Hexactinellid sponge ecology: growth rates and seasonality in deep water sponges

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Abstract

It has been well established that sponges play an important role in benthic ecology as abundant, large, sessile filter-feeders. However, the ecology of one group, the Hexactinellida, whose electrophysiology and cell biology is quite distinct from other Porifera, has received little attention due to the inaccessibility of their preferred deep water habitat. Now, a three year study of a population of the hexactinellid sponge *Rhabdocalyptus dawsoni* (Lambe, 1892) has been carried out in the fjords of British Columbia, Canada. *Rhabdocalyptus* was found to have a patchy distribution in Saanich Inlet, British Columbia, with local abundance reaching 5.3 individuals m^{-2}. The mean length of the tube-like sponges in the inlet was 32 cm (an equivalent of 5.8 l volume) although sponges could reach 87 cm in length (36 l volume). The average growth rate of sponges measured over the course of 3 years was 1.98 cm $year^{-1}$ (min. -0.76 cm $year^{-1}$, max. 5.7 cm $year^{-1}$) or 167 ml $year^{-1}$ (min. -537 ml $year^{-1}$, max. 856 ml $year^{-1}$). The rate of tissue regeneration after artificial wounding in the field was 0.05 ± 0.03 cm^2 day^{-1}, some 40 times the rate of growth. No recruitment was observed during the study, but mortality of large individuals was seen. Using the calculated growth rate (average rate of increase in volume), the age of an average-sized sponge was estimated to be 35 years. With the assumption that growth rate is constant, large individuals (1 m in length) were estimated to be 220 years old. All sponges showed seasonal trends in sloughing of the debris-covered outer spicules during winter months (November to February). Increase in outer spicule coat occurred from March to October and sloughing corresponded to the end of seasonal phytoplankton blooms in October or November. These data suggest that hexactinellid sponges have life history strategies and growth rates similar to those of massive tropical and temperate demosponges and that, despite their deep water habitat, they experience seasonality which influences their growth rates and perhaps reproductive period. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

Hexactinellids, or glass sponges, are unusual in possessing syncytial rather than cellular tissues (Reiswig, 1979; Mackie and Singla, 1983; Leys, 1995). Furthermore, unlike other sponges, they can propagate electrical signals through their tissue to co-ordinate the cessation of their feeding current (Lawn et al., 1981; Mackie et al., 1983; Leys and Mackie, 1997). As remarkable as this mechanism is in a member of the Porifera, its ecological function remains unclear. Few studies have addressed the ecology of the Hexactinellida because they generally inhabit depths only accessible by submersible or dredge. In fact there are only four places in the world where hexactinellids can be reached by SCUBA: Antarctica, southern New Zealand, a submarine cave off southern France, and along the coast of British Columbia and Alaska.

In a pioneering study of long-term subtidal community interactions, Dayton et al. (1974) used underwater photography to monitor Antarctic sponge communities along fixed transects. He showed that although some demosponges grew quite rapidly, growth was only observed in small individuals of one species of hexactinellid over the course of seven years, yet trends of mass mortality were seen (Dayton, 1979). A more recent examination of trophic interactions among sponge species in Antarctic and Weddell Sea sponge communities has demonstrated that sponges, and hexactinellids in particular, play an important role in the well-being of deep water benthic communities by modifying the substrate for colonization by other invertebrates, and as a food source for asteroids and other invertebrates (Barthel, 1992; Barthel and Gutt, 1992).

Despite two attempts since Dayton's work to quantify growth rates in hexactinellids (Marliave, 1992; Tunnicliffe, unpublished), the age of these animals has remained a curiosity. Nothing is known of recruitment to hexactinellid populations, and our only knowledge of larval development comes from an early study of dredged preserved material (Okada, 1928) and from a single population of hexactinellids recently discovered in France (Boury-Esnault and Vacelet, 1994). Furthermore, it is often assumed that unlike their littoral relatives, deep water sponges do not experience seasons which would influence either reproductive or growth periods (Barthel, 1995).

One of the most accessible populations of hexactinellid sponges today is found in depths of 30–60 m in the fjords of Vancouver Island, British Columbia, Canada. The present study investigates population dynamics, growth rates, regeneration, and seasonal regression of the hexactinellid sponge *Rhabdocalyptus dawsoni*.

2. Methods

2.1. Habitat

Populations of *Rhabdocalyptus dawsoni* were studied in Saanich Inlet and in Barkley Sound, British Columbia, Canada.

Saanich Inlet is typical of many of British Columbia's fjords. It reaches 220 m at its deepest point and has a sill at the entrance which causes the lower 70 m to be anoxic. Between August and November dense, oxygen-rich water enters the inlet over the sill

flushing the anoxic water up to as shallow as 60 m for that period (Fig. 1) (Carter, 1932; Tunnicliffe, 1981; Sancetta, 1989). Three species of hexactinellid sponges are found on the fjord walls to depths of 65 m and skeletons of dictyonal hexactinellids (whose fused siliceous skeleton remains when the animal has died) can be seen even deeper which suggests that sponges were able to colonize the now anoxic depths at some point in the past. The fjord walls support numerous other benthic invertebrates (Tunnicliffe, 1981; Austin, 1985 pp. 25–28) and, despite the low circulation of waters in the fjord (Cross and Chandler, 1996), vast numbers of cnidarians and amphipods migrate vertically during the summer months (Mills, 1982; Mackie and Mills, 1983).

Barkley Sound, a wide expanse of water (13^2 km) some 150 m at the deepest point,
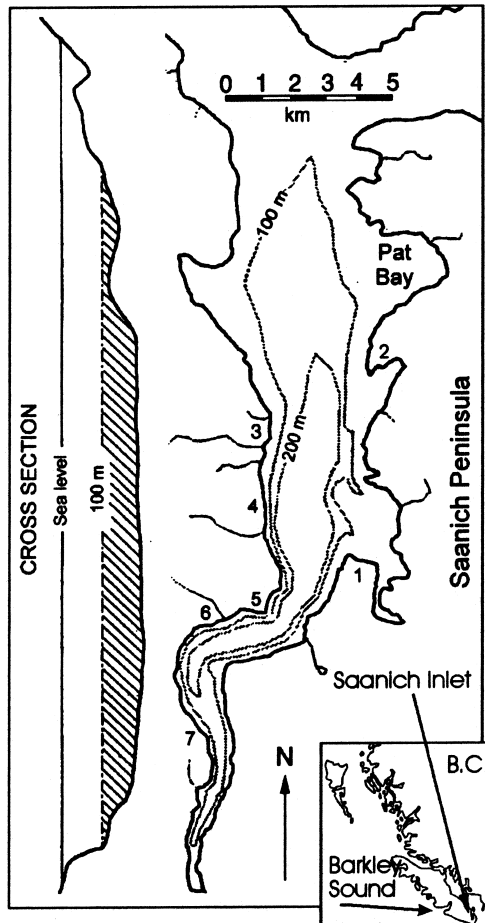

Fig. 1. Map of Saanich Inlet showing bathymetric features and sites surveyed by SCUBA for hexactinellid sponges (numbers correspond to those in Table 1). A cross section through the deepest part of the fjord is shown on the left; the hatched area indicates waters with less than 1 ml 1^{-1} oxygen (adapted from Carter, 1932). Inset shows the relative locations of Saanich Inlet and Barkley Sound in British Columbia.

lies at the south west corner of Vancouver Island (Fig. 1). Ocean swells reach three quarters of the way into the Sound and large tidal exchanges (−0.5–4.4 m recorded extremes) provide good flushing of all the water in the sound.

Rhabdocalyptus dawsoni is a rosellid hexactinellid sponge (its spicules are loose rather than fused) that forms a rough tube with a large atrial cavity. The tissue is white and hangs in cobweb-like fashion over the spicules. Some spicules project approximately a centimetre from the outside walls and are covered by a detritus-laden coat (henceforth termed the outer spicule coat) that is home to a wide variety of invertebrates (see Boyd, 1981), and which can only be dislodged if the sponge is vigorously shaken. In Saanich Inlet *Rhabdocalyptus dawsoni* is solitary and hangs from the rock walls below 25 m with its osculum generally opening down (Fig. 2). In Barkley Sound, *Rhabdocalyptus* is found both on fjord walls, and on nearly flat, silty bottoms where its osculum opens upward.

2.2. Population abundance and size frequency

The abundance and sizes of individuals of *Rhabdocalyptus dawsoni* at seven sites in Saanich Inlet, B.C., Canada (see Fig. 1) were estimated by diving along a transect 20 m
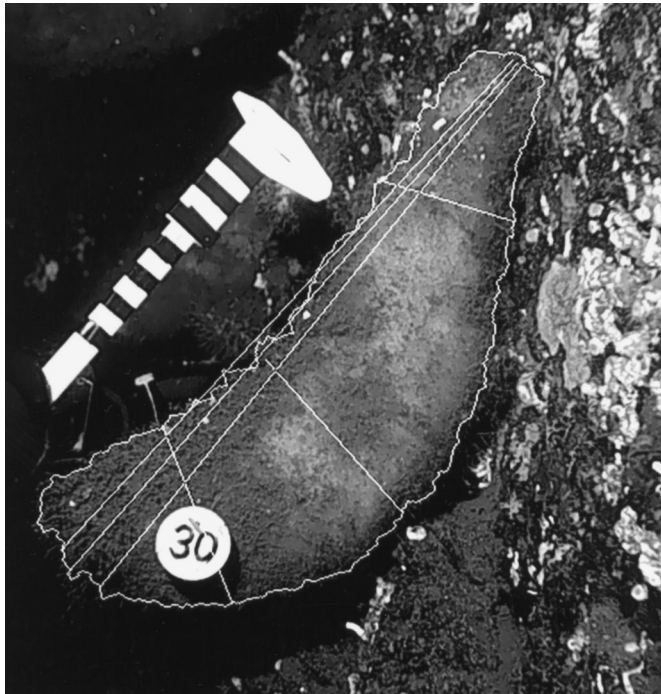

Fig. 2. A photograph of a *Rhabdocalyptus dawsoni* in Saanich Inlet with the measurements of length, width, and area superimposed by computer tracing. Bars on calipers indicate centimetres.

long at 30 m depth at each site and photographing every sponge encountered. The minimum size of sponges detectable using this search method was 2–3 cm in length.

2.3. Measurement of sponges

Photographs of sponges attached to a vertical rock wall were taken with a Nikonos V underwater camera and a SB103 strobe light using a scale for size calibration. Images from photographic slides placed on a light box were grabbed and enhanced using Optimas version three (Optimas Corporation). The average of three measurements each of length (longest line distance between the base and the osculum), diameter (each third of the sponge), and area (computer assisted tracing of the outline of the sponge and calculation of area therein) was recorded (Fig. 2). Volume, including atrial cavity, was calculated by estimating the shape of the sponges to be a cylinder. Area was used to monitor seasonal changes in body form. All measurements included the spicule coat if present. From a sub-sample of ten individuals which were sacrificed for measurements of length, width, and dry weight, length was determined to be the best estimator of sponge size (biomass) for animals less than 25 cm, but for animals greater than 25 cm, volume was a better indicator of sponge size since both diameter and height are incorporated in the measurement.

Because of depth and diving conditions, it was not possible to mount a frame around the sponges to ensure the exact orientation of each photograph was identical. Consequently, the error involved in measurement by repeated photography of the sponges was estimated by photographing a small and large sponge 15 times each, repositioning each time under water. The coefficient of variation for photographs of the small (15 cm) and large (30 cm) sponges was 7.23% and 9.7% respectively for length calculations, and 27.3% and 26.0% for volume calculations. A calculation using this coefficient of variation indicated that error introduced by photographing the animals repeatedly accounts for approximately 13% of the variability in these data.

2.4. Growth rates

Forty sponges at Willis Pt., Saanich Inlet, B.C., were marked in 1991 with numbered plastic discs attached though the sponge body wall with nylon T-shaped tags. The sponge tissue showed no rejection of the nylon tags and appeared to grow around them as it overgrew other debris on the outer surface of the sponge. Because there is very little current in Saanich Inlet (Cross and Chandler, 1996), it was suspected that the few tags that were lost on sponges at the edge of the site closest to the entry point soon after the initial tagging were most likely removed by curious divers. Other tags remained in the sponges for more than five years. In some cases settlement of encrusting bryozoans and polychaete worms on the tags obscured the numbers and the sponges were retagged to make the number more legible in photographs.

From photographs of the tagged sponges taken four times during the first year it was found that there were seasonal variations in sponge size. Therefore, sponges were photographed twice yearly in late February and in early October, before the arrival of spring and before the onset of winter. Growth was calculated as the change in length or

in volume over three years; initial and final measurements were both made during the same season to minimise effects of seasonal changes in body form on growth measurements. No difference in growth or in seasonal changes in size was observed in a few untagged sponges that were in the same photographs as tagged sponges. Sponges were also tagged at San Jose Islets in Barkley Sound, B.C., in order to compare growth rates of sponges in two habitats. However, at San Jose the sponges grow upward from a relatively flat surface, which made it difficult to ensure that photographs of the sponges were taken from the same angle each season. Furthermore, because most sponges at San Jose Islets had buds that made it difficult to measure the growth of an individual, sponges at this site were not used for the growth study.

2.5. Regeneration

Regeneration experiments were carried out in situ at San Jose Islets, Barkley Sound. Thirty-three sponges were cored mid-way down the animal using a cork borer of 2.5 cm internal diameter. The diameter of the hole was measured using callipers immediately after wounding and at monthly intervals thereafter. Rates of healing were calculated from the difference in diameter of the hole at each measurement period divided by the number of days since the last measurement.

2.6. Reproduction

Cores of the body wall of sponges (as described above) were taken from ten sponges at San Jose Islets, Barkley Sound, in February, June, August, September, November, and December. The cores were fixed in Bouins without being removed from a vial of sea water, and taken to the University of Victoria where they were rinsed in sea water, desilicified in 4% hydrofluoric acid, dehydrated to 100% ethanol, and embedded in paraffin. Sections 30 μm thick, measuring 1 cm by 2 cm, were cut on a microtome, stained with Eriochrome Cyanin and examined for the presence of embryos or larvae.

3. Results

3.1. Population abundance and size frequency

Although this study was restricted to depths accessible by SCUBA (40 m), previous work using the PISCES IV submersible has shown that live sponges are not found deeper than 65 m in Saanich Inlet, and that only pelagic animals and larvae inhabit depths where the water is seasonally anoxic (Mackie and Mills, 1983).

Rhabdocalyptus was found to have a patchy distribution at all sites surveyed in Saanich Inlet. Local abundance on steep rock walls with little sediment (e.g. site five) was as high as 5.3 m^{-2}, while at the head of the Inlet, where the Goldstream river enters and the substratum is covered with sediment, there were far fewer sponges (Table 1, Fig. 1).

The average length of the 59 sponges encountered at seven sites in Saanich Inlet was

Table 1
Relative abundance of *Rhabdocalyptus dawsoni* at specific sites in Saanich Inlet, B.C., as indicated in Fig. 1

Site	Latitude, longitude	Substrate	Incline	Abundance of *R. dawsoni*
1 Willis Pt.	48° 34.50′N, 123° 28.73′W	Rock wall	80–90°	4.4/m^2
2 Dyre Rk.	48° 37.49′N, 123° 29.17′W	Rock and boulder with silt	10–20°	0
3 N. Bamberton	48° 35.43′N, 123° 31.15′W	Rock rubble with heavy silt,	45–60°	0.1/m^2
4 S. Bamberton	48° 34.86′N, 123° 31.18′W	Rock rubble and silt	30–45°	0.45/m^2
5 McCurdy Pt.	48° 33.65′N, 123° 31.18′W	Rock wall, small sand shelves	80–90°	5.3/m^2
6 Spectacle Ck.	48° 33.46′N, 123° 32.55′W	Rock wall	80–90°	2/m^2
7 Xmas Pt.	48° 31.98′N, 123° 32.50′W	Rock shelves, rubble with silt	60–75°	1.1/m^2

32 cm. The shortest sponge encountered was 6.7 cm and the longest, 87 cm (Fig. 3). The average volume of sponges was 5.8 l, including atrial volume, (minimum, 103 ml; maximum, 36.8 l) (Fig. 3). The relationship between sponge length and volume (Fig. 4)
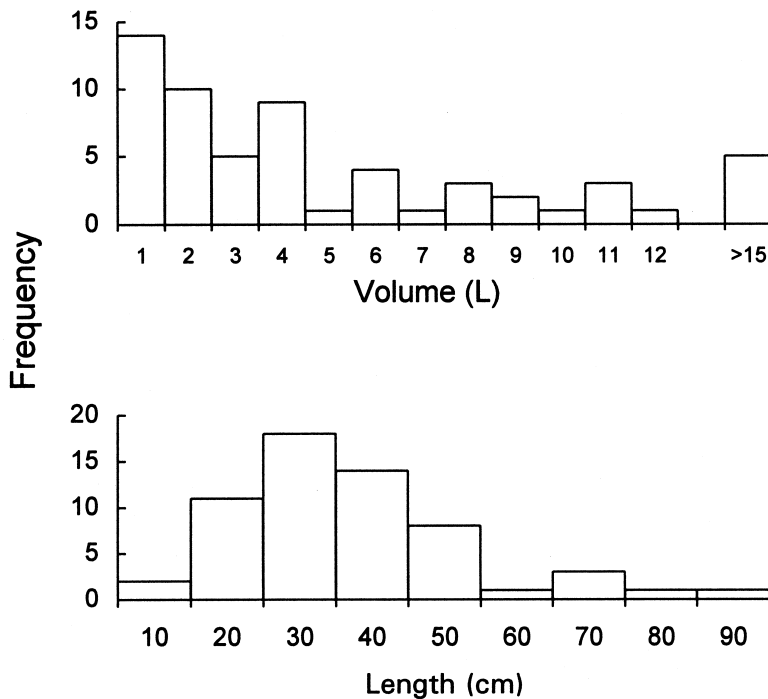

Fig. 3. Size frequency histograms for *Rhabdocalyptus dawsoni* in Saanich Inlet.
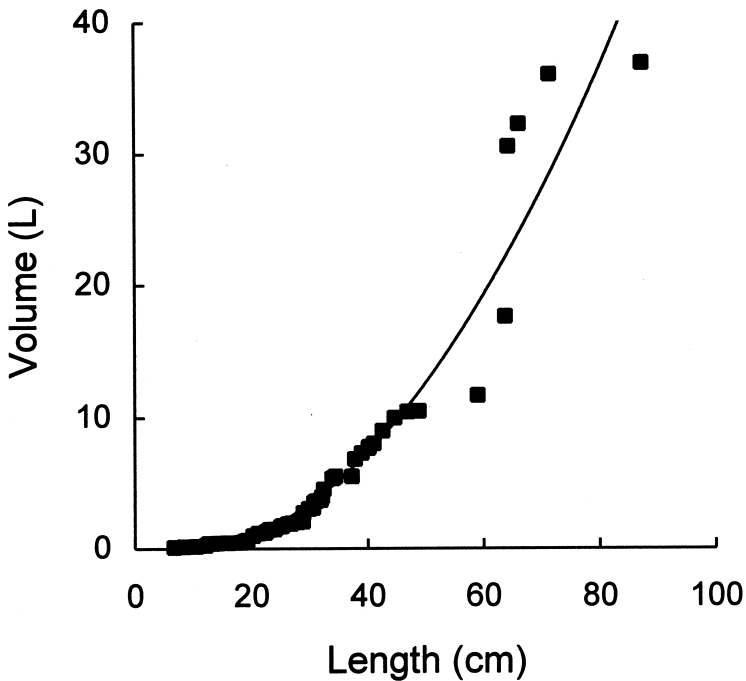
Fig. 4. The relationship of sponge length to volume. The volume of sponges increases linearly with length for sponges less than 25 cm length. Thereafter volume increases more than length, but the diameter and hence volume of the largest sponges is quite variable.

shows that as sponges get longer their diameter becomes more variable, and confirms that, whereas for sponges shorter than 25 cm (approx. 1.6 l) both length and volume are equally good estimators of size (biomass), for sponges longer than 25 cm volume is a better predictor of sponge size.

3.2. Growth rates and estimated ages

Of forty sponges initially tagged it was possible to relocate and photograph 19 animals for three years. Two animals died, at least four lost their tags, and the remaining 15 were not found after two or more measurement periods and may have lost their tags or died. Sponges were considered to have died if they did not regain their outer spicule coat after several seasons. These sponges became pure white and eventually detached from the rock. Poor visibility in these waters (some 3–5 m in summer months and slightly more during winter months) made relocation of tagged animals difficult.

The average growth rate for the 19 individuals which ranged from 6–40 cm in length (0.3–9 l) was 1.98 ± 2.14 cm year^{-1} or 167 ± 408 ml year^{-1}. Sponges shorter than 25 cm grew 12.6% per year in terms of length, while those greater than 25 cm grew 6% per year. In terms of volume, sponges less than 1.6 l grew 20.6% per year, while those over

1.6 l grew 15.4% per year. Some individuals showed no growth while others decreased in size over the three year study.

A Ford–Walford plot, which describes the growth rate of an organism by looking at a cross section of the population at two time periods, shows that the growth rate (solid line) is slightly greater than zero (dotted line) (Fig. 5A). A model 2 regression was used to account for the fact that there is variability in measurement of both *x* and *y* variables, and the data was plotted on a log scale to compensate for greater variability in measurements of larger animals. The same data can be shown on a more traditional plot of specific growth rate (Fig. 5B), which, although less preferred because of the use of initial volume in both axes, nevertheless is useful since it allows ready comparison of the data with that shown in work on tropical sponges (e.g. Reiswig, 1973). Both graphs indicate that growth rate decreases as sponges get larger. The large amount of scatter of the data in both plots indicates that these animals show indeterminate growth.

3.3. Regeneration

Sponges readily regenerated tissue removed by experimental wounds. Of 33 sponges wounded, however, four died and in five the wound first increased in size over several months before regeneration began. There appeared to be no correlation between the size of the wound inflicted relative to the size of the sponge and the ability of the sponge to regenerate. Tissue closed in the circular wound area at a rate of 0.05 ± 0.03 cm^2 day^{-1}, filling in a 5 cm^2 area within 5 months (Fig. 6). Filling in of the circular wound made by the cork borer began first at the atrial side of the sponge; once the wound was closed the sponge tissue filled in to the dermal side. In most cases the area regenerated remained noticeable for at least several years in the form of a scar.

3.4. Reproduction

Groups of archaeocytes, the ''congeries'' of Reiswig (1979) from which embryos develop, were abundant (100–250 per section) during August and September. Congeries were 60 μm in diameter if round, and 60 μm by 100 μm if oval. Parenchymella-like objects, 100–300 μm long and some 60 μm wide, were found some sections from cores collected at all seasons, but one to two such ciliated objects were found in most sections from cores collected in August and September. Identification of these objects as larvae was not conclusive because no free-swimming larvae were found in any live pieces examined. Furthermore, unlike the descriptions of hexactinellid larvae from *Oopsacas minuta* (Boury-Esnault and Vacelet, 1994), these objects appeared to be ciliated all over. A few juvenile sponges conforming to the description of newly metamorphosed juveniles of the hexactinellid *Farrea Sollasii* given by Okada (1928), were found attached to spicules around the base of adult sponges collected at all times of the year.

3.5. Seasonal regression

After photographing the tagged sponges for the first year it became evident that practically all the sponges sloughed their outer spicule coat during winter months (Fig.
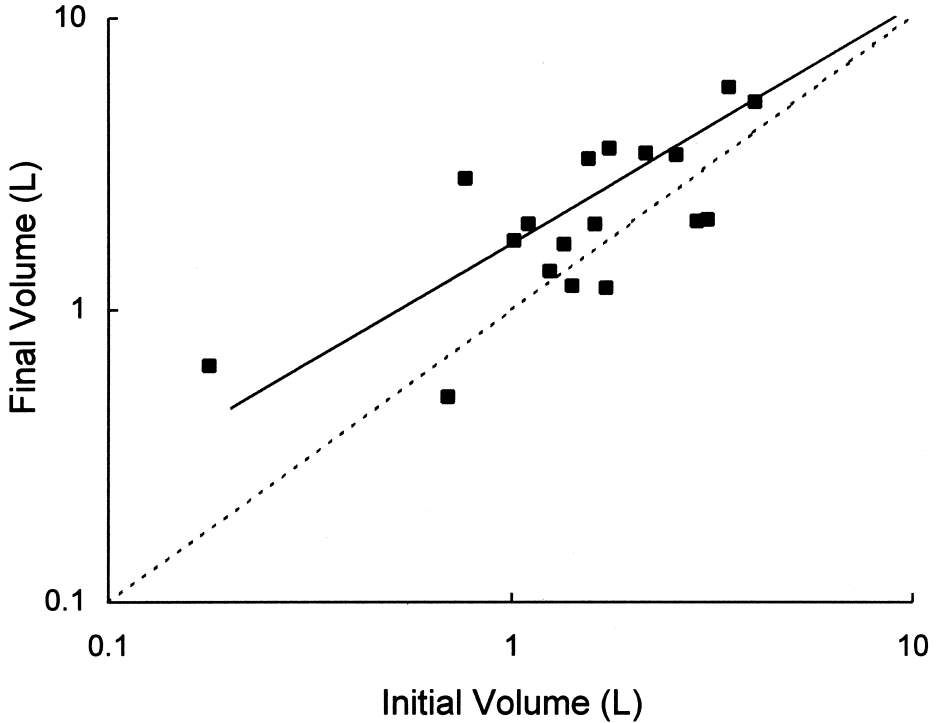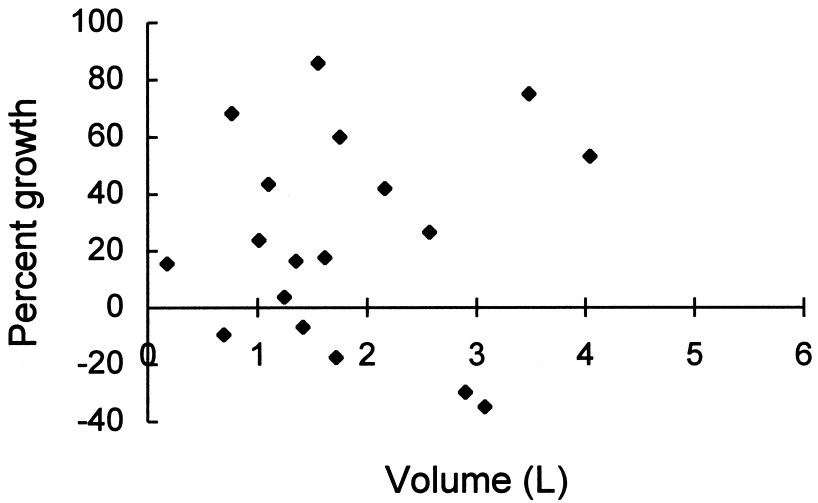
Fig. 5. Growth rate of *Rhabdocalyptus dawsoni*. (A) A Ford–Walford plot showing specific growth rate by a comparison of the sizes of a cross section of the population at two time periods. Initial volume is plotted against the final volume (3 years later) of each animal. The dashed line represents zero growth. A model-2 regression (solid line: $y = 1.15x + 0.31$) was calculated. (B) Specific growth rate. The same data from (a) plotted to show the percent change in volume of each individual over time.
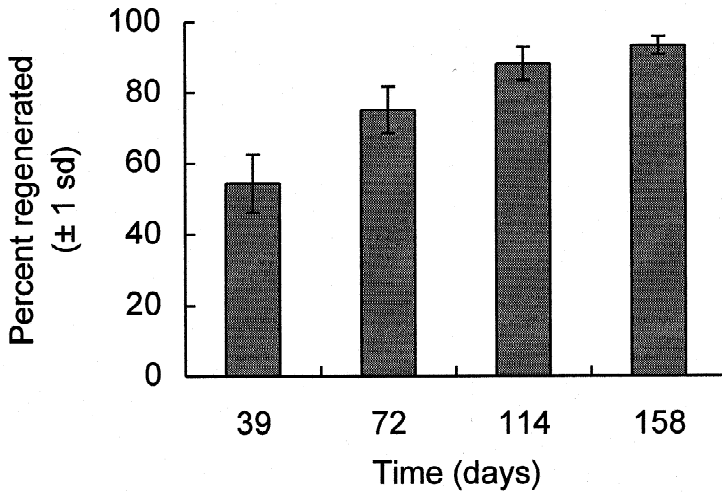
Fig. 6. Average rates of regeneration of cores of tissue removed from the body wall of 33 individuals of *Rhabdocalyptus dawsoni* in situ at San Jose Islets, Barkley Sound, B.C.

7). Most individuals were flaccid to the touch from November to February and one or two individuals never regained their outer spicule coat, and eventually detached from the rock. Although the seasonal trend was quite obvious during several dives throughout the winter and summer months, it was difficult to predict when the sponges would begin to slough in the autumn, or gain their coat again in the spring, and it appeared that they would do this quite rapidly, i.e. from one week to the next. Consequently, if photographed too late in the spring or autumn it was not possible to see the seasonal trend. Area measurements (the computer tracing around the sponge in the photograph) were used to quantify the gain or loss of tissue due to sloughing of the outer spicule coat (Fig. 8). The data indicate there was a 1.5 year fluctuation in outer spicule coat. However, our photography sessions in February (W 93) and October (S 94) 1994 were too late; sponges had already started to gain their summer coat in February, and had begun to slough this coat in late October. The trend of a select individual sponge is shown to indicate the seasonal trend we observed during all our dives.

Growth of sponges accounted for a slight increase in area of the sponges measured each season despite sloughing. Whereas animals photographed at the end of March were on average only 2.8% larger than they were the previous October, in October sponges were on average 11.6% larger than they were the previous March.

4. Discussion

4.1. Habitat and population demographics

Although some 13 species of hexactinellids can be found along the coast of British Columbia (Austin, 1985), *Rhabdocalyptus dawsoni* is the only species with large
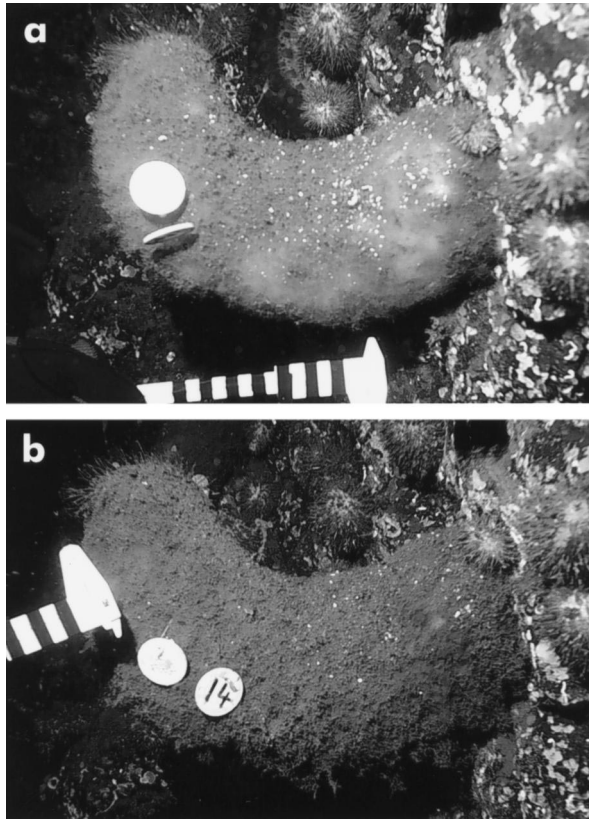
Fig. 7. Seasonal sloughing. Photographs of a tagged sponge (a) in February 1993 and (b) in October 1993. In (a) the sponge appears patchy, its white tissue shows through a very thin outer spicule coat, most of which has been sloughed off during the winter months. In (b) the sponge has regained a thick outer spicule coat over the course of the summer. Bars on the callipers indicate centimetres.

populations readily accessible by SCUBA. In a survey of several sites in Saanich Inlet the abundance of *Rhabdocalyptus* reached 5.3 individuals per square metre on rock walls clear of silt, but the distribution was extremely patchy. The sponges were most abundant at McCurdy Pt. which forms a promontory at a bend in Saanich Inlet. Observations from other sites in Barkley Sound showed that *Rhabdocalyptus* was more likely to be found on walls near promontories, which suggests this species has a preference for sites with greater water exchange.

Small scale patchiness in fauna was reported both in the Porcupine Seabight (northeast Atlantic) and in Antarctic benthic communities where it was thought to be caused by hexactinellid sponge spicule mats, which modify the substrate promoting colonization by other invertebrates (Bett and Rice, 1992; Barthel and Gutt, 1992). In Antarctica these spicule mats can form 50 to 70% of the sediment bulk reaching 0.5 m in thickness (Dayton et al., 1970). Dayton (1979) suggested that the patchy distribution of sponges in
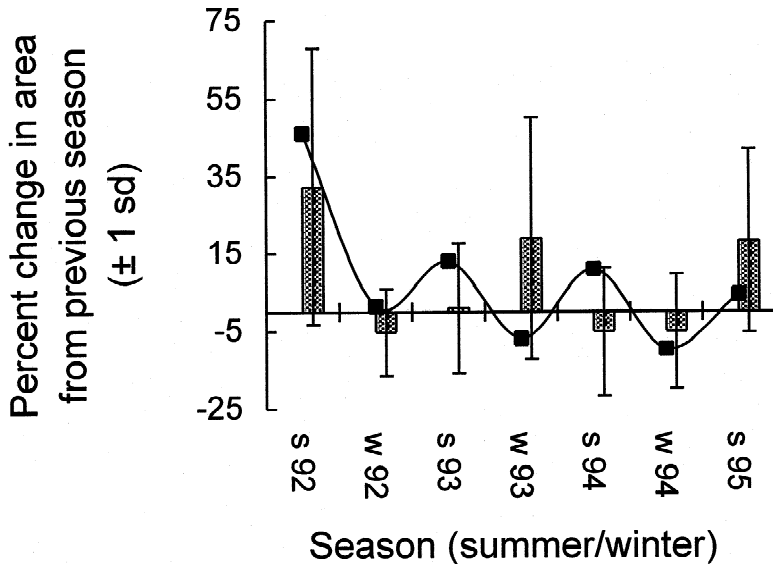
Fig. 8. Seasonal sloughing in *Rhabdocalyptus dawsoni*. Seasonal change in area of the sponges as an indication of gain or loss in outer spicule coat (Mean±1 SD; see text for methods). The line indicates the trend shown by an individual sponge.

McMurdo Sound could also be due to the predominance of asexual reproduction by budding and the lack of water movement which would otherwise disperse the buds. In Saanich Inlet, however, the walls to which the sponges are attached are often too steep (see Table 1) to allow a build up of spicule debris or for buds to stay near parent sponges. Here patchiness could result from selective recruitment to areas already colonised by sponges, or from a limited dispersal range of the larvae.

The size-frequency histogram of sponges encountered in Saanich Inlet is skewed to the left reflecting domination of the population at that depth by small or young individuals. This distribution could result from high mortality rates at all sizes, from selective mortality of large individuals (suggesting the sponges could function optimally at smaller sizes), or from an infrequent high recruitment event (Sebens, 1987), and it is quite possible that all three phenomena affect this population. Several large individuals (nearly 1 m in length) died within two weeks, both within the study site in Barkley Sound, and at another site visited less frequently. Dayton (1979) also observed mortality of large sponges in Antarctica and suggested that disturbance by divers or wounding by asteroids increased the susceptibility of large animals to further attack by predators. However, only the sea star *Pteraster tesselatus* was found to eat the soft tissues of *Rhabdocalyptus*, and less than five attacks on individual sponges were observed in over 150 dives during 5 years. Since demosponges are known to reproduce by fragmentation (Wulff, 1990) it is possible that mortality of large individuals might be a means of reproducing, although no viable pieces were found during a rough examination of dying sponge tissue during dives. Alternatively, large sponges may be more susceptible to

starvation during the winter months because of the increased food resources they require, but more information on nutrient requirements and metabolism in these sponges is needed before further speculation can be made.

It is not clear when or where recruitment takes place. Although small (1 cm^3) individuals of a dictyonal hexactinellid *Aphrocallistes vastus* were seen on the rock walls at McCurdy Pt., no *Rhabdocalyptus* smaller than 6 cm length were found. Marliave (1992) found juveniles (less than 3 cm long) of *Rhabdocalyptus* in Howe Sound, B.C., during the autumn, and speculated that reproduction must therefore occur in the summer. Hexactinellids are thought to reproduce year round, but their larvae are seldom seen. The only descriptions of larvae come from early studies on dredged specimens (Ijima, 1904; Okada, 1928) and, more recently, from a population of hexactinellids (*Oopsacas minuta*) in a submarine cave on the southern coast of France (Boury-Esnault and Vacelet, 1994). *Oopsacas* is the only hexactinellid from which live larvae have been observed, and although it does reproduce throughout the year, due to the fragile environment of its cave habitat no more is yet known about recruitment or population dynamics of the sponge population.

Paraffin sections of Bouins-fixed material collected monthly from the body walls of representative sizes of *Rhabdocalyptus* suggest that groups of archaeocytes, from which embryos develop, are most abundant in August and September, and parenchymella-like objects some 100–300 μm in length were found in individuals at all months, but were more common sponge pieces collected in August and September. Juveniles (<1 cm length) were found infrequently among the spicule coat of adults over the course of this study, and H. Reiswig (personal communication) reports finding many small individuals of *Rhabdocalyptus* (<1 cm) on the hairy tunicate *Halocynthia*. These observations suggest that *Rhabdocalyptus* may reproduce year round, but is more active toward the end of the summer months in these waters. It is possible, however, that unlike *Oopsacas*, *Rhabdocalyptus* allocates more resources to growth and reproduces sexually less frequently.

4.2. Growth rates

The growth rate of hexactinellid sponges calculated here (ca. 2cm year^{-1}; 167 ml year^{-1}) is faster than previously appreciated, and is even comparable to rates of growth of massive tropical and temperate demosponges (Reiswig, 1973; Hoppe, 1988). The Ford-Walford plot of those animals measured in Saanich Inlet suggests that for *Rhabdocalyptus* growth rate decreases marginally with increasing size of animals. However, the scatter of data around the regression reflects the immense variability in growth rates among individuals and suggests that the population shows indeterminate growth (see Sebens, 1987). The fact that the sponges measured in this 3-year study did not cover the entire size range of individuals inhabiting the inlet, and that even larger sponges have been found in other inlets, suggests that the maximum size attainable for *Rhabdocalyptus* depends on environmental conditions.

Dayton (1979) monitored a population of hexactinellids in Antarctica for 10 years and saw little evidence of growth in *Scolymastra joubini* and *Rosella nuda*, but found that *Rosella racovitzae* grew rapidly, small individuals increasing on average 22% in length

in one year and 98% in 3 years. He also noted that growth rates were highly variable. More recently, Tunnicliffe (unpublished) and Marliave (1992) each tracked six and 13 individuals of *Rhabdocalyptus dawsoni* respectively, the former using photography from a submersible of unmarked sponges along a chain hung vertically at McCurdy Pt. in Saanich Inlet, and the latter using direct measurement of both marked and unmarked sponges in Howe Sound, British Columbia. Tunnicliffe calculated a mean rate of growth (increase in length) of 3.3 ± 1.72 cm year^{-1} over three years in individuals ranging from 3–15 cm initial length. Marliave found that while small sponges (2–3 cm initial length) grew 71% in 6 months, large sponges (25 to 100 cm initial length) grew only 20% in the same time. While I have no data on growth rates in very small sponges, sponges longer than 25 cm grew at only 6% per year which is somewhat slower than the rate calculated by Marliave (1992) and may reflect the difference in methods of measurement used.

4.3. Estimated ages

The average length of sponges measured in the survey of Saanich Inlet was 32 cm or 5.8 l. At the mean rate of growth of 167 ml year^{-1} (if growth rate is considered to be constant) sponges this size would be 35 years old. The largest individuals of *Rhabdocalyptus* measured in the present study were 36.8 l, nearly 1 m long, which is comparable to the size of the largest hexactinellids photographed by Dayton et al. (1974) in Antarctica. Assuming those sponges grew at a constant rate of 167 ml year^{-1} their age can be estimated at 220 years. Even if the largest sponges measured here grew at the fastest rate of growth recorded they would be at least 42 years old. However, considering that many sponges in this study had years during which they regressed or shrank rather than grew (e.g. those individuals below the zero growth line in Fig. 5A), and considering that growth rate is not constant but decreases as sponges get larger, these are quite possibly conservative estimates of the ages of large hexactinellids.

4.4. Regeneration

The ability of numerous individuals of *Rhabdocalyptus* to regenerate rapidly from artificial wounds suggests that these sponges are resilient when damaged and would readily recover from occasional predatory attacks. However, because four of the 33 sponges that were wounded died, and in five other sponges the wound grew larger before healing, it is likely that the susceptibility of sponges to bacterial infection varies. In this study the sponges were wounded in the summer months, which is the time of year that the tissue produces the best tissue cultures in the lab (Leys, 1997).

Numerous experiments have been conducted on wound regeneration in temperate and tropical sponges and corals (e.g. Storr, 1964; Bak et al., 1977; Jackson and Palumbi, 1979; Ayling, 1983; Hoppe, 1988), but since different sizes of wound have been inflicted in each study a true comparison of rates cannot be made. Complete filling in of the wound in *Rhabdocalyptus* took up to 5 months for a wound 5 cm^2, a rate more than 40 times the rate of growth of new tissue. In cellular sponges regeneration occurs by the deployment of amoeboid cells into the wound area from neighbouring tissue (Harrison, 1972). In cases of extreme wound damage new cells are thought to be produced by

archaeocytes in a manner similar to the development of sponges from aggregates or reduction bodies (Brøndsted, 1953; Korotkova, 1970). Hexactinellids, on the other hand, begin wound healing by flooding the area with streams of cytoplasm from the multinucleate trabecular syncytium (Wyeth et al., 1996). Given that the rate of cytoplasmic streaming is faster than the rate of crawling of individual cells (Leys, 1995), regeneration might be expected to occur faster in hexactinellids than in cellular sponges. Wound healing is nonetheless insufficiently rapid to prevent settlement of debris or of invertebrates, such as annelids, which often become encased within the wall of the sponge by newly regenerated tissue, apparently without detriment to the sponge.

4.5. Seasonality

It has been argued that the lack of a clear seasonal reproductive pattern in Antarctic sponges suggests that there is no seasonal cycle in sponge communities that are too deep to be influenced by light (Barthel, 1995). Although groups of archaeocytes, which form embryos, were more abundant in tissue collected at the end of the summer, because so few juveniles were found during the three years of this study it was difficult to ascertain whether *Rhabdocalyptus* has seasonal reproductive period. However, a seasonal fluctuation in outer spicule coat (also reported by Marliave, 1992) was quite apparent to us on all our dives. While we do not have histological data on the tissue or spicules which are lost during sloughing, we did note that the loss of the outer spicule coat of *Rhabdocalyptus* was correlated with a lack of firmness of the whole sponge, and with a reduced ability of the tissue to form aggregates in culture in the laboratory (Leys, 1997).

Although seasonality in growth and reproductive period has been well documented in intertidal and subtidal demosponges (Stone, 1970; Reiswig, 1973; Elvin, 1976; Ayling, 1983; Rader and Winget, 1985), sloughing has only been reported in the intertidal sponge *Halichondria panicea* where it was shown to occur as an antifouling response (Barthel and Wolfrath, 1989). Where sloughing is found in other marine invertebrates and plants it is generally seen as a means of preventing fouling by epiphytes or sediment (e.g. Johnson and Mann, 1986; Riegl, 1995), but in some cases sloughing may also play a role in maintaining the biomechanical properties of a thallus during periods of rapid tissue growth (Keats et al., 1994).

Rhabdocalyptus could slough to rid itself of the debris and associated epifauna which would either compete for food or obstruct the water flow into the sponge, but this explanation seems inappropriate since the sponges did not slough for the full six months they were covered in debris, and since the tissue of the sponges was firm and showed good adhesive properties in culture during this time, and was flaccid and showed poor adhesive properties after sloughing. Alternatively, these sponges may slough after expending energy on the production of embryos, which this study suggests may be more abundant in the tissues in late summer. However, it is also possible that seasonal sloughing by *Rhabdocalyptus* may simply correspond to the end of seasonal phytoplankton blooms in British Columbia waters (Sancetta, 1989). Considering that seasonal fallout of phytodetritus influences the distribution and abundance of organisms in other deep sea communities (Billet et al., 1983; Lampitt, 1985; Gooday, 1988), it is possible

that *Rhabdocalyptus* populations thrive on phytodetrital fallout during the summer months and starve during the winter, which prompts sloughing.

5. Summary

(1) *Rhabdocalyptus* has a patchy distribution in Saanich Inlet, British Columbia, with local abundance reaching 5.3 individuals m^{-2}.

(2) The average growth rate of 19 sponges measured over 3 years was 167 ml $year^{-1}$ (min. –537 ml $year^{-1}$, max. 856 ml $year^{-1}$) or 1.98 cm $year^{-1}$ (min. –0.76 cm $year^{-1}$, max. 5.7 cm $year^{-1}$).

(3) Using the average rate of increase in volume, the age of an average-sized sponge (32 cm length, 5.8 l volume) was estimated to be 35 years old. Large individuals (1 m in length) may be 220 years old, if growth rate is constant. This population showed indeterminate growth.

(4) Tissue regeneration occurred rapidly after wounding in the field (0.05 cm^2 day^{-1}).

(5) All sponges showed seasonal trends in sloughing during winter months (November to February). Gain of a thick outer spicule coat occurred from March through October, and sloughing corresponded to the end of seasonal phytoplankton blooms.

Acknowledgements

References

Austin, W.C., 1985. An Annotated Checklist of Marine Invertebrates in the Cold Temperate Northeast Pacific. Khoyatan Marine Laboratory, Cowichan Bay, B.C., and Institute of Ocean Sciences, Fisheries and Oceans, Sidney, B.C., Victoria.

Ayling, A.L., 1983. Growth and regeneration rates in thinly encrusting demospongiae from temperate waters. Biol. Bull. 165, 343–352.

Bak, R.P.M., Brouns J.J.W.M., Heys, F.M.L., 1977. Regeneration and aspects of spatial competition in the scleractinian corals *Agaricia agaricites* and *Montastrea annularis*. In: Taylor, D.L. (Ed.), Proceedings of the Third International Coral Reef Symposium. Rosentiel School of Marine and Atmospheric Science, Miami, pp. 144–148.

Barthel, D., 1992. Do hexactinellids structure Antarctic sponge associations? Ophelia 36, 111–118.

Barthel, D., 1995. Tissue composition of sponges from the Weddell Sea Antarctica: not much meat on the bones. Mar. Ecol. Prog. Ser. 123, 149–153.

Barthel, D., Gutt, J., 1992. Sponge associations in the eastern Weddell Sea. Antarctic Sci. 4, 137–150.

Barthel, D., Wolfrath, B., 1989. Tissue sloughing in the sponge *Halichondria panicea*: a fouling organism prevents being fouled. Oecologia 78, 357–360.

Bett, B.J., Rice, A.L., 1992. The influence of hexactinellid sponge (*Pheronema carpenteri*) spicules on the patchy distribution of macrobenthos in the porcupine seabight (Bathyl NE Atlantic). Ophelia 36, 217–226.

Billet, D.S.M., Lampitt, R.S., Rice, A.L., Mantoura, R.F.C., 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature 302, 520–522.

Boury–Esnault, N., Vacelet, J., 1994. Preliminary studies on the organization and development of a hexactinellid sponge from a Mediterranean cave, *Oopsacas minuta*. In: van Soest, R.W.M., van Kempen, T.M.G., Braekman, J. (Eds.), Sponges in Time and Space. AA Balkema, Rotterdam, pp. 407–416.

Boyd, I., 1981. The Spicule Jungle of *Rhabdocalyptus dawsoni*: A Unique Microhabitat. Honours Thesis. University of Victoria, Victoria, B.C., Canada.

Brøndsted, H.V., 1953. The ability to differentiate and the size of regenerated cells after repeated regeneration in *Spongilla lacustris*. Q. J. Micros. Sci. 94, 177–184.

Carter, N.M., 1932. The Oceanography of the Fjords of Southern British Columbia. Progress reports of the Pacific Biological Station, Nanaimo, B.C., and Fisheries Experimental Station, Prince Rupert, B.C., 12, pp. 7–11

Cross, S.P., Chandler, P.C.P., 1996. Surface circulation patterns. Saanich Inlet Study. B.C. Ministry of the Environment, Lands and Parks, p. 7.

Dayton, P.K., 1979. Observations of growth, dispersal and population dynamics of some sponges in McMurdo Sound, Antarctica. In: Lévi, C., Boury–Esnault, N. (Eds.),Colloques internationaux du C.N.R.S., 291, pp. 271–282.

Dayton, P.K., Robilliard, G.A., DeVries, A.L., 1970. Benthic faunal zonation as a result of anchor ice at McMurdo Sound, Antarctica. Antarctic Ecol. 1, 244–258.

Dayton, P.K., Robilliard, G.A., Paine, R.T., Dayton, L.B., 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecol. Monographs 44, 105–128.

Elvin, D.W., 1976. Seasonal growth and reproduction of an intertidal sponge, *Haliclona permollis* (Bowerbank). Biol. Bull. 151, 108–125.

Gooday, A.J., 1988. A response by benthic Foraminifera to the deposition of phytodetritus in the deep sea. Nature 332, 70–73.

Harrison, F.W., 1972. The nature and role of the basal pinacoderm of *Corvomeyenia carolinensis* Harrison (Porifera: Spongillidae). Hydrobiologia 39, 495–508.

Hoppe, W.F., 1988. Growth, regeneration and predation in three species of large coral reef sponges. Mar. Ecol. Prog. Ser. 50, 117–125.

Ijima, I., 1904. Studies on the Hexactinellida. Contribution IV. (Rossellidae). J. College Sci. Imperial Univ. Tokyo 18, 13–307.

Jackson, J.B.C., Palumbi, S.R., 1979. Regeneration and partial predation in cryptic coral reef environments: preliminary experiments on sponges and ectoprocts. In: Lévi, C., Boury–Esnault, N. (Eds.), Colloques Internationaux du C.N.R.S., 291, pp. 303–308.

Johnson, C.R., Mann, K.H., 1986. The crustose coralline alga *Phymatolithon* Foslie, inhibits the overgrowth of seaweeds without relying on herbivores. J. Exp. Mar. Biol. Ecol. 96, 127–146.

Keats, D.W., Wilton, P., Maneveldt, G., 1994. Ecological significance of deep-layer sloughing in the eulittoral zone coralline alga, *Spongites yendoi* (Foslie) Chamberlain (Corallinaceae, Rhodophyta) in South Africa. J. Exp. Mar. Biol. Ecol. 175, 145–154.

Korotkova, G.P., 1970. Regeneration and somatic embryogenesis in sponges. Zool. Soc. Lond. 25, 423–436.

Lampitt, R.S., 1985. Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. Deep-Sea Res. 32, 885–897.

Lawn, I., Mackie, G.O., Silver, G., 1981. Conduction system in a sponge. Science 211, 1169–1171.

Leys, S.P., 1995. Cytoskeletal architecture and organelle transport in giant syncytia formed by fusion of hexactinellid sponge tissues. Biol. Bull. 188, 241–254.

Leys, S.P., 1997. Sponge cell culture: a comparative evaluation of adhesion to a native tissue extract and other culture substrates. Tissue Cell 29, 77–87.

Leys, S.P., Mackie, G.O., 1997. Electrical recording from a glass sponge. Nature 387, 29–30.

Mackie, G.O., Mills, C.E., 1983. Use of the *Pisces* IV submersible for zooplankton studies in coastal waters of British Columbia. C. J. Fish. Aquatic Sci. 40, 763–776.

Mackie, G.O., Singla, C.L., 1983. Studies on hexactinellid sponges. I. Histology of *Rhabdocalyptus dawsoni* (Lambe 1873). Phil. Trans. Royal Soc. Lond. B. 301, 365–400.

Mackie, G.O., Lawn, I.D., Pavans de Ceccatty, M., 1983. Studies on hexactinellid sponges. II Excitability, conduction and coordination of responses in *Rhabdocalyptus dawsoni* (Lambe, 1873). Phil. Trans. Royal Soc. Lond. B. 301, 401–418.

Marliave, J.B., 1992. Environmental monitoring through natural history research. Canadian Tech. Report Fisheries Aquatic Sci. 1879, 199–209.

Mills, C.E., 1982. Patterns and Mechanisms of Vertical Distribution of Medusae and Ctenophores. Ph.D Thesis. University of Victoria, Victoria, B.C., Canada.

Okada, Y., 1928. On the development of a hexactinellid sponge, *Farrea sollasii*. J. Fac. Sci. Imperial Univ. Tokyo 4, 1–29.

Rader, R.B., Winget, R.N., 1985. Seasonal growth rate and population dynamics of a freshwater sponge. Hydrobiologia 123, 171–176.

Reiswig, H.M., 1973. Population dynamics of three Jamaican demospongiae. Bull. Mar. Sci. 23, 191–226.

Reiswig, H.M., 1979. Histology of Hexactinellida (Porifera). In: Lévi, C., Boury–Esnault, N. (Eds.), Colloques Internationaux du C.N.R.S., 291, pp. 173–180.

Riegl, B., 1995. Effects of sand deposition on scleractinian and alcyonacean corals. Mar. Biol. 121, 517–526.

Sancetta, C., 1989. Spacial and temporal trends of diatom flux in B.C. Fjords. J. Plankton Res. 11, 503–520.

Sebens, K.P., 1987. The ecology of indeterminate growth in animals. Annual Rev. Ecology Systematics 18, 371–407.

Stone, A.R., 1970. Growth and reproduction of *Hymeniacidon perleve* (Montagu) (Porifera) in Langstone Harbour. Hampshire. J. Zool. Lond. 161, 443–459.

Storr, J.F., 1964. Ecology of the gulf of Mexico commercial sponges and its relation to the fishery. Special Science Report Fisheries 466, 1–73.

Tunnicliffe, V., 1981. High species diversity and abundance of the epibenthic community in an oxygen-deficient basin. Nature 294, 354–357.

Wulff, J.L., 1990. Patterns and processes of size change in Caribbean demosponges of branching morphology. In: Rützler, K. (Ed.), New Perspectives in Sponge Biology. Smithsonian Institution, Washington, pp. 425–434.

Wyeth, R.C., Leys, S.P., Mackie, G.O., 1996. Use of sandwich cultures for the study of feeding in the hexactinellid sponge *Rhabdocalyptus dawsoni* (Lambe, 1892). Acta Zool. 77 (3), 227–232.