. Sponges in foreground are *Heterochone calyx,* about 1 m in height, and in the middle distance (centre of photo) the bush-like sponges are *Farrea occa*.

large-volume (0.75 m^3) samples of the reef surface. Examination of sponge skeletons by scanning electron microscope clearly shows attachment of younger sponges to other sponge skeletons, commonly of different species (Neuweiler, 2000). None of the Hexactinosan sponges described here are known to anchor in muddy or sandy seafloor sediments.

Evidence of Mechanical Destruction of Sponge Reefs by Trawling

Figure 7 shows a sidescan sonar image of sponge reef areas in southern Queen Charlotte Sound (southernmost sponge reef area, Fig. 1), which have been subject to bottom trawling by fishing vessels. The parallel tracks visible on the images, which are usually 70-80 m apart, correspond to the marks created by trawl net doors. Data collected in 1988 over the same areas did not display these abundant trawl marks, which traverse many kilometres of seafloor (Fig. 8). Trawl marks can also be observed on sidescan sonar records collected at the northern periphery of the Hecate Strait complex (Fig. 1). Data

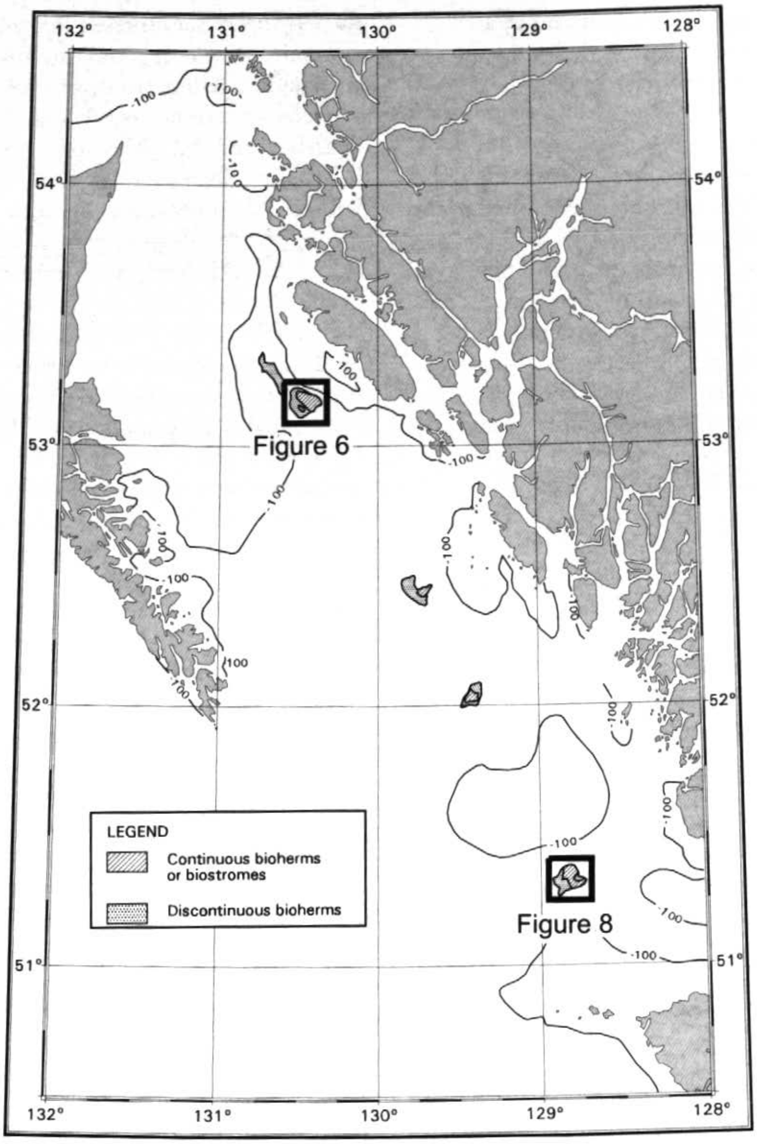


Figure 4 Location of sponge reef complexes on the western Canadian continental shelf, shown in more detail in Figures 6 and 8. Each area is composed of a core of more dense, continuous bioherms or biostromes, and a peripheral zone of smaller, discontinuous bioherms.

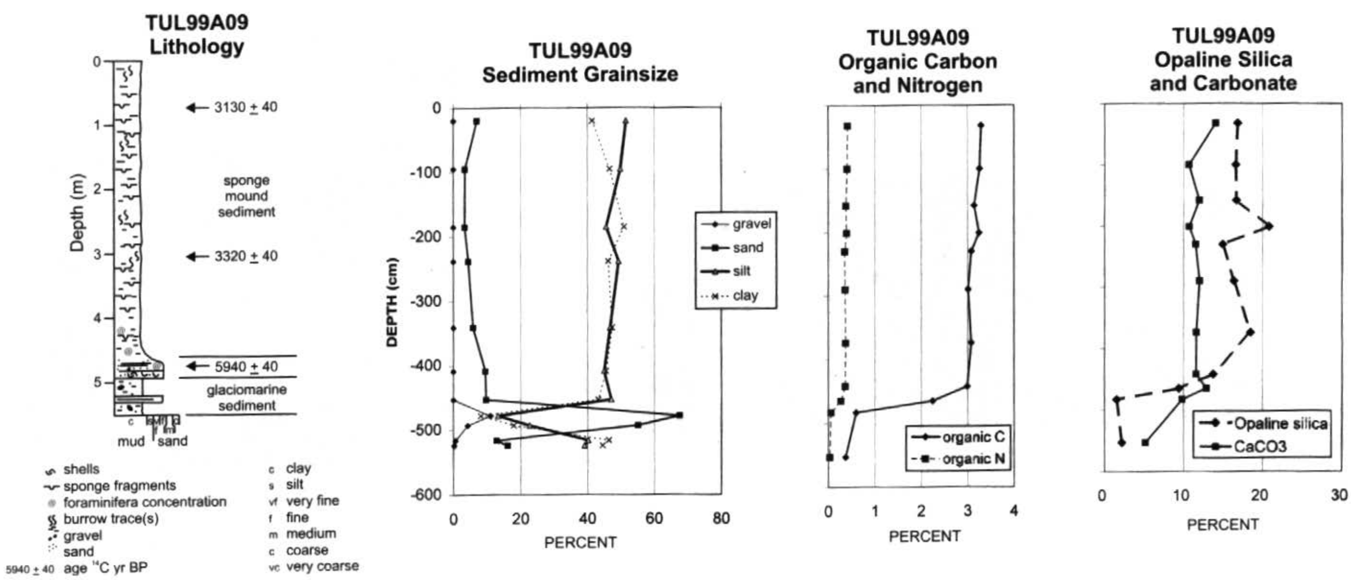


Figure 5 Lithology of core from Hecate Strait including grain size, radiocarbon ages, and sediment chemistry.

provided by the Department of Fisheries and Oceans confirm active and widespread trawling is ongoing throughout the areas where the sponge reefs are found.

In northern and southern Hecate Strait, areas of sponges lying broken off at the seafloor were observed during submersible dives. In some areas, broken projections of sponges ("stumps") and sponges with abraded distal edges were seen. In undisturbed settings, the sponge skeletons remain in place after death, eventually becoming blanketed with sediment (Fig. 3). At one site in Hecate Strait a linear ridge or berm of sponge skeletal debris to a height of approximately 40 cm was observed. This debris ridge probably represents a ploughed reef surface where the skeletal remains of sponges have been piled by mobile fishing gear.

DISCUSSION

The sponge reefs occupy the troughs on the continental shelf where a relict seafloor allows growth in an undisturbed, stable setting. The only significant, modern sediments in the vicinity of the sponge reefs are those that are incorporated into the reef itself (Conway *et al.*, 1991). A large proportion of this sediment appears to be biogenic (up to 34%), especially opaline silica and carbonate. Much of the volume of the sponge reef complexes is thus of biological origin. The high levels of organic carbon, >3 weight percent (wt.%), are similar to those found at modern deltas on the west coast (Bornhold, 1978), and this contributes to reducing conditions within the sediments. Reducing conditions are indicated by the smell of H_2S detected during recovery of core and large-volume grab samples. Organic carbon measured elsewhere on the shelf in Holocene muds in Queen Charlotte Sound, suggests typical values of 0.8 wt.% (Luternauer *et al.*, 1989a). The paucity of bivalves within the reef sediments, again compared to Holocene muds cored elsewhere, is probably due to this factor. The bivalve genus found most commonly in the sponge reefs, *Thyasira*, is known to favour hypoxic, reducing conditions (P. Johnston, personal communication, 2000).

The pattern of distribution in the sponge reef complexes suggests a central zone of reef building construction extending laterally out from an inner core of the complex, with small mounds being built at the periphery (Barrie *et al.*, 2000). Orientation of the constituent mounds within the sponge reef complex, parallel to the trough axis, (Fig. 6) is due mainly to the focussing of tidal currents through bathymetric constraints (Conway *et al.*, 1991). Complete sidescan sonar coverage allowing construction of a mosaic of the same area also confirms this orientation. The sediments brought to the sponge mounds are entrained in bottom currents, and direct observation indicates that flocs of fine mud and organic particles clumped as aggregates, or "marine snow," are the most common types of sediment particles delivered to, and trapped by, the sponge reefs.

A framebuilding process is responsible for the multi-generational habitation of the reefs by sponges. This use of skeletal remains as an attachment substratum is a similar process to that of coral reef construction. The only attachment substrate available to benthos is the skeletons of hexactinosan sponges in an organic-rich, biogenic and siliciclastic matrix. This is the first documented study showing framework construction by modern hexactinellid sponges (Neuweiler, 2000). In addition to other unique attributes of these reefs, the sponge reef complexes can thus be differentiated from other sponge build-ups, including modern sponge spicule mats, on this basis. The sponge reefs found on the western Canadian shelf have not been found elsewhere, although similar fossilized bioconstructions are found in the Upper Jurassic of the northern Tethys and adjacent Atlantic basins (Krautter *et al.*, 2000). The sponge reefs therefore offer an analogue for the study of ancient sponge reefs, reef mounds, and sponge facies that, until now, lacked any close modern analogue (Leinfelder *et al.*, 1994).

The distribution of the sponge reefs coincides with the distribution of a

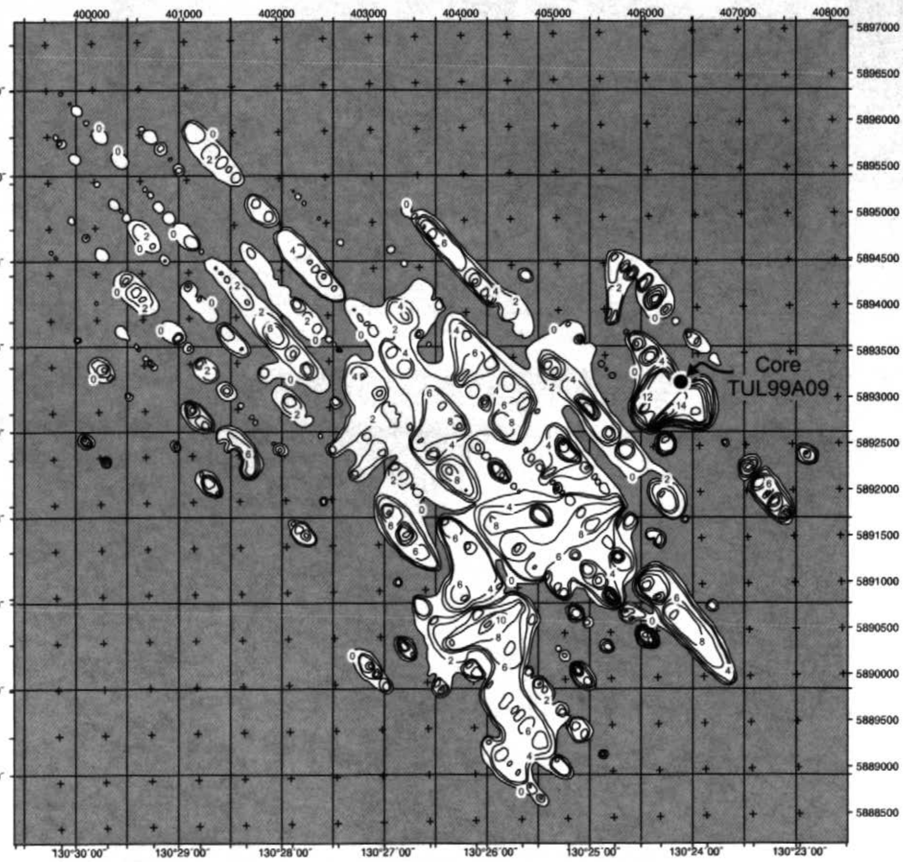
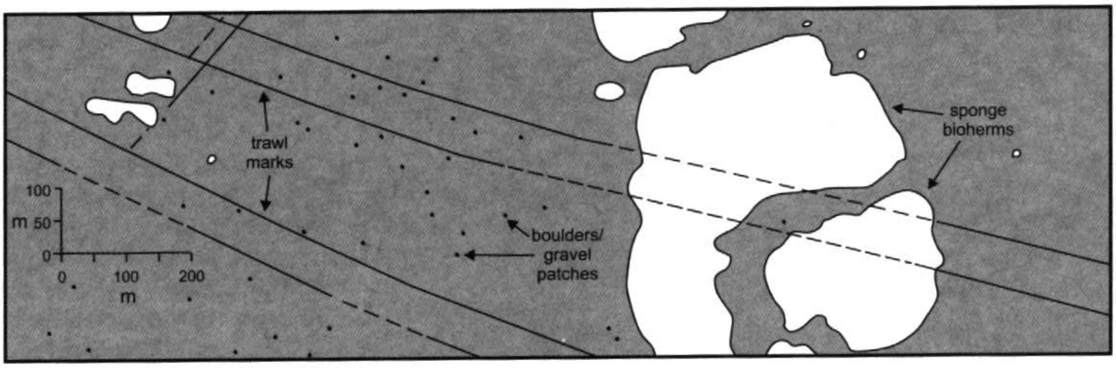


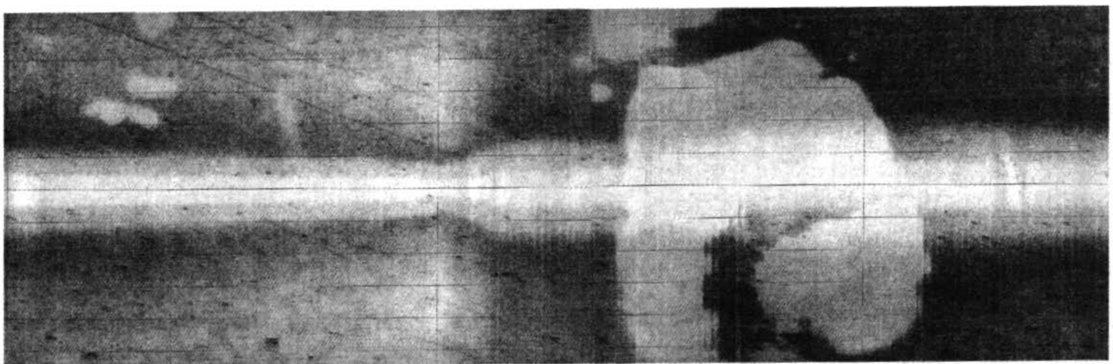
Figure 6 Thickness of sponge reef sediments in reef complex in northern Hecate Strait. Contour interval is 2 m. Isopach was prepared by analysis of Huntec seismic records and by reference to sidescan sonar mosaic for sponge reef boundaries. Location of core TUL99A09 is shown.

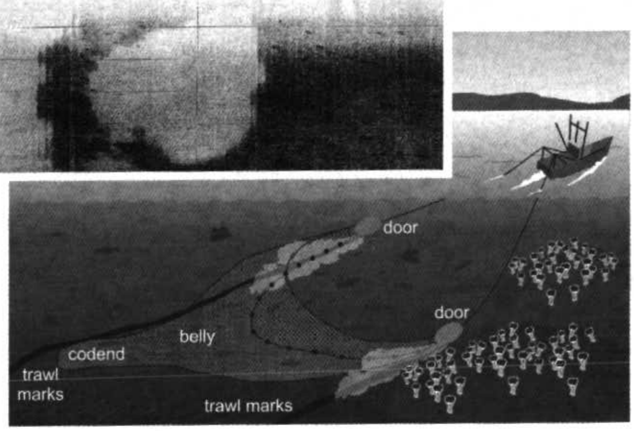
relict iceberg-furrowed seafloor, and this suggests a close direct relationship between the availability of long-term, stable or relict seafloor conditions and the development of the sponge reefs. A requirement for low or very low sedimentation rates and suitable substratum for initiation of the reefs is implied. The iceberg-furrowed seafloor areas provide the proper "growth medium" for the sponge reefs because of the opportunity provided for attachment of sponges to exhumed and concentrated boulders on the shoulders or berms of the furrows (Conway, 1991). These relict iceberg-furrows are the sites where bioherms are initiated and development of the sponge reefs begins.

The cyclical nature of coverage of the reef by sediment followed by renewed sponge growth suggests that a negative feedback effect on sedimentation rate must be in operation as the sponges become covered by sediment. If this were not the case the reefs would soon become buried and, because of the requirement of the hexactinosan sponges for solid attachment surfaces, no further opportunity for renewed sponge growth would exist. A cleaning mechanism for the surfaces of living sponges is suggested by the proximity of completely sediment-covered sponges adjacent to pristine, clean examples of the same species (Conway *et al.*, 1991). Given the nearly continuous delivery by bottom currents of "marine snow" observed in dives at some reef sites, this self-cleaning mechanism may be a critical biological process allowing the sponges to keep from being smothered by the suspended sediment, and also an important process in sediment capture and deposition. The apparent paradox of low sedimentation rates and continuous delivery of suspended particles is explained by the bottom current velocities that are sufficient to keep the flocculated material in suspension where sponges are not present (Conway *et al.*, 1991). In addition to the above-mentioned framebuilding capacity of hexactinosan sponges, biological controls on sponge reef development probably also include such unknown factors such as hexactinosan reproduction.

The awareness of the importance of structural elements as part of the marine habitat and the damage caused by mobile fishing gear to invertebrate species has been growing (Messieh *et al.*, 1991; Freese *et al.*, 1999). The physical structure provided by organisms like corals and sponges is an important habitat for many species, including rockfish, prawns, shrimp, and crabs. Direct studies of the effects of trawling on seabed invertebrates have shown detrimental affects ranging from complete removal of epifauna to increased rates of benthos mortality







(after Christen, 1999)

Figure 7 Sidescan sonar showing paired trawl marks on seafloor crossing sponge bioherms. These marks are created when net doors, weighing up to 2 tonnes, are dragged across the seafloor. Lower right sketch after Christen, 1999.

related to physical damage. In addition to the direct physical impact of trawl doors and weighted nets, the turbidity associated with the plowing action of the doors may be detrimental to filter feeding, sedentary organisms (Churchhill, 1989). It is probable that, when the framework skeletons become fragmented due to physical impacts, the physical structural support provided by the skeletons is greatly reduced. If these substrate skeletons become completely fragmented or buried by ploughing, recruitment of new sponges, anchoring to the reef surface, will be negatively affected. The sponges that form the framework of the reefs are known to grow slowly, with hexactinosan growth rates inferred from cable fouling to be on the order of 1-7 cm·a^{-1}(Levings and McDaniel, 1974; W. Austin, written communication, 2000). In view of these slow growth rates, recovery of damaged or destroyed reef areas is likely to occur only slowly, and the time frame of recovery of a destroyed sponge reef is suspected to be on the order of 50-100 years. The mode and rates of reproduction of hexactinosan sponges are completely unknown, and the degree to which these organisms can recolonize a reef surface once removed is therefore uncertain.

CONCLUSIONS

The existence of living, large-scale reef structures built by hexactinellid sponges offers an observatory or window onto past times when shelf sponge reefs were common, not an exception or anomaly. The modern reefs are similar to deeper-water hexactinellid and lithistid sponge reefs that spread over a belt 7000 km long during the Upper Jurassic along the northern margin of the Tethys Sea and into the Atlantic Basin (Krautter, 1997). This reef belt was the largest bioconstruction that has ever existed on Earth. The understanding of sponge reef mounds that developed earlier in geologic time, during the Paleozoic (Brunton and Dixon, 1994; and references therein), will also benefit from the study of the modern sponge reefs. In addition, as a general case of development of a simple reef type, study of the modern sponge reefs may help shed light on various extinct reef types, including stromatoporoid reefs, which are widespread and economically important as fossil reefs in Alberta and elsewhere.

The sponge reefs have been subject to damage by seafloor trawling in the past decade, and the smaller, lower-profile bioconstructions appear to be especially vulnerable to trawling impacts as the peripheries of the reef complexes are fished. Further study is required to examine the ecological relationships between the sponges and associated fauna. The sponge reefs may play an important role in the continental shelf ecosystem through direct biological activity and also by providing a complex seafloor habitat.

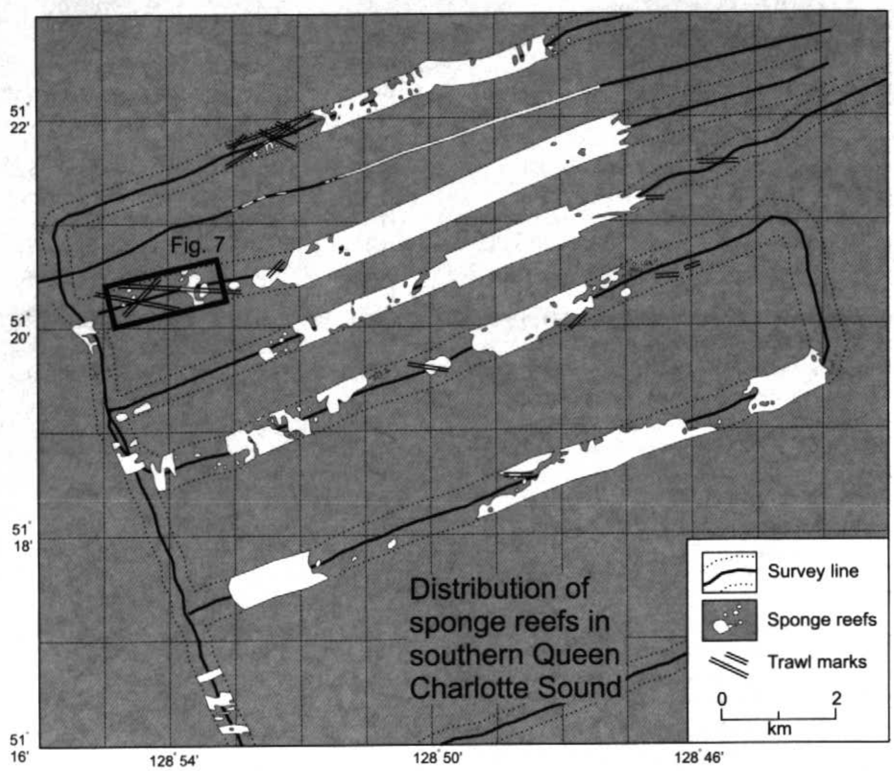


Figure 8 Map of southern sponge reef complex showing areas where trawl marks were observed. The distribution of sponge reefs and trawl marks was mapped using sidescan sonar data.

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