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Environmental Flow Regimes for *Dysidea avara* Sponges

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Abstract The aim of our research is to design tank systems
to culture *Dysidea avara* for the production of avarol. Flow
information was needed to design culture tanks suitable for
effective production. Water flow regimes were character-
ized over a 1-year period for a shallow rocky sublittoral
environment in the Northwestern Mediterranean where
D. avara sponges are particularly abundant. Three-dimen-
sional Doppler current velocities at 8–10-m depths ranged
from 5 to 15 cm/s over most seasons, occasionally spiking
to 30–66 cm/s. A thermistor flow sensor was used to map
flow fields in close proximity (≈2 cm) to individual sponges
at 4.5-, 8.8-, and 14.3-m depths. These "proximal flows"
averaged 1.6 cm/s in calm seas and 5.9 cm/s during a storm,
when the highest proximal flow (32.9 cm/s) was recorded
next to a sponge at the shallowest station. Proximal flows
diminished exponentially with depth, averaging 2.6 cm/s±
0.15 SE over the entire study. Flow visualization studies
showed that oscillatory flow (0.20–0.33 Hz) was the most
common regime around individual sponges. Sponges at the
4.5-m site maintained a compact morphology with large
oscula year-around despite only seasonally high flows.
Sponges at 8.8 m were more erect with large oscula on tall
protuberances. At the lowest-flow 14.3-m site, sponges
were more branched and heavily conulated, with small
oscula. The relationship between sponge morphology and
ambient flow regime is discussed.

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Introduction

Dysidea avara (Schmidt 1862), a violet-colored, encrust-
ing, and heavily conulated dictyoceratid sponge, is known
from mostly sciaphilic microhabitats of the rocky sublittoral
Mediterranean to 80-m depths (Uriz et al. 1992). It is the
natural source of avarol and related metabolites that have
shown antitumoral, antibacterial, antiviral, and anti-inflam-
matory activities (Müller et al. 1985; Minale et al. 1974;
Uriz et al. 1996). Avarol is currently being tested on
humans in Germany as an additive to a skin cream for
treating psoriasis (Pietschmann et al. 2004). Early clinical
results have been promising, and projections for an
expanded market have begged the question of a sustainable
source of supply. Aquaculture of *D. avara*, both in situ and
ex situ, has been proposed and preliminarily investigated
(Sipkema et al. 2005). Aquaculture for the production of
drugs from other sponges has been reviewed by Battershill
and Page (1996). Recently, Bannister et al. (2007) identified
hydrodynamic features of the environment as key param-
eters for selecting suitable sites for bath sponge aquaculture
on the Great Barrier Reef, in Australia.

Bidder (1923) was the first to relate the general
morphology of a sponge to environmental flow and oscular
output. Bell and Barnes (2000), and Bell et al. (2002a,b,
2006) studied the influences of bathymetry and flow on
morphology and distribution of a number of sponge
species. They showed more massive and encrusting forms

dominated in high-energy sites, whereas arborescent forms dominated at low current sites. Riedl (1977) working with colonial cnidarians and sponges also showed that as depth increased, morphology changed from more compact forms at the surface to more erect, taller, plumate forms in the deeper zones. Pronzato et al. (1998) studied morphological adaptations of three species of the genus *Spongia* along an 80-m submerged vertical cliff and found distinct morphological differences that could be separated by depth, i.e., differences in ambient flow speeds.

Palumbi (1984, 1986) studied acclimation, body plan limitations, and morphological changes of *Halichondria panicea* in relation to varying flow regimes within a large coastal inlet in Alaska. He found that individuals at the entrance of the inlet (higher flows) had thicker colonies and added skeletal mass (i.e., spicules) as a means of resisting stronger wave forces. Kaandorp (1999) studied the relationship between water flow and the form (degree of compactness) of the sponge *Haliclona oculata*, a hydrozoan, and a hard coral using an algorithmic method and found increasingly more compact morphologies along a gradient of exposure to water movement.

Barthel (1991) presented relevant data on the influence of differing flow regimes on the growth form of the cosmopolitan sponge *H. panicea*. In a subtidal oscillating flow regime, the form was thickly encrusting globe, whereas at a sheltered "cave-like" setting, the sponge formed long slender, partly anastomosing branches extending upward from a relatively small base. Meroz-Fine et al. (2005) studied changes in morphology and physiology of *Tetilla* sp. sponges in the East Mediterranean in relation to light, depth, and water flow from differing habitats. They found that tide-pool-inhabiting sponges (higher wave forces) had significantly larger body volume and more skeletal silica than did cohorts inhabiting subtidal caves or a nearby 30-m site. Transplants from the deeper (calmer) site to a shallow (turbulent) site significantly increased spicule content to match the shallow-living individuals. Hill and Hill (2002) looked at morphological plasticity in a tropical sponge in relation to wave energy and predation pressures. They found that treatments in higher wave force habitats or those challenged with artificial predation increased their spicule density as a means of defense against the potentially damaging forces of high wave energy or increased levels of predation.

The overall aim of our research is to design tank systems to culture *D. avara* for the production of avarol. Sponges are notoriously sensitive organisms that are difficult to culture ex situ (Sipkema et al. 2005). So far, we have not been successful in our attempts to grow *D. avara* in tanks. Effects of food quality and quantity gave unsatisfactory results in growth experiments (Sipkema et al. 2006). During collections of *D. avara*, it became apparent that the flow

regime we applied in our tanks differed from the natural regime. We immediately noticed that *Dysidea* was usually present in habitats protected from strong currents. In addition, we noticed different morphologies at different sites, which we suspected were related to local flow conditions. We planned to do flow tank experiments to study the interaction of flow and particle uptake by the sponges. Therefore, we would need to know natural flow conditions to set starting parameters in the flow tank. Hence, the need for comprehensive field studies was indicated.

The specific aim of this research was to measure flow regimes within a rocky sublittoral cove on the northeast coast of Spain, where *D. avara* was known to be more abundant and attain larger size than from other similar environments nearby. Bulk current flow and flow in very close proximity to individual sponges in both calm and stormy seas would be determined at different depths where sponges showed different morphologies.

Materials and Methods

Site Selection, Sponge Selection, Identification, and Sampling Periods

Field studies were conducted in northeastern Spain on the Costa Brava in the vicinity of L'Escala, Girona, at Punta del Romani and within the Cala Illa Mateua (CIM) cove (global positioning system coordinates: 42°06.863′ N, 003°10.116′ E). Five field trips were conducted: 26–30 September, 2005; 3–30 March, 29 May–2 June, 25–28 July, and 27–31 October, in 2006. The sublittoral rocky plateaus of the point, with its many small caves, tunnels, and rocky overhangs, provided ideal habitats for the sponges. Using a self-contained underwater breathing apparatus, study sites were selected at three depths just west of the point: site A, at 4.5–5.0-m depths; site B, 8.8 m; and site C, 14.3 m. Each of the sites comprised two subsites ("main" and "annex") located in close proximity to one another, which were a priori differentiated as distinct flow microhabitats.

Site A The shallowest site was located closest to the shore and in the lee of the point. The A main site at 5.5 m was located in a "minicave" where many healthy *D. avara* sponges were found. The A annex site was located within a small cleft in the rock at 4.5-m depth where a number of small but healthy-appearing *D. avara* were found. A total of six sponges were selected (three at each subsite).

Site B The intermediate-depth 8.8-m B site was the least exposed of the three sites studied. It was located at the base of a steep, west-facing rock wall and protected from the west by

giant boulders and from the east and south by steep rock walls. Three large sponges were selected from inside a minicave (B main subsite) on the west-facing wall and three from a B annex subsite at the same depth but on an exposed rock shelf just outside of the minicave. Adjacent to the minicave and just before the south wall, a large tunnel connected to a large vertical tube, which opened into shallower water.

Site C The deepest of the three study sites (14.3 m) was the furthest from the shore and the protection of the submarine portions of the point. Given that wave forces diminish exponentially with depth and in proportion to wave length (Sverdrup et al. 1961), protection for the sponges at site C came by virtue of their depth, not rock cover. The C annex subsite was located a bit closer to the lowest rock shelves of the point but still at 14.3-m depth, so potentially, the annex sponges could receive some protection from the rocks—especially in an easterly sea. The sampled sponges (three main and three annex) were found encrusting on large rocks, which were mostly buried in sand. The maximum depth visited at Site C was 15.1 m, the deepest range for *D. avara* sponges within the study cove.

3-D Doppler Velocimeter

Bulk current flows within the cove were measured using a 16-MHz MicroADV acoustic Doppler velocimiter (Sontek, San Diego, CA, USA, e.g., Voulgaris and Trowbridge 1998). The acoustic Doppler velocimeter (ADV) measures the velocity of moving water by the Doppler principle, where the frequency of sound at a receiver is shifted from the transmitted frequency in proportion to the speed of the water moving through an acoustical sampling volume located 5 cm below the sender transducer. From signals received from a triangular array of receivers, water velocity vectors in three-directional components (*XYZ* Cartesian) were recorded. By vector addition, the resultant flow speed (V_{net}) was computed and displayed on *X–Y* coordinates in relation to time.

The ADV was deployed onto the sea bottom from an inflatable diver-towed miniraft and affixed to a sturdy steel tripod placed on the sea bottom. Recordings were made at each of the three depth sites for varying periods (usually for no less than 3 h). In operation, raw flow data were transmitted up the cable connecting the ADV to its signal-processing electronics housed on the inflatable. The analog signal (900 MHz) was radioed directly to a shore-based computer in real time.

Thermistor Flow Sensor and Recorder

An advanced thermistor flow sensor and recorder was specially designed and built to measure water flow speeds

in close proximity to individual sponges. The principle of operation is based on the rate of heat removed from a submerged, electrically heated thermistor (temperature sensitive electrical resistor), which is related to the speed of the water mass moving past it (Reiswig 1971, 1974; Vogel 1977). The nondirectional flow probe comprised a 0.9-mm diameter glass bead-covered thermistor silicone sealed onto the distal end of a 2-mm diameter stainless steel tube. The electrical connections ran down the core of the tube and connected to a 1.5-m-long electrical cable connecting the probe to the recorder. A second ambient temperature compensation thermistor was molded onto the outside of the recorder case. A liquid crystal display screen under a clear plastic lid showed the flow-related meter readings and magnet-operated function buttons.

The thermistor probe was calibrated in a commercial tow tank (Delft Hydraulics, The Netherlands) but only through a limited range of 0.17–13 cm/s. For speeds in excess of 13 cm/s, calibration relied upon the wider-ranged temperature response curve of the thermistor, which was stored onto the firmware of the instrument's circuitry. Before each measurement, the stored temperature response curve was electronically referenced to recalibrate the probe to the ambient temperature. We estimated measurement errors increased from ±2% at the lowest speeds to approximately ±15% at the highest speeds encountered in this study.

The measurement protocol in the field called for recording a series of individual flow speeds at four different placements of the probe around the periphery and two placements over the top of a sponge all within 10–15 min. Flow was measured approximately 2 mm from the surface of the sponge. At the underwater site, a lead-weighted, tri-footed stainless steel platform served as a stable mount for holding the thermistor probe, which was attached to a length of a flexible aluminum rod. The rod was shaped and bent to position the thermistor at the exact spot next to the sponge where the flow measurement was to be made. The setup during a typical field measurement is shown in Fig. 1.

Flow Visualization

Water flow regimes around individual sponges were visualized using an array of miniflags made of thin strips of fluorescent orange surveyor's tape pinned onto a sponge. The flags rotated freely on the pins and waved in response to the slightest water movement. A companion method employed milky suspensions of micrometer-sized white latex particles aspirated over a sponge from a syringe. The current-induced motions of the flags and latex clouds were recorded as short video movies on a Nikon® Cool-Pix 5200 camera. Flow visualization studies were used prior the proximal flow measurements as a tool to set up these measurements. Prior to thermistor probe experiments,
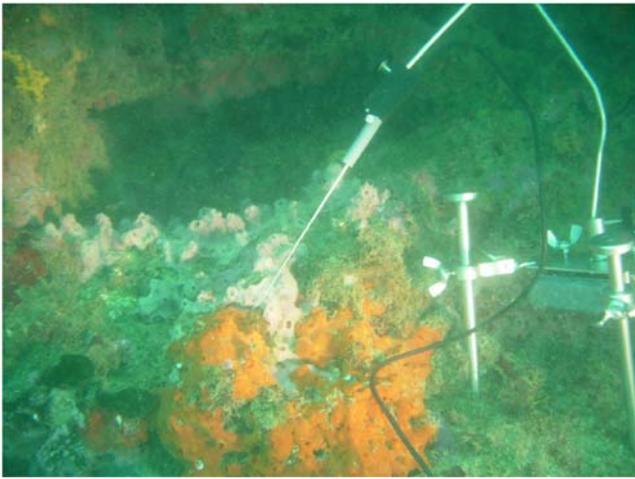
Fig. 1 Setup for proximal flow measurements with the thermistor probe around the purple *Dysidea avara* specimen (note: orange-colored sponge in front of *D. avara* is *Crambe crambe*)

obstacles that could affect the flow (such as the miniflags) were removed.

Results

Weather and Sea Conditions

Mild weather conditions and calm seas prevailed during the Sept. 2005 and March, July, and Oct. 2006 sampling periods. Underwater visibility during these calm periods was 10–15 m. During the May–June 2006 fieldtrip, strong "Tramuntana" winds (Beaufort scale 5–6) blew toward the study site from across the Gulf of Roses with swells and breaking waves cresting to 1–2 m. Underwater visibility during this storm was 3–4 m, attributable to entrained bottom sediments and air from the sea surface.

Bulk Current Profiles (ADV Recordings)

Calm Seas Three-dimensional Doppler flow profiles were recorded from inside the minicave at the A main subsite (5.5 m) in Sept., 2005. Recording showed oscillating flows with mean amplitude of approximately ±12 cm/s and periodicity of 12–20 cpm (0.20–0.33 Hz). The smallest component of the three-axis recording (±2 cm/s) was in the Z direction, i.e., the up/down flow component with respect to the water surface.

During calm seas on March 2006, the resultant flow speed (V_{net}) of the bulk current flow recorded at four different placements along a 50-m transect crossing the 10–12-m depth contours ranged from 3 to 13 cm/s. During summer (July 2006) at 8.8 m near site B and for the first 0.75 h of recording, V_{net} ranged from 5 to 30 cm/s with only a few

surges to 50–66 cm/s. For the remaining 1.75 h, V_{net} reduced to the 5–10-cm/s range with a few surges to 15–20 cm/s. V_{net} at 9 m (close to site B) during the fall sampling period (Oct. 2006) was in the range of 3–13 cm/s for the entire 3-h recording. All ADV recordings during calm seas could be characterized as oscillating flows with 3–5-s periodicity.

Stormy Seas Despite the very stormy sea surface generated by the seasonal Tramuntana winds of early summer, V_{net} at 9.3 m (close to site B) remained in the low range of 3–8 cm/s for most of the 3-h recording period.

Proximal Flows Around Individual Sponges

Figures 2, 3, and 4 display all proximal flow measurements made at each of the three depth/sites over the entire 7-month study period.

Site A Sponges at the shallowest site experienced the highest speed and the widest range of proximal flows: average=4.0 cm/s±0.3 SE, range 0.4–32.9 cm/s (Fig. 2). During the storm of 1 June, sponge A-1 at the shallowest 4.5-m A annex subsite experienced the highest proximal flows of any sponge: average=19.0 cm/s±6.2 SE, range 7.4–32.9 cm/s. Four days after the full strength of the storm had passed, proximal flows around this same sponge reduced to an average=4.7 cm/s±2.0 SE, range 1.9–12.4 cm/s, and in calm seas, sponge A-1 experienced flows in the range of 0.4–4.0 cm/s.

Site B The 7-month average flow speed at the intermediate depth site was 2.3 cm/s±0.1 SE, range 0.3–16.3 cm/s (Fig. 3). On 5 June, after the full force of the Tramuntana storm had passed, sponge B-6 (B annex subsite) experi-
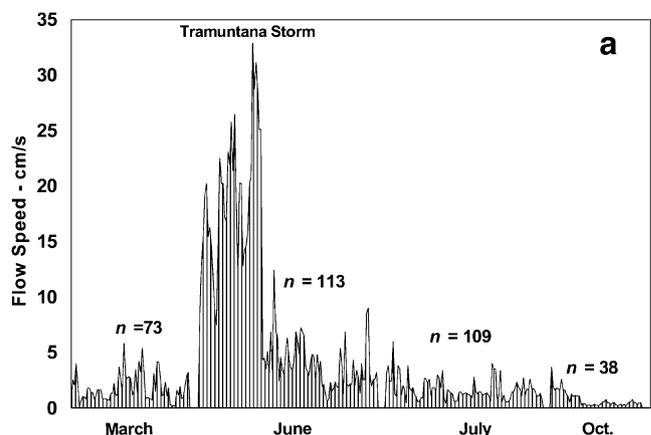
Fig. 2 Proximal flows at the 4.5-m site A, March through October 2006. The Tramuntana storm period of late May–early June is labeled, as are the number of measures for each of the fieldtrips
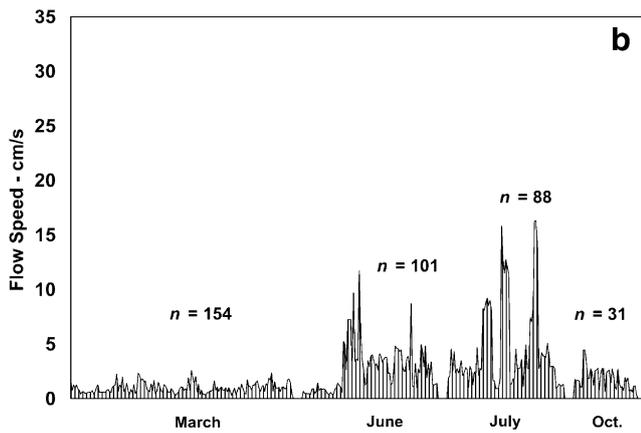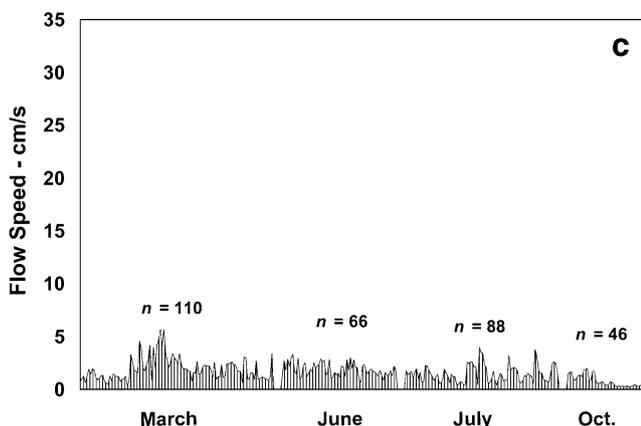
Fig. 3 Proximal flows at the 8.8-m site B, March through October 2006. The number of measures for each of the fieldtrips is shown above the corresponding month
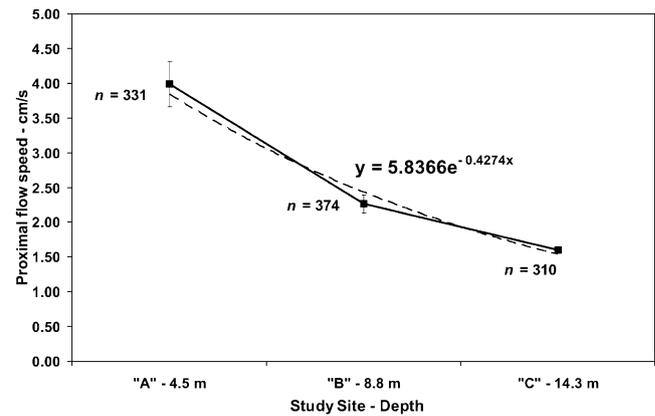

Fig. 5 Proximal flows (cm/s) measured close to *Dysidea avara* sponges in relation depth and site from March to October 2006. *Error bars* show ±1 standard error of the means (the very small error bars for the "C" site data are not visible). The *dashed trendline* shows a best-fit exponential equation to the mean data points at each depth

enced the highest flows recorded at the B site (seven measures >5 cm/s, one measure 11.8 cm/s). Less expected were the high flows recorded for the same sponge in calm seas on 25 July (six measures >7 cm/s, highest, 16.3 cm/s).

Site C The 7-month average flow speed at the deepest of the three sites was 1.6 cm/s±0.05 SE, range 0.2–5.67 cm/s (Fig. 4).

Figure 5 presents results of 1,015 thermistor flow-sensor measurements made in close proximity (i.e., ≈2 cm of the sponge surface) to 15 *D. avara* sponges (five each from sites A, B, and C) over the four fieldtrips in 2006. The overall average proximal flow speed for all depths, sea conditions, and seasons was 2.6 cm/s±0.15 SE. In calm seas, the average flow was 1.6 cm/s±0.03 SE. In stormy seas, the average proximal flow was 5.9 cm/s±1.7 SE. Proximal flows followed the expected distribution (decreasing exponentially with depth) with the highest flows and

greatest variability recorded at the shallowest site, followed by the intermediate site, with the deepest site showing the lowest proximal flow speeds and the smallest variation. Flows at the three depths differed significantly from each another (single-factor analysis of variance, $P \le 0.001$).

Flow Visualization

Fifty-seven 1–2-min movies were made of flow regimes around individual sponges. The results showed that the most prevalent flow regime at all depths and at all times of year was oscillatory, i.e., back-and-forth flow over and around a sponge in a more or less horizontal plane, with smaller-magnitude vertical flow components overlain. Mean periodicity of the oscillation was timed at 12–20 cpm (0.20–0.33 Hz). Mean residence time of a given mass of water hovering and lingering over a particular sponge was timed at 0.75–1.5 min depending on the oscillation frequency.

Sponge Morphotypes

Figure 6a–c shows the distinctive sponge morphotype predominating at each of the three main depth sites. Site A sponges (4–5-m depths, Fig. 6a) were in general smaller, more compact, and more thinly incrusting than the sponges at either of the other two sites. Site A sponges generally possessed smaller oscula than did site B sponges; however, most specimens possessed a few larger oscula placed on raised but not conspicuously elevated protuberances.

The sponges located under the protected overhang of the minicave of the B main subsite (Fig. 6b) exhibited more erect and massive body forms than did sponges from either sites A or C. Sponges at the B main subsite had large oscula (up to 10 mm diameter) each located at the apex of a thick protuberance rising 3–5 cm above the mean body surface. B

Fig. 4 Proximal flows at the 14.3-m site C, March through October 2006. The number of measures for each of the fieldtrips is shown above the corresponding month

Fig. 6 Typical morphotypes of *Dysidea avara* sponges from the three depth sites. **a** Site A, 4.5 m; *arrows* point to oscula on two short, connected protuberances; **b** site B, 8.8 m; *arrow* points to large osculum on tall protuberance; note: thermistor probe positioned over very large osculum; **c** site C, 14.3 m; thermistor probe is seen positioned near base of sponge and to the *right* in photo. Note: buildup of organic matter on the substratum between the erect, heavily conulated "fingers" of this specimen

annex subsite sponges were of a more flattened morphotype than those inside the minicave, but they also possessed elevated, thick protuberances with large terminal oscula.

Sponges at site C (Fig. 6c) were always distinctly erect, heavily branched, and heavily conulated with conspicuously small oscula not placed at the highest extremities of their branches.

Oscula of the sponges were not open in all cases. Under high-flow conditions (e.g., during the Tramuntana storm in early June), oscula exposed to these higher flow conditions were closed. An example of such an event is shown in Fig. 7. This is a sponge at site B, where the oscula on the front side are exposed to high-flow conditions and are closed, while oscula at the backside are protected against flow (facing the wall of the cave) and are open.
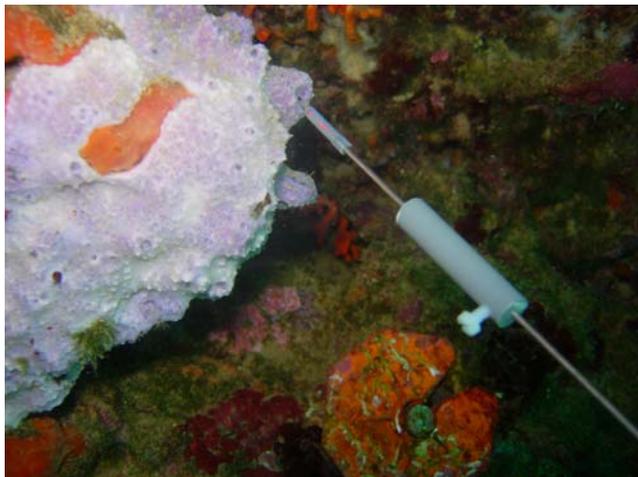
Fig. 7 Sponge at site B, with the thermistor probe placed above an osculum. The *left side* of the sponge shows oscula that are facing the unprotected opening of the "minicave" and are exposed to higher-flow conditions. The *right side* of the sponge is facing the rear cave wall where there is less flow; and the oscula are open

Discussion

Proximal vs. Vicinity Flow Regimes

We found proximal flows around individual sponges quite low, ranging from 1.6 to 4.0 cm/s (except during infrequent storms). Our use of two complimentary flow-measuring instruments showed us that the local bulk ocean current velocity (which averaged 10–12 cm/s over the course of our study) is significantly higher than the flow very close to the sponges. Our findings agree with classical physical oceanographic works, which instruct that water velocity near the bottom in the shallow sublittoral zone will be much lower than the bulk current velocity in the local water column (Hiscock 1983; Nowell and Jumars 1984; Sverdrup et al. 1961).

Flow Visualization Studies

Under the influence of surface waves, the near-bottom flow regime in the shallow sublittoral is mostly oscillatory (Bascom 1964; Hiscock 1983; Nowell and Jumars 1984). Our results confirmed this axiom and showed that a given water mass in an oscillating regime hovered and lingered over an individual sponge for a longer period than would a water mass transported by unidirectional flow of the same mean velocity. As each oscillation passed through the near-zero velocity crossover point, the latex particles slightly heavier than water (mimics of natural planktonic food) sank a bit closer toward the surface of the sponge. The morphology of the sponge then came into play acting to further extract momentum from the moving water mass and increase the particle settling rate (as was demonstrated in modeling studies for various classes of benthic organisms by Abelson et al. 1993).

From published studies on sponge fluid mechanics (Riisgård et al. 1993; Vogel 1977, 1994), we know that

the micrometer-sized ostia take in food particles under a slight negative pressure generated by the pumping action of the choanocytes driving water out of the oscula. Premised on our field observations and supported by the findings of others who studied the consequences of oscillatory flow and particle capture for other benthic invertebrates and macrophytes (Denny et al. 1985; Hunter 1989; Koehl 1982; Leonard et al. 1988), we initiated flow tank and computer modeling studies to test the hypothesis that an oscillatory flow regime worked together with sponge morphology to enhance food particle inflow rates in *D. avara.*

Sponge Body Forms and Water Flow Regimes

Results of modeling studies Denny et al. (1985) and Denny (1994) concluded that the mechanical limits of strength of tissues dictate that benthic invertebrates are smaller in size in wave-swept zones than their cohorts from deeper more protected zones. A more recent study (Denny 2006) calculated safety factors against breakage for a number of organisms living in the wave-swept environment and concluded that there was a significant amount of "overde-sign" (or adaptation) in body plans to cope with the extreme forces under which these organisms normally live. Koehl (1999), following on the original work of Alexander (1981) on the distribution of strengths and stresses in populations of animals, proposed the concept of "environmental stress factor," which she suggests is an "age- and season-dependent safety factor."

When compared to sponges from the deeper B and C sites, the more compact site A sponges support the theoretical models of these authors. The smaller, more rounded, and compacted body shapes of the A site sponges can be considered an adaptation to their seasonal exposure to the large forces generated by storm-driven waves. The intermediate-depth B main subsite sponges were the largest of all sponges surveyed. They possessed the tallest protuberances with the largest terminal oscula. Their shape is correlated with the generally low flows found within their protected minicave habitat and is supported by the concept that oscula placed high on protuberances help insure maximum separation of ejected metabolic wastes and new oxygenated water and food particles entering the ostia at the surface of the sponge (Vogel 1977, 1994).

Also interesting for the B site, overall, are the interme-diate-level proximal flows (7–16 cm/s) recorded during the June and July study periods (Fig. 6). These could be explained by the "alley-like" bathymetry of the site and the presence of the large through tunnel, which, together, acted to funnel wave energy back and forth through the rather narrow-walled site and up-and-back through the tunnel, increasing local flows—especially for the more exposed B

annex sponges. During periods of higher flow at B site (e.i., >5 cm/s) we observed that oscula exposed to the full force of the flow were generally closed. Oscula protected by virtue of their location on the sponge (i.e., those located closer to the rock walls) were generally open. During periods of low flow at B site (i.e., >3–4 cm/s) most oscula on most sponges observed were generally open.

C main and C annex sponges showed the same highly branched and heavily conulated body forms, reflecting the generally low-flow regimes found throughout the C site. Their tall, scalloped-edged, finger-like processes together with the occurrence of many small oscula could be viewed as adaptations to increased levels of sedimentation (Jackson 1979; Bell and Barnes 2000). Although site C sponges were never observed to be smothered with sediment (which is mostly larger-grained sand in this zone), we did commonly see layers of fine organic matter built up on the substratum spaces between the finger-like processes of C site sponges (visible in Fig. 6c). Associated with this organic matter are large populations of microorganisms, which (together with ultrafine organic particles) could become food for the sponge whenever portions of the trapped debris were resuspended by local flow and thereafter possibly settled out onto the ostial fields of the sponge.

Anatomical Adaptations to High Flow

D. avara is not supported by a stiff silicious skeleton as are other species known from stronger-flow regimes (Palumbi 1986; Bell and Barnes 2000). Its skeleton is composed of crisscrossing spongin fibers. Considering its relatively fragile body type, one might conclude that this sponge runs the risk of being torn apart by high wave forces such as those encountered seasonally at our site A.

However, *Dysidea* exhibit three behaviors and/or ana-tomical adaptations that contribute to its ability to colonize and survive in high-flow environments. First is its habit of taking up sand grains and other inorganic particles to stiffen primary skeletal fibers (Teragawa 1986). Second is its ability to grow into a compact drag-reducing body form in high-flow regimes. And the third is its tensile structure body plan (Otto 1962) first demonstrated by Teragawa (1985) with *Dysidea etheria*, when she showed that the surface membrane was under constant tension while the membrane-supporting main skeletal fibers were in constant compression.

Thus, the entire *Dysidea* body plan allows the organism to bend, flex, and deform under the influence of the forces imparted by waves. We observed such adaptive flexing, bending, and vibrating of the site A sponges during the early-summer Tramuntana storm as they resisted the potentially damaging forces of the waves.

Conclusions and Culture Tank Design

We have shown that at one rocky coastal site on the Northwestern Mediterranean coast, *D. avara* sponges live primarily in low, oscillating-flow microhabitats afforded protection by rock cover and/or depth. The sponge adjusts and adapts its body plan to the prevailing flow regime attaining a variety of morphotypes found at differing depths and flow microhabitats.

These findings have implications for in situ ecological studies of feeding, growth, and behavior of sponges in general. Moreover, the information gained should help aquaculturists set or select optimal flow regimes for tank or in-sea cultures of *D. avara* for natural product production.

Proximate flows are low (<5 cm/s). In our culture tanks, flow is generally higher (e.g., Khalesi et al. 2007, worked with flows in the range of 3–20 cm/s). For successful ex situ cultivation, the flow conditions need to be adapted to conditions found in nature. Indeed, at these lower-flow regimes, we are now able to maintain *D. avara* in the laboratory for extended periods.

It was clearly demonstrated that variations in the low flow observed in the field resulted in different morphologies of the sponges. The consequence of different flow regimes and morphologies will be further studied in our laboratory using a flow tank and particle-tracking velocimetry. Results from these studies should provide us the flow information needed to facilitate the design of culture tanks and water mixing systems for effective production of *D. avara* biomass for extraction of avarol.

References

Abelson A, Miloh T, Loya Y (1993) Flow patterns induced by substrata and body morphologies of benthic organisms, and their role in determining availability of food particles. Limnol Oceanogr 38:1116–1124

Alexander R McN (1981) Factors of safety in the structure of animals. Sci Prog 67:109–130

Bannister RJ et al (2007) The distribution and abundance of dictyoceratid sponges in relation to hydrodynamic features: identifying candidates and environmental conditions for sponge aquaculture. Mar Fresh Res 58:624–633

Barthel D (1991) Influence of different current regimes on the growth form of *Halichondria panicea* Pallas. In: Reitner J, Keupp H (eds) Fossil and recent sponges. Springer, Berlin

Battershill CN, Page MJ (1996) Sponge aquaculture for drug production. Aquac Update 16:5–6

Bascom W (1964) Waves and beaches. The dynamics of the ocean surface. Doubleday, New York

Bell JJ, Barnes DKA (2000) The influence of bathymetry and flow regime upon the morphology of sublittoral sponge communities. J Mar Biol Assoc UK 80:707–718

Bell JJ, Barnes DKA, Shaw C (2002a) Branching dynamics of two species of arborescent demosponge: the effect of flow regime and bathymetry. J Mar Biol Assoc UK 82:279–294

Bell JJ, Barnes DKA, Turner JRT (2002b) The importance of micro and macro morphological variation in the adaptation of a sublittoral demosponge to current extremes. Mar Biol 140:75–81

Bell JJ, Burton M, Bullimore B, Newman PB, Lock K (2006) Morphological monitoring of subtidal sponge assemblages. Mar Ecol Prog Ser 311:79–91

Bidder GP (1923) The relation of the form of a sponge to its currents. Quart J Microscop Soc 67:292–323

Denny MW (1994) Extreme drag forces and the survival of wind and water-swept organisms. J Exp Biol 194:97–115

Denny MW (2006) Ocean waves, nearshore ecology, and natural selection. Aqua Ecol 40:439–461

Denny MW, Daniel TL, Koehl MAR (1985) Mechanical limits to size in wave-swept organisms. Ecol Monogr 55:69–102

Hill MS, Hill AL (2002) Morphological plasticity in the tropical sponge *Anthosigmella varians*: responses to predators and wave energy. Biol Bull 1202:86–95

Hiscock K (1983) Water movement. In: Earll R, Erwin D (eds) Sublittoral ecology. Clarendon, Oxford

Hunter T (1989) Suspension feeding in oscillatory flow: the effect of colony morphology and flow regime on plankton capture by the hydroid *Obelia longissima*. Biol Bull 176:41–49

Jackson JBC (1979) Morphological strategies of sessile animals. In: Larwood G, Roser BR (eds) Systematics association special volume no. 11. "Biology and Systematics of Colonial Organisms". Academic, New York, pp 499–555

Kaandorp JA (1999) Morphological analysis of growth forms of branching marine sessile organisms along environmental gradients. Mar Biol 134:295–306

Khalesi MK, Beeftink HH, Wijffels RH (2007) Flow-dependent growth in the zooxanthellate soft coral *Sinularia flexibilis*. J Exp Mar Biol Ecol 351:106–113

Koehl MAR (1982) The interaction of moving water and sessile organisms. Sci Am 247:124–132

Koehl MAR (1999) Ecological biomechanics of benthic organisms: life history, mechanical design and temporal patterns of mechanical stress. J Exp Biol 202:3469–3476

Leonard AB, Strickler JR, Holland ND (1988) Effects of current speed on filtration during suspension feeding in *Oligometra serripinna* (Echinodernata Crinoidea). Mar Biol 97:111–125

Meroz-Fine E, Shefer S, Ilan M (2005) Changes in morphology and physiology of an East Mediterranean sponge in different habitats. Mar Biol 147:243–250

Minale L, Riccio R, Sodano G (1974) Avarol, a novel sesquiterpenoid hydroquinone with a rearranged drimane skeleton from the sponge *Dysidea avara*. Tetrahedron Lett 38:3401–3404

Müller WEG, Maidhof A, Zahn RK, Schröder HC, Gasic MJ, Heidemann D, Bernd A, Kurelec B, Eich E, Sibert G (1985) Potent antileukemic activity of the novel cytostatic agent avarone and its analogues in vitro and in vivo. Cancer Res 45:4822–4827

Otto F (ed) (1962) Tensile structures, vols. 1–2. MIT, Cambridge

Nowell ARM, Jumars PA (1984) Flow environments of aquatic benthos. Annu Rev Ecol Syst 15:303–328

Palumbi SR (1984) Tactics of acclimation: morphological changes of sponges in an unpredictable environment. Science 225:1478–1480

Palumbi SR (1986) How body plans limit acclimation: responses of a demosponge to wave force. Ecol 67:208–214

Pietschmann R, Shatton M, Schatton W (2004) EU patent number EP1391197. Application number EP20030016673 20030801. Munich, DE

Pronzato R, Bavestrello G, Cerrano C (1998) Morpho-functional adaptations of three species of *Spongia* (Porifera, Demospongiae) from a Mediterranean vertical cliff. Bull Mar Sci 63:317–328

Reiswig HM (1971) In situ pumping activities of tropical Demospongiae. Mar Biol 9:38–50

Reiswig HM (1974) Water transport, respiration and energetics of three tropical marine sponges. J Exp Mar Biol Ecol 14:231–249

Riedl R (1977) Water movement. In: Kinne O (ed) Marine ecology. Wiley, Chichester

Riisgård HU, Thomassen S, Jakobsen H, Weeks JM, Larsen PS (1993) Suspension feeding in marine sponges *Halichondria panicea* and *Haliclona urceolus*: effects of temperature on filtration rate and energy cost of pumping. Mar Ecol Prog Ser 96:177–188

Sipkema D, Osinga R, Schatton W, Mendola D, Tramper J, Wijffels RH (2005) Large-scale production of pharmaceuticals by marine sponges: sea, cell or synthesis? Biotechnol Bioeng 90:201–222

Sipkema D, Yosef NAM, Adamczewski M, Osinga R, Mendola D, Tramper J, Wijffels RH (2006) Hypothesized kinetic models for describing growth of globular and encrusting demosponges. Mar Biotechnol 8:40–51

Sverdrup HV, Johnson MV, Fleming RH (1961) The oceans, their physics, chemistry and general biology. Prentice-Hall, Englewood, NJ, p 518, 519, 585

Teragawa C (1985) Mechanical function and regulation of the skeletal network in *Dysidea*. In: Rützler K (ed) New perspectives in sponge biology. Third International Conference on Biology of Sponges. Woods Hole, MA, USA. Smithsonian Institution, Washington, DC, pp 252–258

Teragawa C (1986) Particle transport and incorporation during skeleton formation in a keratose sponge: *Dysidea etheria*. Biol Bull 170:321–334

Uriz MJ, Rosell D, Martin D (1992) The sponge population of the Cabrera archipelago (Balearic Islands): characteristics, distribution and abundance of the most representative species. PSZN I: Mar Ecol 113:101–117

Uriz MJ et al (1996) New light on the cell location of avarol within the sponge *Dysidea avara* (Dendroceratida). Cell Tissue Res 285:519–527

Vogel S (1977) Current-induced flow through living sponges in nature. Proc Natl Acad Sci USA 74:2069–2071

Vogel S (1994) Life in moving fluids, 2nd edn. Princeton University Press, Princeton, NJ

Voulgaris G, Trowbridge JH (1998) Evaluation of the acoustic Doppler velocimeter (ADV) for turbulence measurements. J Atmos Ocean Technol 15:272–289