Exhalant jet speed of single-osculum explants of the demosponge Halichondria panicea and basic properties of the sponge-pump

Sponges are modular organisms in which each aquiferous module draws water through a canal system by means of pumping units (choanocyte chambers, CC), and the filtered water leaves the module as an exhalant jet through a single opening (osculum). A constant density of CCs in sponges would imply that the filtration rate must be proportional to the sponge volume, but it is less obvious how the osculum cross-sectional area (OSA) scales to sponge volume. Here, we present data obtained on single-osculum sponge explants (i.e. single aquiferous modules) of the demosponge Halichondria panicea to gain insight into important basic properties of the sponge-pump. In the experimental study of 27 explants (volume $V_s=14$ to 1977mm$^3$), osculum cross sectional area (OSA), exhalant jet speed ($U_0$) and filtration rate ($F=OSA \times U_0$) were measured. The observed scaling with size ($OSA \sim V_s^{0.66}$; $U_0 \sim OSA^{0.45}$; $F \sim OSA^{1.45}$) was found to be close to that inferred from the hypothesis of volume based CC density. Thus, the volume-specific filtration rate (= pumping rate) could be approximated as $F (\text{mlmin}^{-1})=2.3V_s^{0.66}(\text{cm}^3)$ which is of the same order of magnitude as that of the demosponge Haliclona urceolus, $F (\text{mlmin}^{-1})=3.5V_s(\text{cm}^3)$. This suggests that for the two sponge species CCs are very likely of similar size, with similar individual pumping rate, and of similar uniform distribution over the sponge volume. By comparing the observed increase of $U_0$ with increasing OSA to literature data on other leuconoid sponge species this revealed a power function with an identical exponent 0.45 and maximum values of $U_0=6$ to 8cm$^{-1}$. This indicates that $U_0$ of a single-osculum explant, or $U_0$ of an individual osculum in a multi-oscula sponge approaches an upper limit as the sponge grows, implying that a module of a multi-oscula sponge may increase only to a certain size. Time-lapse video-microscope recordings of sponge explants showed temporal variation in OSA during spontaneous contractions. Exposure to a neurotransmitter (GABA) as well as overloading with ink particles triggered contractions that correlated with both decreasing OSA and $U_0$ that eventually became zero. Video-microscope recordings revealed that it was contraction of the endopinacoderm lining the excurrent canals that effectively restricted or stopped the water flow.

Hydrodynamic functionality of the lorica in choanoflagellates

Choanoflagellates are unicellular eukaryotes that are ubiquitous in aquatic habitats. They have a single flagellum that creates a flow toward a collar filter composed of filter strands that extend from the cell. In one common group, the loricate choanoflagellates, the cell is suspended in an elaborate basket-like structure, the lorica, the function of which remains unknown. Here, we use Computational Fluid Dynamics to explore the possible hydrodynamic function of the lorica. We use the choanoflagellate Diaphanoeana grandis as a model organism. It has been hypothesized that the function of the lorica is to prevent refiltration (flow recirculation) and to increase the drag and, hence, increase the feeding rate and reduce the swimming speed. We find no support for these hypotheses. On the contrary, motile prey are encountered at a much lower rate by the loricate organism. The presence of the lorica does not affect the average swimming speed, but it suppresses the lateral motion and rotation of the cell. Without the lorica, the cell jiggles from side to side while swimming. The unsteady flow generated by the beating flagellum causes reversed flow through the collar filter that may wash away captured prey while it is being transported to the cell body for engulfment. The lorica substantially decreases such flow, hence it potentially increases the capture efficiency. This may be the main adaptive value of the lorica.
Hydrodynamics of the leucon sponge pump
Leuconoid sponges are filter-feeders with a complex system of branching inhalant and exhalant canals leading to and from the close-packed choanocyte chambers. Each of these choanocyte chambers holds many choanocytes that act as pumping units delivering the relatively high pressure rise needed to overcome the system pressure losses in canals and constrictions. Here, we test the hypothesis that, in order to deliver the high pressures observed, each choanocyte operates as a leaky, positive displacement-type pump owing to the interaction between its beating flagellar vane and the collar, open at the base for inflow but sealed above. The leaking backflow is caused by small gaps between the vaned flagellum and the collar. The choanocyte pumps act in parallel, each delivering the same high pressure, because low-pressure and high-pressure zones in the choanocyte chamber are separated by a seal (secondary reticulum). A simple analytical model is derived for the pump characteristic, and by imposing an estimated system characteristic we obtain the back-pressure characteristic that shows good agreement with available experimental data. Computational fluid dynamics is used to verify a simple model for the dependence of leak flow through gaps in a conceptual collar–vane–flagellum system and then applied to models of a choanocyte tailored to the parameters of the freshwater demosponge Spongilla lacustris to study its flows in detail. It is found that both the impermeable glycocalyx mesh covering the upper part of the collar and the secondary reticulum are indispensable features for the choanocyte pump to deliver the observed high pressures. Finally, the mechanical pump power expended by the beating flagellum is compared with the useful (reversible) pumping power received by the water flow to arrive at a typical mechanical pump efficiency of about 70%.
Hydrodynamic functionality of the lorica in choanoflagellates
Choanoflagellates are unicellular microswimmers that are ubiquitous in aquatic habitats. They have a single flagellum that creates a flow toward the collar, the filtration apparatus composed of closely spaced filter strands. Loricate choano flagellates have evolved a basket-like “skeleton” around the cell, the lorica, the function of which remains unknown. Here, we use Computational Fluid Dynamics (CFD) to explore the possible hydrodynamic function of the lorica by studying the choanoflagellate Diaphanoeca grandis, with and without its lorica. We study the flow rate, the flow recirculation, and the resulting clearance rate for the capture of motile and non-motile prey by the freely swimming choanoflagellate. We find no support for several previous hypotheses regarding the effects of the lorica. Rather, our simulations suggest that the main function of the lorica is to enhance the capture efficiency, but this happens at the cost of lower encounter rate with motile prey.

Swim and fly: escape strategy in neustonic and planktonic copepods
Copepods can respond to predators by powerful escape jumps that in some surface-dwelling forms may propel the copepod out of the water. We studied the kinematics and energetics of submerged and out-of-water jumps of two neustonic pontellid copepods, Anomalocera patersoni and Pontella mediterranea, and one pelagic calanoid copepod, Calanus helgolandicus (euxinus). We show that jumping out of the water does not happen just by inertia gained during the copepod’s acceleration underwater, but also requires the force generated by the thoracic limbs when breaking through the water’s surface to overcome surface tension, drag and gravity. The timing of this appears to be necessary for success. At the moment of breaking the water interface, the instantaneous velocity of the two pontellids reached 125 cm s⁻¹, while their maximum underwater speed (115 cm s⁻¹) was close to that of similarly sized C. helgolandicus (106 cm s⁻¹). The average specific power produced by the two pontellids during out-of-water jumps (1700-3300 W kg⁻¹ muscle mass) was close to that during submerged jumps (900-1600 W kg⁻¹ muscle mass) and, in turn, similar to that produced during submerged jumps of C. helgolandicus (1300 W kg⁻¹ muscle mass). The pontellids may shake off water adhering to their body by repeated strokes of the limbs during flight, which leads to a slight acceleration in the air. Our observations suggest that out-of-water jumps of pontellids are not dependent on any exceptional ability to perform this behavior but have the same energetic cost and are based on the same kinematic patterns and contractive capabilities of muscles as those of copepods swimming submerged.
In a recent paper, Specht & Fuchs (2018; Mar Ecol Prog Ser 589:129−140) claim that 2 ciliary suspension-feeding bivalves, the blue mussel *Mytilus edulis* and the hard clam *Mercenaria mercenaria*, differ in how they respond to viscosity. For *M. mercenaria*, the authors found no change in filtration rate or beat frequency of water-pumping cilia in response to changes in viscosity at constant temperature. For *M. edulis* on the contrary, a previous study found these parameters to depend on manipulated viscosity at constant temperature in the same way as viscosity changes with temperature. To reconcile the opposing views, Specht & Fuchs suggested that the 2 bivalves may fundamentally differ in their responses to viscosity. But this suggestion is unwarranted. In addition to other shortcomings, we show for example that Specht & Fuchs likely misidentified compound laterofrontal cirri as lateral cilia, leading to erroneous conclusions. Furthermore, general fluid mechanical aspects were not considered by Specht & Fuchs, although many studies have shown that temperature-dependent viscosity of the ambient water controls or strongly affects bio-mechanical activity, such as beat frequency of water-pumping cilia in suspension-feeding bivalves, as well as water flows in general.

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**Too much food may cause reduced growth of blue mussels (*Mytilus edulis*) — Test of hypothesis and new "high Chl a BEG-model"**

Growth of the blue mussel (*Mytilus edulis*) is closely related to the biomass of phytoplankton (expressed as concentration of chlorophyll *a*, Chl *a*), but the effect of too much food in eutrophicated areas has so far been overlooked. The hypothesis addressed in the present study suggests that high Chl *a* concentrations (> about 8μgChl *a* l⁻¹) result in reduced growth because mussels are not evolutionarily adapted to utilize such high phytoplankton concentrations and to physiologically regulate the amount of ingested food in such a way that the growth rate remains high and constant. We first make a comparison of literature values for actually measured weight-specific growth rates (μ, %d⁻¹) of small (20 to 25mm) *M. edulis*, either grown in controlled laboratory experiments or in net bags in Danish waters, as a function of Chl *a*. A linear increase up to about μ=8.3%d⁻¹ at 8.1μgChl *a* l⁻¹ fits the “standard BEG-model” after which a marked decrease takes place, and this supports the hypothesis. A "high Chl *a* BEG-model", applicable to newly settled post-metamorphic and small juvenile (non-spawning) mussels in eutrophicated Danish and other temperate waters, is developed and tested, and
new data from a case study in which the growth of mussels in net bags was measured along a Chl a gradient are presented. Finally, we discuss the phenomenon of reduced growth of mussels in eutrophicated areas versus a possible impact of low salinity. It is concluded that it is difficult to separate the effect of salinity from the effect of Chl a, but the present study shows that too much food may cause reduced growth of mussels in eutrophicated marine areas regardless of high or moderate salinity above about 10psu.

Filter-Feeding Zoobenthos and Hydrodynamics
This chapter summarizes recent years’ studies on zoobenthic filter feeding in the sea. General principles are extracted based on experiments and mathematical modeling, mainly from own studies in shallow temperate Danish waters, in order to present primary characteristics of the sophisticated interplay between benthic filter feeders and hydrodynamics. Starting from the general concept of grazing potential and typical data on benthic population densities its realization is considered, first at the level of the individual organism through the processes of pumping and trapping of food particles for ingestion which relies on hydrodynamics. Studies have shown the importance of biomixing giving increased vertical seston flux due to mixing induced by exhalant jets of filter feeders, particularly in stagnant water but likely also in benthic boundary layers over mussel beds at moderate flow velocities. Mathematical models for such flows are discussed. At the scale of benthic boundary layers, mussels experience flows that are usually turbulent, but at the smaller scale of sublayers, colonies of bryozoans experience viscous-dominated flow that needs modeling. Finally, a case study from a particular shallow water area illustrates the effects of tide, current, and wind on vertical mixing, growth rates, and ecological implications. The main biophysical processes that may allow or prevent dense populations of filter feeders to control the phytoplankton biomass in shallow waters are presented along with remaining challenges for development of improved models for the benthic boundary layers, including effects of wall roughness, biomixing, and oscillating flows caused by waves.
Biomixing in stagnant water above population of blue mussels (*Mytilus edulis*). 
Dense beds of filter-feeding mussels can exert a considerable grazing impact on phytoplankton in many marine areas depending on downmixing promoted by current, wave- and wind action. But downmixing may also be promoted by biomixing caused by the action of the strong exhalent jets of water from the mussels. Here we study the strength of biomixing exerted by large actively filtering blue mussels *Mytilus edulis* in stagnant water. Vertical concentration profiles of added algal cells (*Rhodomonas salina*) were measured (as chl a) over a 70 cm high and stagnant water column in an aquarium above a population of 48 ind.m⁻² of mussels of shell length 69.5 ± 2.3 mm. Due to the intense agitation (biomixing) generated by exhalent jets of the actively feeding mussels the profiles remained nearly uniform over the full water column while decreasing exponentially with time, reaching a level of about 40% of the initial level after 120 min, which implied a population filtration rate of about 0.3 m³·h⁻¹·m⁻² in agreement with prior clearance measurements. Comparing to numerical solutions of a one-dimensional diffusion model, varying the eddy diffusivity, a value of $D = 550 \times 10^{-6} \text{ m}^2\cdot\text{s}^{-1}$ was estimated. This high strength of biomixing far exceeds those of previous similar studies on the filter-feeding polychaete *Nereis diversicolor* ($0.3 \times 10^{-6} \text{ m}^2\cdot\text{s}^{-1}$) and the ascidian *Ciona intestinalis* ($150 \times 10^{-6} \text{ m}^2\cdot\text{s}^{-1}$) and suggests that biomixing in moderate benthic boundary layer flows past mussel beds may contribute to the downmixing of phytoplankton.

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Growth-Prediction Model for Blue Mussels (*Mytilus edulis*) on Future Optimally Thinned Farm-Ropes in Great Belt (Denmark)
A recently developed BioEnergetic Growth (BEG) model for blue mussels (*Mytilus edulis*), valid for juvenile mussels, has been further developed to an ‘extended model’ and an alternative ‘ad hoc BEG model’ valid for post-metamorphic mussels, where the latter accounts for changing ambient chl a concentration. It was used to predict the growth of *M. edulis* on optimally thinned farm-ropes in Great Belt (Denmark), from newly settled post-metamorphic mussels of an initial shell size of 0.8 mm to marketable juvenile 30–35 mm ‘mini-mussels’. Such mussels will presumably in the near future be introduced as a new Danish, smaller-sized consumer product. Field data for actual growth (from Day 0 = 14 June 2011) showed that size of ‘mini-mussel’ was reached on Day 109 (Oct 1) and length 38 mm on Day 178 (Dec 9) while the corresponding predictions using the extended model were Day 121 (Oct 13) and Day 159 (Nov 20). Similar results were obtained by use of the ad hoc BEG model which also demonstrated the sensitivity of growth prediction to levels of chl a concentration, but less to temperature. The results suggest that it is possible (when the conditions are optimal, i.e., no intraspecific competition ensured by sufficient thinning) to produce ‘mini-mussels’ in Great Belt during one season, but not the usual marketable 45-mm mussels. We suggest that the prediction model may be used as a practical instrument to evaluate to what degree the actual growth of mussels on farm ropes due to intraspecific competition may deviate from the potential (optimal) growth under specified chl a and temperature conditions, and this implies that the effect of thinning to optimize the individual growth by eliminating intraspecific competition can be rationally evaluated.
Physiologically regulated valve-closure makes mussels long-term starvation survivors: test of hypothesis

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Filter feeding in mussels is a secondary adaptation where the gills have become W-shaped and greatly enlarged, acting as the mussel filter–pump. Water pumping and particle capture in the blue mussel, Mytilus edulis, have been studied over many years. Here, we give a short status of the present understanding of ciliary structure and function of the mussel...
filter–pump, supplemented with new photo-microscope and scanning electron microscopy (SEM) pictures of gill preparations. Pumping rate (filtration) and pressure to maintain flow have been extensively studied so the power delivered by the mussel pump to the water flow is known (1.1% of total respiratory power), but the actual cost based on gill respiration is much higher (19%), implying that the cost of maintaining of the large gill pump is considerable and that only relatively little energy can be saved by stopping or reducing the activity of the water-pumping cilia so that continuous feeding with a ‘minimal scaled’ pump is cheaper than discontinuous feeding with a correspondingly larger pump. According to the present view, the pump proper is the beating lateral cilia (lc) on the gill filaments and particle capture is accomplished by the action of laterofrontal cirri (lfc) transferring particles from the main water current to the frontal gill filament currents driven by frontal cilia (fc). Unexplained aspects include retention efficiency according to particle size and the role of pro-laterofrontal cirri (p-lfc) placed between the lfc and fc. The structure of cilia and the mode of ciliary beating have been re-examined in this study by new high-resolution light and scanning electron microscopy of isolated gill preparations exposed to serotonin (5-HT) stimulation which can activate the lc and lfc at low concentrations (10^{-6} M), but removes the lfc from the interfilament canals at higher concentrations (10^{-5} M).

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Allometric equations for maximum filtration rate in blue mussels Mytilus edulis and importance of condition index
The relationship between body dry weight (W) and shell length (L) of blue mussels, Mytilus edulis, can be expressed by the condition index (CI = W/L^3) which varies from population to population and during the year. Here, we examine the influence of CI on the relationships between maximum filtration rate (F, l h^{-1}), W (g), and L (mm) as described by the equations: FW = aW^b and FL = cL^d, respectively. This is done by using available and new experimental laboratory data on M. edulis obtained by members of the same research team using different methods and controlled diets of cultivated algal cells. For all data, it was found that FW = 6.773W^{0.678} and FL = 0.00135L^{2.088} which are very similar to equations for mussels with ‘medium condition’ (CI = 4–6 mg cm^{-3}): FW = 6.567W^{0.681} and FL = 0.00135L^{2.091}, with b- and d-values within a few percent of the theoretically expected of 2/3 and 2, respectively. Further, based on the present data, we propose a correction factor expressed by the empirical relation FW/FL = 0.3562CI^{2/3} which implies that FW tends to underestimate the actual filtration rate (FL) when CI<4.70 and to overestimate the filtration rate when CI>4.70.

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Dwarfism of blue mussels in the low saline Baltic Sea — growth to the lower salinity limit

Mussels within the Baltic Mytilus edulis × M. trossulus hybrid zone have adapted to the low salinities in the Baltic Sea which, however, results in slow-growing dwarfed mussels. To get a better understanding of the nature of dwarfism, we studied the ability of M. trossulus to feed and grow at low salinity (7 psu) compared with its performance at relatively high-salinity (20 psu) in controlled laboratory experiments, supplemented with field (Great Belt) growth experiments with M. trossulus and M. edulis in net-bags. Subsequently, the growth of M. trossulus transplanted in cages to various localities in the northern Baltic Sea was used to evaluate the effect of very low salinities, down to 3.4 psu. The laboratory feeding experiments with M. trossulus at 7 psu showed that the growth in shell length was negligible, whereas the body dry weight nearly doubled during the 15 d experiment, with a weight-specific growth rate of 3.7% d⁻¹. The same parameters measured at 20 psu showed a pronounced growth in both shell length and body dry weight, with a weight-specific growth rate of 2.2% d⁻¹. The growth rates of M. trossulus and M. edulis in suspended net-bags in the Great Belt (22 psu) were similar: 5.6 and 6.8% d⁻¹, respectively. M. trossulus in cage experiments had positive growth rates at locations with salinities above 4.5 psu, up to 2.60% d⁻¹, but negligible increase in the shell length, and at sites with salinities below about 4.5 psu, the somatic growth was negative, around −0.3% d⁻¹, which indicates valve closure and respiratory weight loss. A trend line in a plot of all available growth data for both mussel species as a function of salinity indicates that the growth of mussels is steadily hampered by reduced salinities from 30 psu down to about 10 psu, below which the growth is rapidly reduced to become negative below 4.5 psu. We suggest that reduced ability to produce shell material at extremely low salinity may explain dwarfism of mussels in the Baltic Sea. Reduced bio-calcification at low salinity, however, may impede shell growth, but not somatic growth, and this may at first result in an increased condition index, as seen in the benthic Baltic Sea mussels transferred to cages suspended in the water column.
Potential for production of ‘mini-mussels’ in Great Belt (Denmark) evaluated on basis of actual and modeled growth of young mussels Mytilus edulis

The present study is a first step towards evaluation of the potential for line-mussel production in the Great Belt region between the Kattegat and Baltic Sea, Denmark. We present experimental results for actual growth rates of juvenile/adult mussels Mytilus edulis in suspended net bags in terms of shell length and dry weight of soft parts during extended periods (27–80 days) in the productive season in the first 6 series of field experiments, including 4 sites in Great Belt and 2 sites in Limfjorden, Denmark. Data were correlated and interpreted in terms of specific growth rate (μ, % day−1) as a function of dry weight of soft parts (W, g) by a previously developed simple bioenergetic growth model μ = aW −0.34. Results were generally in good agreement with the model which assumes the prevailing average chlorophyll a concentration at field sites to essentially account for the nutrition. Our studies have shown that M. edulis can grow from settlement in spring to 30 mm in shell length in November. We therefore suggest line farming of 30 mm ‘mini-mussels’ during one growth season, recovering all equipment at the time of harvest and re-establishing it with a new population of settled mussel larvae at the beginning of the next season, thus protecting the equipment from the damaging weather of the Danish winter season. The growth behavior during the fall–winter season was recorded in an additional 7th series of mussel growth experiments on farm-ropes to show the disadvantage of this period.

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Somatic growth of mussels Mytilus edulis in field studies compared to predictions using BEG, DEB, and SFG models
Prediction of somatic growth of blue mussels, Mytilus edulis, based on the data from 2 field-growth studies of mussels in suspended net-bags in Danish waters was made by 3 models: the bioenergetic growth (BEG), the dynamic energy budget (DEB), and the scope for growth (SFG). Here, the standard BEG model has been expanded to include the temperature dependence of filtration rate and respiration and an ad hoc modification to ensure a smooth transition to zero ingestion as chlorophyll a (chl a) concentration approaches zero, both guided by published data. The first 21-day field study was conducted at nearly constant environmental conditions with a mean chl a concentration of C=2.7μgL−1, and the observed monotonous growth in the dry weight of soft parts was best predicted by DEB while BEG and SFG models produced lower growth. The second 165-day field study was affected by large variations in chl a and temperature, and the observed growth varied accordingly, but nevertheless, DEB and SFG predicted monotonous growth in good agreement with the mean pattern while BEG mimicked the field data in response to observed changes in chl a concentration and temperature. The general features of the models were that DEB produced the best average predictions, SFG mostly underestimated growth, whereas only BEG was sensitive to variations in chl a concentration and temperature. DEB and SFG models rely on the calibration of the half-saturation coefficient to optimize the food ingestion function term to that of observed growth, and BEG is independent of observed actual growth as its predictions solely rely on the time history of the local chl a concentration and temperature.

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Bioenergetic model predictions of actual growth and allometric transitions during ontogeny of juvenile blue mussels Mytilus edulis

The growth rates of blue mussels Mytilus edulis on ropes in the Great Belt (Denmark) have been studied during the growth season of one year, from settling to about 30 mm shell length mussels, covering >4 decades of body mass. Measured shell length (L, mm) and dry weight of soft parts (W, μg) for L > 10 mm followed a power-law (W = 2.15L^{3.40}) which supplemented an existing power-law for L < 10 mm (W = 24.7 L^{2.42}) to establish that somatic growth changes character at L ≈ 10 mm and W ≈ 10 mg. Results of specific growth rates based on dry weight of soft parts (μ = dlnW/dt) compared well with predictions based on a previously developed bioenergetic growth model (BEG) for W > 10 mg (μ = aW^b, a = 0.871×C – 0.986; b = -0.34, with μ in % d^{-1} and W in g) which explicitly takes into account the prevailing chla concentration C (μg L^{-1}). Results for W < 10 mg also correlated well by the power-law (μ = aW^b), now with exponent b = -0.13 close to the suggested value (b = -0.1) from experimentally established correlations for filtration and respiration rate of post-metamorphic mussels. Using the stated W(L)-relation for L > 10 mm the growth model has been expressed in terms of shell length specific growth rate (μL ≡ dlnL/dt = αL^β) by which data on shell length was well correlated, including the influence of chla concentration. Supplementary growth data from mussels in suspended net-bags at the same site illustrated differences ascribed to lack of competition for space and food, and literature data on shell length from cage-growth of mussels in the brackish Baltic Sea support the present correlations. It is argued that the allometric transitions that take place around W ≈ 10 mg and L ≈ 10 mm during the ontogeny of M. edulis is most likely universal and not restricted to first year growth of juvenile (young) mussels during the productive season.

Growth of mussels Mytilus edulis at algal (Rhodomonas salina) concentrations below and above saturation level for reduced filtration rate

Average filtration and growth rates of groups of juvenile Mytilus edulis (n =2545 of 22-35 mm shell length) were measured at different concentrations of an algal cell monoculture in 9 laboratory experiments of duration 14-30 days, 4 experiments below and 5 above the limit of incipient saturation concentration (C_{sat} ≈ 6000-7000 Rhodomonas salina cells ml^{-1}). From a nearly constant filtration rate (F ≈ 30 ml min^{-1} for a 30 mm shell length) at measured algal concentrations below C_{sat} the steady-state filtration rate decreased approximately as 1/C for increasing algal concentrations (C) above C_{sat} to levels as low as 12-9 % of the former value. Corresponding calculated gross ingestion rates (I = F x C) increased linearly below C_{sat} and remained nearly constant above C_{sat}. However, the measured weight-specific growth rates (μ) decreased sharply above C_{sat} from a maximal value of about 9.5 % day^{-1} to about 1.5 % day^{-1}. Below C_{sat}, on the other hand, measured μ values increased linearly with increasing algal concentration which was in good agreement with an earlier advanced bioenergetic growth model. The overall functional response of M. edulis resembles a Type I in terms of gross ingestion, but with a rapid decrease instead of a constant above C_{sat} in terms of actual ingestion and growth. The
physiological implications of the functional response remain uncertain. The response to increasing food concentration with possible regulation of net ingestion appears only to come into play when \( C_{\text{sat}} \) is exceeded and then as partial valve closure and reduced filtration and growth rates along with production of pseudo-faeces. A survey of naturally occurring phytoplankton biomass in the sea shows that this is generally below \( C_{\text{sat}} \) except for the short spring bloom periods; hence mussels generally feed at optimal rates depending on the composition and concentration of biomass exceeding the minimal concentration below which the mussels close their valves and reduce or cease filtering.

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**Field data and growth model for mussels Mytilus edulis in Danish waters**
Growth rates of blue mussels, *Mytilus edulis*, in suspended net-bags were measured in field experiments conducted in Limfjorden and Great Belt, Denmark, for extended periods of time (22 69 days) with up to 8 intermediate data samplings during the period. The resulting time series of growth of different overlapping size-classes of *M. edulis* were analysed individually and after being assembled to cover the full range of sizes, as full time series in terms of weight specific growth rate (\( \mu = \frac{1}{W} \frac{dW}{dt}, \% \text{ day}^{-1} \)) as a function of dry weight of soft parts (\( W, \text{g} \)). The results were compared to a simple bioenergetic growth model for mussels (\( \mu = aW^b \), \( a = 0.871 \times C - 0.986, b = -0.34 \)), and observed power-law relations of growth data were in good agreement with the model, which takes into account the prevailing average chlorophyll a (chl a) concentration (\( C, \mu \text{ g chl a l}^{-1} \)) at field sites. Thus, the b-values of data were close to the predicted -0.34 while the a-value was in one case lower than estimated due to suboptimal conditions during part of the growth period. As a supplementary interpretation the growth data have been expressed in terms of the time to double the dry weight of soft parts for a given size of mussel and at a given experimental site.

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Validation of the flow-through chamber (FTC) and steady-state (SS) methods for clearance rate measurements in bivalves

To obtain precise and reliable laboratory clearance rate (filtration rate) measurements with the 'flow-through chamber method' (FTC) the design must ensure that only inflow water reaches the bivalve's inhalant aperture and that exit flow is fully mixed. As earlier recommended these prerequisites can be checked by a plot of clearance rate (CR) versus increasing through-flow (FI) to reach a plateau, which is the true CR, but we also recommend to plot percent particles cleared versus reciprocal through-flow where the plateau becomes the straight line CR/FI, and we emphasize that the percent of particles cleared is in itself neither a criterion for valid CR measurement, nor an indicator of appropriate 'chamber geometry' as hitherto adapted in many studies. For the 'steady-state method' (SS), the design must ensure that inflow water becomes fully mixed with the bivalve's excurrent flow to establish a uniform chamber concentration prevailing at its incoming flow and at the chamber outlet. These prerequisites can be checked by a plot of CR versus increasing FI, which should give the true CR at all through-flows. Theoretically, the experimental uncertainty of CR for a given accuracy of concentration measurements depends on the percent reduction in particle concentration (100P) from inlet to outlet of the ideal 'chamber geometry'. For FTC, it decreases with increasing values of P while for SS it first decreases but then increases again, suggesting the use of an intermediate value of P. In practice, the optimal value of P may depend on the given 'chamber geometry'. The fundamental differences between the FTC and the SS methods and practical guidelines for their use are pointed out, and new data on CR for the blue mussel, Mytilus edulis, illustrate a design and use of the SS method which may be employed in e.g. long-term growth experiments at constant algal concentrations.

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Drag reduction by air release promotes fast ascent in jumping emperor penguins—a novel hypothesis

To jump out of water onto sea ice, emperor penguins must achieve sufficient underwater speed to overcome the influence of gravity when they leave the water. The relevant combination of density and kinematic viscosity of air is much lower than for water. Injection of air into boundary layers ('air lubrication') has been used by engineers to speed movement of vehicles (ships, torpedoes) through sea water. Analysis of published and unpublished underwater film leads us to present
a hypothesis that free-ranging emperor penguins employ air lubrication in achieving high, probably maximal, underwater speeds (mean ± SD: 5.3 ± 1.01 m s⁻¹), prior to jumps. Here we show evidence that penguins dive to 15 to 20 m with air in their plumage and that this compressed air is released as the birds subsequently ascend whilst maintaining depressed feathers. Fine bubbles emerge continuously from the entire plumage, forming a smooth layer over the body and generating bubbly wakes behind the penguins. In several hours of film of hundreds of penguins, none were seen to swim rapidly upwards without bubbly wakes. Penguins descend and swim horizontally at about 2 m s⁻¹; from simple physical models and calculations presented, we hypothesize that a significant proportion of the enhanced ascent speed is due to air lubrication reducing frictional and form drag, that -buoyancy forces alone cannot explain the observed speeds, and that cavitation plays no part in -bubble formation.

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**The exhalant jet of mussels Mytilus edulis**

The exhalant jet flow of mussels in conjunction with currents and/or other mussels may strongly influence the mussels' grazing impact. Literature values of mussel exhalant jet velocity vary considerably and the detailed fluid mechanics of the near-mussel flow generated by the exhalant jet has hitherto been uncertain. Computational modelling of this phenomenon depends on knowledge of the velocity distribution near the exhalant siphon aperture of mussels to provide appropriate boundary conditions for numerical flow models. To be useful such information should be available for a range of mussel shell lengths. Here, we present results of a detailed study of fully open mussels Mytilus edulis in terms of filtration rate, exhalant siphon aperture area, jet velocity, gill area and body dry weight, all as a function of shell length (mean +/- SD) over the range 16.0 +/- 0.4 to 82.6 +/- 2.9 mm, with the corresponding scaling laws also presented. The exhalant jet velocity was determined by 3 methods: (1) measured clearance rate divided by exhalant aperture area, (2) manual particle tracking velocimetry (PTV) using video-microscope recordings, and (3) particle image velocimetry (PIV). The latter provides detailed 2-component velocity distributions near the exhalant siphon in 5 planes parallel to the axis of the jet and the major axis of the oval aperture, and hence estimates of momentum and kinetic energy flows in addition to mean velocity. Data obtained on particles inside the exhalant jet of filtered water was verified by the use of titanium dioxide seeding particles which were de-agglomerated by ultrasound to a size range of 0.7 to 2 μm prior to addition, to avoid retention by the gill filter of the mussels. We found that exhalant jet velocity was essentially constant at similar to 8 cm s⁻¹, and independent of shell length. Based on geometric similarity and scaling of mussel pump-system characteristics we found that these characteristics coincide approximately for all sizes when expressed as pressure head versus volume flow divided by shell length squared.

**General information**
Particle-capture mechanisms in suspension-feeding invertebrates

A large number of suspension-feeding animals (e.g. bivalves, polychaetes, ascidians, bryozoans, crustaceans, sponges, echinoderms, cnidarians) have specialized in grazing on not only the 2 to 200 µm phytoplankton but frequently also the 0.5 to 2 µm free-living bacteria in the aquatic environment, or they have specialized in capturing larger prey, e.g. zooplankton organisms. Here we give an overview of the different types of particle-capture mechanisms in order to illustrate the many different solutions to the common problem of nourishing on a dilute suspension of microscopic food particles. Despite the many differences in morphology and living conditions, particle-capture mechanisms may be divided into 2 main types. One type of mechanism (i) is some form of filtering or sieving (e.g. through mucus nets, stiff cilia, filter setae), which is found in both passive suspension feeders, that rely on external currents to bring suspended particles to the filter, and in active suspension feeders that themselves produce a feeding flow by a variety of pump systems. Here the inventiveness of nature does not lie in the capture mechanism but in the type of pump system and filter pore-size. The other type of mechanism (ii) involves some paddle-like flow manipulating system (e.g. cilia, cirri, tentacles, hair-bearing appendages) that acts to redirect an approaching suspended particle, often along with a surrounding ‘fluid parcel’, to a strategic location for arrest or further transport. Examples include (i) sieving (e.g. through microvilli in sponge choanocytes, mucus nets in polychaetes, acidians, salps a.o., filter setae in crustaceans, “ciliary sieving” by stiff laterofrontal cilia in bryozoans and phoronids), (ii) “cirri trapping” in mussels and other bivalves with eu-laterofrontal cirri, ciliary “catch-up” in bivalve and gastropod veliger larvae, some polychaetes, entoprocts, and cyclophores. These capture mechanisms may involve contact with a particle, and possibly mechanoreception or chemoreception, or may include redirection of particles by the interaction of multiple currents (e.g. in scallops and other bivalves without eu-laterofrontal cirri). Based on the review, we discuss the current physical and biological understanding of the capture process and suggest a number of specific problems related to particle capture, which may be solved using advanced theoretical, computational and experimental techniques.
Ciliary-propelling mechanism, effect of temperature and viscosity on swimming speed, and adaptive significance of 'jumping' in the ciliate Mesodinium rubrum

Beating cilia are important organelles, not only for water pumping in many active filter-feeding organisms, but also for the swimming activity of ciliates and other aquatic organisms that use cilia for propulsion. The present study concerns the effect of temperature-dependent viscosity of the ambient seawater on the swimming velocity of the 'jumping' ciliate Mesodinium rubrum in which the propulsion is due to the active beat of an equatorial ring of swim-cilia. This was done by using videomicroscope recordings of ciliates at different temperatures and, at constant temperature, by addition of a high molecular weight polymer (PVP) to manipulate the viscosity. Both 'large' (45 mm long) and 'small' (22 mm) M. rubrum were studied in order to characterize the jumping behaviour and swimming mechanism in more details. For large M. rubrum, the swimming velocity decreases with decreasing temperature, hence increasing viscosity, from 9.6 +/- 0.3 mm/s at 21°C to 5.2 +/- 0.7 mm/s at 9.8°C for seawater, and down to 3.7 +/- 0.5 mm/s at a temperature equivalent Te = 5.8°C for PVP-manipulated viscosity, and further, the swimming velocity was found to decrease with increasing viscosity according to the power law Vs ~ μ^-n, n~1.93. For small M. rubrum, swimming velocity decreased from 6.1 +/- 1.3 mm/s at 21.1°C to 3.8 +/- 0.3 mm/s at 9.5°C, while the power-law exponent was n ~ 1.4 and 3 for changing temperature and temperature equivalent, respectively, but with n ~ 1.96 for all data taken together. The results, supplemented with an analysis of a hydrodynamic model for self-propagation of an idealized micro-organism, support the hypothesis that the response is mainly physical/mechanical rather than biological. Since the jump-speed of M. rubrum is nearly the same for all tracks of varying jumplengths at a given viscosity, this indicates that the swim-cilia may frequently have more than one beat cycle per jump, and possibly at times less than one beat cycle. The jump-length to jump-time for large ciliates is larger (~0.5 mm to 101 ms) than for small ciliates (~0.15 mm to 30 ms). However, swim-velocities - when reaching the near-constant level - show less difference, being about 5 mm/s on the average for the temperature range studied. The beat frequency of swim-cilia in jumping ciliates is estimated to be about 60 Hz, which is high but likely necessary for attaining the high swimming velocities observed.

Viscosity and not biological mechanisms often controls the effects of temperature on ciliary activity and swimming velocity of small aquatic organisms

A number of studies have shown that temperature-dependent viscosity of the ambient water controls or strongly affects bio-mechanical activity such as beat frequency of water-pumping cilia in mussels and ascidians, swimming velocity of sperm cells, ciliates and small (micro- and meso-scale) aquatic organisms using cilia or small appendages for propulsion. Here we summarize results from the literature and from own studies on bio-mechanical activities in response to changing...
temperature or manipulated viscosity at constant temperature, both having the same change in kinematic viscosity. The survey is used to assess to what extent the response is purely physical/mechanical or biological. We argue that a power-law dependence of bio-mechanical activity (a) on kinematic viscosity (ν), i.e. a ∼ ν^−m, should be applied to available data. Based on a general close matching of the response data to power-law regressions for viscosity manipulation (by means of an additive) and/or temperature we suggest that viscosity and not biological mechanisms often control the response. This knowledge enhances our basic understanding of the effect of temperature not only on the swimming and feeding behaviour of small aquatic organisms, but also on larger ciliary suspension-feeding bivalves and ascidians.

Effect of temperature and viscosity on swimming velocity of the copepod Acartia tonsa, brine shrimp Artemia salina and rotifer Brachionus plicatilis

Beating cilia are important organelles for swimming in many zooplanktonic aquatic organisms, including many invertebrate larvae, rotifers and ciliates, but other planktonic organisms, such as copepods and brine shrimps, use muscle-powered swimming appendages. In recent studies we found that the temperature-dependent viscosity of seawater is the key physical/mechanical factor that controls the beat frequency of water-pumping cilia in mussels and the swimming velocity in a ciliate. The present study on the swimming velocity of 3 zooplankton organisms, however, shows that the response of swimming velocity to a change in viscosity is different when due to a change in temperature or, at constant temperature, due to a manipulation of viscosity by addition of a high-molecular-weight polymer (polyvinyl pyrrolidone, PVP) to the ambient seawater. There is a biological effect (fraction of total reduction of swimming velocity for a 10 degrees C temperature reduction) that is found to be largest for the brine shrimp Artemia salina nauplius (37%) and the rotifer Brachionus plicatilis (26%), but negligible for the copepod Acartia tonsa (4%). We suggest that experimental data on change in swimming velocity (V) due to change in kinematic viscosity (ν) be correlated in terms of a power law, V proportional to ν^(-m). The present data on swimming velocity of copepods, brine shrimps and rotifers show values of exponent m approximate to 1.5 to 3, with a trend of decreasing values for increasing size of species. Differences in m-values may be ascribed to differences in propulsion system, body drag and size.
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Filter-feeding zoobenthos and importance of hydrodynamics in the shallow Odense Fjord (Denmark) - earlier and recent studies, perspectives and modelling

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Interplay between filter-feeding zoobenthos and hydrodynamics in the shallow Odense Fjord (Denmark) - earlier and recent studies, perspectives and modelling

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Viscosity of seawater controls beat frequency of water-pumping cilia and filtration rate of mussels Mytilus edulis

Down-mixing of phytoplankton above filter-feeding mussels - interplay between water flow and biomixing

Measurement of mean rotation and strain-rate tensors by using stereoscopic PIV

A technique is described for measuring the mean velocity gradient (rate-of-displacement) tensor by using a conventional stereoscopic particle image velocimetry (SPIV) system. Planar measurement of the mean vorticity vector, rate-of-rotation and rate-of-strain tensors and the production of turbulent kinetic energy can be accomplished. Parameters of the Q
criterion and negative $\lambda_2$ techniques used for vortex identification can be evaluated in the mean flow field. Experimental data obtained for a circular turbulent jet issuing normal to a crossflow in a low speed wind tunnel for a jet-to-crossflow velocity ratio of 3.3 are presented to show the applicability of the proposed technique. The results reveal the presence of a secondary counter-rotating vortex pair (SCVP) which is located within the jet core and has a sense of rotation opposite to that of the primary one (PCVP). Consistency of the measurements is verified by the agreement of data obtained in two perpendicular planes. Accuracy of the data is discussed and algebraic relations for some measurement uncertainties are presented.

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**Water flow analysis and particle capture in ciliary filter-feeding scallops (Pectinidae)**

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**Water pumping and analysis of flow in burrowing zoobenthos - a short overview**
Burrowing animals maintain contact with the water above the sediment by pumping water through a tube system and therefore measurements of water pumping rate of burrowing animals is of crucial importance for the study of many processes both within and above the sea floor. This review deals with the measuring of water pumping and the analysis of flow generated by burrowing deposit- and filter-feeding zoobenthos in order to determine the type of pump and mechanisms involved, flow rate, pump pressure, and pumping power. The practical use of fluid mechanical principles is examined, and it is stressed that not only the pump pressure that a burrowing animal can apply is of interest for assessing the energy cost of pumping, but also the distribution of excess pressure along its burrow is of importance for assessing the seepage flow of oxygen-rich water into the sediment surrounding the burrow because this bioirrigation exerts a considerable effect on the chemistry and microbiology of sediments. Dense populations of burrowing filter-feeding zoobenthos also interact with the water above the sediment interface and this is reflected in the development of phytoplankton concentration profiles above the filter-feeding animals. In stagnant situations the near-bottom water may be depleted of food particles, depending on the population filtration rate and the intensity of the biomixing induced by the filtering activity. But moderate currents and the biomixing can presumably generate enough turbulence to facilitate mixing of water layers at the sea bed with the layers above where food particle concentrations are relatively higher. Following a brief summary of types of burrowing benthic animals, common methods for measuring pumping rates are described along
with examples. For estimating the required pump pressure, biofluid mechanical theory for flow in tube–pump systems is summarised (elaborated in Appendix A). Specific examples are given to illustrate general principles and to give an idea of typical values of flow rate, pressure drop and power involved. Finally, some flow effects generated by burrowing animals in and above the sediment are described.

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### Down-mixing of phytoplankton above benthic filter feeders - interplay between water flow and biomixing

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Measurement of rotation and strain-rate tensors by using stereoscopic PIV

A simple technique is described for measuring the mean rate-of-displacement (velocity gradient) tensor in a plane by using a conventional stereoscopic PIV system. The technique involves taking PIV data in two or three closely-spaced parallel planes at different times. All components of the mean rate-of-displacement tensor are then calculated by using finite difference formulas. Planar measurements of the mean vorticity vector, rate-of-rotation and rate-of-strain tensors and the production of turbulent kinetic energy can be accomplished. Parameters of the Q-criterion and negative-λ_2 techniques used for vortex identification can be evaluated in the mean flow field. Dissipation rate of the turbulent kinetic energy in a non-isotropic three-dimensional flow field may also be estimated. Experimental data obtained for a round turbulent jet normal to a crossflow in a low-speed wind tunnel are presented to show the applicability of the proposed technique. The PIV cameras and light sheet optics shown in Fig. 1a are mounted on the same traverse mechanism in order to displace the measurement plane accurately. Data obtained in constant-y and -z planes are presented. Fig. 1b shows a contour plot of the normalized production rate of turbulent kinetic energy P*=PD/U^3 in the z/D=2 plane (D is the jet diameter, U is the crossflow velocity). P* is evaluated by using its exact definition, i.e., all nine additive terms in the definition are included. Smoothness of the contour plot indicates the successful implementation of the technique. Measurement uncertainties are discussed and algebraic relations for uncertainties in P and the parameter of the Q-criterion are presented. Consistency of the measurements is verified by showing agreement of two data sets obtained in two perpendicular planes. Accuracy of the data can be improved if optimal spacing between velocity vectors is employed. The feasibility of measuring the truncation error in the rotation- and strain-rate tensors is also demonstrated.

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Simulation of particle transport in electrostatic precipitators

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Swirling flow structures in electrostatic precipitator

General information
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Organisations: Fluid Mechanics, Department of Mechanical Engineering
Three-dimensional flow and turbulence structure in electrostatic precipitator by stereo PIV

Turbulence studies of negative corona ESP

Flow in a Centrifugal Pump Impeller at Design and Off-design Conditions. Part 1: PIV and LDV measurements
Laser Doppler anemometry study of a turbulent jet in crossflow

General information
Publication status: Published
Organisations: Fluid Mechanics, Department of Mechanical Engineering
Contributors: Özcan, O., Larsen, P. S.
Pages: 1614-1616
Publication date: 2003
Peer-reviewed: Yes

Publication information
Journal: AIAA Journal
Volume: 41
Issue number: 8
ISSN (Print): 0001-1452
Ratings:
Scopus rating (2003): SJR 1.178 SNIP 1.327
Web of Science (2003): Indexed yes
Original language: English
Source: orbit
Source-ID: 25563
Research output: Contribution to journal › Journal article – Annual report year: 2003 › Research › peer-review

EFP-2000 - Electrostatic Precipitation - Reduction of Emissions and Energy Consumption

General information
Publication status: Published
Organisations: Department of Mechanical Engineering, Fluid Mechanics
Contributors: Larsen, P. S., Ullum, T. U., Özcan, O.
Publication date: 2002

Publication information
Original language: English
Source: orbit
Source-ID: 62636
Research output: Book/Report › Report – Annual report year: 2002 › Communication

Filtrerende bryozoer (mosdyr) - partikler og strømmende vand

General information
Publication status: Published
Organisations: Department of Mechanical Engineering
Contributors: Riisgård, H. U., Larsen, P. S., Nielsen, C.
Pages: 12-23
Publication date: 2002
Peer-reviewed: Unknown
On ciliary pumping and sieving in bryozoans

Based on video-microscope observations of trajectories of particles in the feeding currents of individual isolated bryozoans Bowerbankia imbricata, Flustrellidra hispida and Electra pilosa the velocity fields above and in the lophophore have been determined. The flow into the lophophore, which is a result of water currents driven out between tentacles by the water pumping lateral cilia, is characterised by nearly parabolic profiles with highest velocity along the centreline of the lophophore. In intact animals, the centreline velocity first increases from its value at the inlet to a maximal value about 20 to 25% down into the lophophore and then decreases to low values as the flow stagnates at the mouth. In a narcotised animal, whose laterofrontal filter was inactive, the centreline velocity was found to decrease monotonously from its inlet value. An approximate expression is derived for the relation between velocity distribution in the lophophore and variation of pumping rate along tentacles. Typical variations are given and compared to those obtained by a more accurate two-dimensional numerical solution. Based on observed velocity distributions in the lophophore, particle tracks and tentacle flicks, a description is given of the feeding mechanisms. Particles entering the central region are brought to the mouth by the high velocity feeding current in the central part of the lophophore. Particles entering further out either escape between tentacles or are stopped by the laterofrontal cilia sieve and, in the distal region of tentacles, are brought back into the central feeding current by flicks of tentacles. The relative velocity between fluid and particle during a flick recovery phase ensures particle release. Particles stopped in the proximal region of the lophophore appear to be transferred to and conveyed by the frontal cilia bands on tentacles. The added load on laterofrontal cilia from viscous drag on a food particle retained by the cilia is found to be of the same order of magnitude or greater than the "background load" of viscous drag from fluid passing the laterofrontal cilia in the absence of a particle. This is hypothesised to stimulate the sensing mechanism triggering observed flicks. The energy cost of pumping is estimated at 1 to 4% of the metabolic power of a "standard" zooid. Keywords: Feeding in bryozoans; Flow in lophophore; Ciliary sieving; Particle retention; Bryozoan model.

Particle deposition in low-speed, high-turbulence flows

The experimental and numerical study considers the concentration of airborne particulate contaminants, such as spores of spoilage fungi, and their deposition on a surface, in a petri dish, and on a warm box-shaped product placed in a food-processing environment. Field measurements by standard, active and passive samplers provide typical values of airborne concentrations and specific deposition fluxes. Velocity and turbulence data from field studies are used as input in LES simulations of the process, and estimates of deposition fluxes are of the same order of magnitude as those deduced from field measurements. Particle deposition is shown to be associated with near-wall coherent structures. Flow reversal, simulated by impulsive start, is shown to give higher deposition rates than steady mean flows. Key word index: Spoilage fungi; spores; food processing plant; deposition flux; large eddy simulation.

General information
Publication status: Published
Organisations: Department of Mechanical Engineering
Contributors: Larsen, P. S., Riisgård, H. U.
Pages: pp. 181-195
Publication date: 2002
Peer-reviewed: Yes
Point and planar LIF for velocity-concentration correlations in a jet in cross flow

Simultaneous measurements of velocities and concentration with Planar Laser Induced Fluorescense (PLIF) combined with Particle Image Velocimetry (PIV) are compared to similar measurements with pointwise Laser Doppler Anemometer (LDA). The flow considered is the mixing of a jet in a fully developed cross flow in a square duct with a width of 10 jet diameters. Both a laminar flow case, Re=675, and a turbulent flow case, Re=33750, are presented. For both flows, the ratio jet-to-duct mean velocities was R=3.3. Result of mean velocities, mean concentration and Reynolds fluxes in the symmetry plane of the jet are presented for PIV and PLIF measurements. The LIF measurements performed with the LDA equipment was in general in good agreement with the PIV/PLIF measurements. The cross sections selected for comparison are challenging, since these involve areas with high velocity- and concentration gradients, which in turn amplifies the effect of a finite measurement volume in the two measurement systems. In addition, the concentration measurement was realized by injecting clean water into the dye seeded main flow. This "inverse" configuration resulted in a deeper insight to the concentration measurement process, itself. The comparison of LDA/LIF and PIV/LIF data also resulted in better understanding of the two measurement systems.

Temperature and velocity fields in natural convection by PIV and LIF

Natural convection in a cubical cavity (L = 250 mm) filled with water is created by heating a square plate (0.5 L) centred in the bottom wall and by cooling the sidewalls, while the remaining walls are insulated. The Rayleigh number based on cavity side length and temperature difference between plate and cooled walls is 1.4×10^{10}. The flow is turbulent and is similar to some indoor room flows. Combined Particle Image Velocimetry (PIV) and Planar Light Induced Fluorescence (LIF) are used to measure local velocities and temperatures. Data measured in a symmetry plane parallel to a sidewall are presented in terms of mean velocities and temperature and in terms turbulent quantities including Reynolds fluxes. The flow consists a plume rising above the heated plate into an almost stagnant fluid with a weakly stratified temperature field, as well as thin buoyancy driven boundary layers down the sidewalls. The measured Reynolds fluxes show that the dominating heat transport is in the plume in vertical direction. This transport relates to hot parcels of fluid rising due to buoyancy. A considerable heat transport in horizontal direction from the plume to the surrounding, stagnant fluid maintains the stratified temperature field.
Three-dimensional flow and turbulence structure in electrostatic precipitator

Stereo PIV is employed to study the three-dimensional velocity and turbulence fields in a laboratory model of a negative corona, barbed-wire, smooth-plate, electrostatic precipitator (figure 1). The study is focused on determining the parametric effects of axial development, mean current density $J_m$ and bulk velocity $U_0$ on secondary flows and turbulence levels and structures due to the action of the three-dimensional electrostatic field on the charged gas. At constant bulk velocity ($U_0 = 1$ m/s) and current density ($J_m = 0.4$ mA/m²), secondary flows in the form of rolls of axial vorticity with swirl numbers up to $S = 0.3-0.4$ are found to level off after 4-5 electrodes, being most regular in the central unit cells defined by the periodic geometry of pin-electrodes. The corresponding image-mean turbulence intensity increases to about 20% from the 1st to the 7th electrode with a consistent anisotropy of normal Reynolds stresses. The effects of $U_0$ and $J_m$ on $S$ and $T_u$ (at fixed position between 6th and 7th electrode) are reasonably correlated by the electrohydrodynamic modulus $\text{NEHD} = (J_m/b_i)ly/(\frac{1}{2}rU_0^2)$, where $b_i$ denotes the ion mobility and $ly$ the electrode-plate distance.

Water pumping and analysis of flow in burrowing zoobenthos - a short overview

Measurement of water pumping rates of burrowing animals is of crucial importance for the study of many processes both within and above the sea floor. This short review deals with water pumping and analysis of flow, including available techniques and bio-fluid mechanical theory, in burrowing deposit- and filter-feeding zoobenthos. A number of examples serve to illustrate general principles.
Colony growth rate of encrusting marine bryozoans (Electra pilosa and Celleporella hyalina)

General information
Publication status: Published
Organisations: Department of Mechanical Engineering
Contributors: Hermansen, P., Larsen, P. S., Riisgård, H. U.
Pages: 1-3
Publication date: 2001
Peer-reviewed: Yes

Publication information
Journal: Journal of Experimental Marine Biology and Ecology
Volume: 263
Issue number: 1
ISSN (Print): 0022-0981
Ratings:
Scopus rating (2001): SJR 1.39 SNIP 1.26
Web of Science (2001): Indexed yes
Original language: English
Source: orbit
Source-ID: 64110
Research output: Contribution to journal › Journal article – Annual report year: 2001 › Research › peer-review

Minireview: ciliary filter feeding and bio-fluid mechanics - present understanding and unsolved problems

General information
Publication status: Published
Organisations: Department of Mechanical Engineering
Contributors: Riisgård, H. U., Larsen, P. S.
Pages: pp. 882-891
Publication date: 2001
Peer-reviewed: Yes

Publication information
Journal: Limnology and Oceanography
Volume: Vol. 46, No. 4
ISSN (Print): 0024-3590
Ratings:
Scopus rating (2001): SJR 2.934 SNIP 1.904
Web of Science (2001): Indexed yes
Original language: English
Source: orbit
Source-ID: 64112
Research output: Contribution to journal › Journal article – Annual report year: 2001 › Research › peer-review

Particle deposition in low-speed, high-turbulence flows

General information
Publication status: Published
Organisations: Department of Mechanical Engineering, Technical University of Denmark
Contributors: Reck, M., Larsen, P. S., Ullum, U.
Publication date: 2001

Host publication information
Title of host publication: Proceedings of 5th World Conference on Experimental Heat Transfer, Fluid Mechanics and Thermodynamics
Simultaneous measurement of velocity and concentration in a jet in channel-crossflow

General information
Publication status: Published
Organisations: Department of Mechanical Engineering, Fluid Mechanics
Contributors: Özcan, O., Meyer, K. E., Larsen, P. S., Westergaard, C. H.
Publication date: 2001

Host publication information
Title of host publication: Proceedings of FEDSM2001-18220
Publisher: American Society of Mechanical Engineers
Source: orbit
Source-ID: 64185

Stereoscopic PIV measurements in a jet in crossflow

General information
Publication status: Published
Organisations: Fluid Mechanics, Department of Mechanical Engineering
Contributors: Meyer, K. E., Özcan, O., Larsen, P. S., Westergaard, C. H.
Publication date: 2001

Host publication information
Title of host publication: Proceedings of the Second International Symposium on Turbulence and Shear Flow Phenomena
Place of publication: Stockholm
Publisher: KTH
Source: orbit
Source-ID: 64155

A comment on experimental techniques for studying particle capture in filter-feeding bivalves

General information
Publication status: Published
Organisations: Department of Energy Engineering
Contributors: Riisgård, H. U., Larsen, P. S.
Pages: 1192-1195
Publication date: 2000
Peer-reviewed: Yes

Publication information
Journal: Limnology and Oceanography
Volume: 45
Issue number: 5
ISSN (Print): 0024-3590
Ratings:
Scopus rating (2000): SJR 3.128 SNIP 2.038
Web of Science (2000): Indexed yes
Original language: English
Source: orbit
Source-ID: 177277
Research output: Contribution to journal › Journal article – Annual report year: 2000 › Research › peer-review
Downstream collecting in ciliary suspension feeders: the catch-up principle

Based on observations of feeding structures and currents in the polychaete Spirorbis tridentatus, the entoproct Loxosoma pectinariola and the cyclophore Symbion pandora, which all possess compound cilia, it is hypothesized that their capture mechanism is based on the catch-up principle. According to this principle, the compound cilia constitute the pump which generates a flow with suspended particles that enters the ciliary region. In this region the same cilia, during their power stroke, catch up with suspended particles and transfer the particles to a food groove, or a mouth cavity. In the particle-size retention spectrum, the lower limit depends on spacing between cilia in phase, while the upper end depends on cilia length which may or may not allow particles to enter the ciliary region. On the basis of fluid mechanical considerations and literature descriptions of structure and function of the ciliary bands of some rotifers and of the various types of trochophora larvae of annelids, molluscs and entoprocts, it is hypothesized that the feeding mechanisms of these organisms are based on the catch-up principle.
Experimental study of temporal and spatial structures in fence-on-wall test case

General information
Publication status: Published
Organisations: Department of Energy Engineering
Contributors: Ullum, U., Schmidt, J. J., Scheel Larsen, P.
Pages: 25-37
Publication date: 1999

Host publication information
Title of host publication: Simulation and Identification of Organized Structures in Flows
Place of publication: Dordrecht
Publisher: Kluwer Academic Publishers
Source-ID: 169345
Research output: Chapter in Book/Report/Conference proceeding – Article in proceedings – Annual report year: 1999 – Research – peer-review

Hysteresis Model for Oil-Soaked Insulation in Flat HTDC-Cable

General information
Publication status: Published
Organisations: Department of Energy Engineering
Contributors: Larsen, P. S.
Number of pages: 6
Publication date: 1999

Publication information
Original language: English
Source: orbit
Source-ID: 172232

Numerical investigation of turbulent flow and heat transfer in channel with ribs
The performance of three different low-Reynolds number turbulence models has been explored for the benchmark test of fully developed (periodic) flow in a ribbed plane channel. Results are presented for two values of the Reynolds number (based on mean velocity and hydraulic diameter), \( \text{Re} = 37,200 \) and \( \text{Re} = 12,600 \), for which experimental data are available for the flow field and heat transfer, respectively. Comparison with experimental data includes the Nusselt number distribution along ribbed surface and profiles of mean velocity.

General information
Publication status: Published
Organisations: Department of Energy Engineering
Contributors: Myllerup, L., Larsen, P. S.
Pages: 391-398
Publication date: 1999

Host publication information
Title of host publication: Progress in Engineering Heat Transfer
Place of publication: Gdansk, Polen
Publisher: Institute of Fluid-Flow Machinery Publ.
Source: orbit
Source-ID: 174422
Research output: Chapter in Book/Report/Conference proceeding – Article in proceedings – Annual report year: 1999 – Research – peer-review
Bryozoan filter feeding in laminar wall layers: flume experiments and computer simulation

General information
Publication status: Published
Organisations: Department of Energy Engineering, University of Southern Denmark
Contributors: Larsen, P. S., Matlok, S., Riisgård, H. U.
Pages: 309-319
Publication date: 1998
Peer-reviewed: Yes

Publication information
Journal: Vie Milieu (Special Issue: Sediment-Water Interface)
Volume: 48
Original language: English
Source: orbit
Source-ID: 170640
Research output: Contribution to journal › Journal article – Annual report year: 1998 › Research › peer-review

Center Contract INTERFLOW: Status rapport No. 2 for the period 1-1-97 to 31-12-97

General information
Publication status: Published
Organisations: Department of Energy Engineering
Contributors: Larsen, P. S.
Publication date: 1998

Publication information
Original language: Danish
Source: orbit
Source-ID: 174402
Research output: Book/Report › Report – Annual report year: 1998 › Research › peer-review

Computational and Experimental Fluid Mechanics: Final report for period 1-1-93 to 31-12-97

General information
Publication status: Published
Organisations: Department of Energy Engineering
Contributors: Larsen, P. S.
Publication date: 1998

Publication information
Original language: English
Source: orbit
Source-ID: 174401
Research output: Book/Report › Report – Annual report year: 1998 › Research › peer-review

Computational results on test cases TC-2C and TC-2D; twodimensional, incompressible flows with recirculation

General information
Publication status: Published
Organisations: Department of Energy Engineering, Technical University of Denmark
Contributors: Schmidt, J. J., Scheel Larsen, P.
Pages: 103-110
Publication date: 1998
Peer-reviewed: Yes

Publication information
Journal: Notes on Numerical Fluid Mechanics
Volume: 65
Original language: English
Source: orbit
Source-ID: 169422
Mixing Studies in a 1:60 scale model of a cornerfired boiler with OFA

General information
Publication status: Published
Organisations: Department of Energy Engineering, Department of Informatics and Mathematical Modeling, Burmeister & Wain Scandinavian Contractor A/S
Contributors: Matlok, S., Scheel Larsen, P., Gjernes, E., Følum-Hansen, J.
Publication date: 1998

Host publication information
Title of host publication: CD proceedings of the 8th int symp on flow visualization
Publisher: Editors: Professor G M Carломагно, Università degli Studi di Napoli Federico II, Italy and professor I Grant, FLIC, Heriot Watt University, Edinburgh EH14 4AS, Scotland, UK
Source: orbit
Source-ID: 169424
Research output: Chapter in Book/Report/Conference proceeding > Article in proceedings – Annual report year: 1998 > Research > peer-review

Om at beregne og måle strømninger og hvirvler

General information
Publication status: Published
Organisations: Department of Energy Engineering
Contributors: Larsen, P. S., Sørensen, J. N., Michelsen, J. A.
Pages: 365-374
Publication date: 1998
Peer-reviewed: No

Publication information
Journal: Naturens Verden
Volume: 9
Original language: Danish
Source: orbit
Source-ID: 174400
Research output: Contribution to journal > Journal article – Annual report year: 1998 > Research

PIV and PLIF investigation of biomixing by model filter-feeders

General information
Publication status: Published
Organisations: Department of Energy Engineering
Contributors: Ullum, U., Adrian, R., Larsen, P. S.
Publication date: 1998

Host publication information
Title of host publication: Proceedings of the 9th International Symposium on Application of Laser Techniques to Fluid Mechanics, Lisbon, Portugal, 13-16 July
Source: orbit
Source-ID: 176154
Research output: Chapter in Book/Report/Conference proceeding > Article in proceedings – Annual report year: 1998 > Research

Statistical analysis and accuracy of PIV data

General information
Publication status: Published
Organisations: Department of Energy Engineering, Dantec Dynamics
Pages: 85-97
Publication date: 1998
Peer-reviewed: Yes
Synthesis of test cases TC-2C and TC-2D - Twodimensional incompressible flows past wall-mounted obstacles

Biomixing generated by benthic filterfeeders: A diffusion model for near-bottom phytoplankton depletion

Simulation of laminar flume flow past row of filter-feeding bryozoa (ectoprocts) - A preliminary report

Skin-friction and turbulent data for low Renumber bump-on-wall test case

Statistical analysis and accuracy of PIV data
Temporal evolution of the perturbed and unperturbed flow behind a fence: PIV analysis and comparison with LDA data

**General information**
Publication status: Published
Organisations: Department of Energy Engineering, Dantec Dynamics
Publication date: 1997

**Host publication information**
Title of host publication: Proceedings of the 7th International Conference on Laser Anemometry Advances and Applications
Source: orbit
Source-ID: 169346
Research output: Chapter in Book/Report/Conference proceeding › Article in proceedings – Annual report year: 1997 › Research › peer-review

Biologiske filter-pumper

**General information**
Publication status: Published
Organisations: Department of Energy Engineering, University of Southern Denmark
Contributors: Riisgård, H. U., Larsen, P. S.
Pages: 307-318
Publication date: 1996
Peer-reviewed: Yes

**Publication information**
Journal: Naturens Verden
Volume: 8
Original language: English
Source: orbit
Source-ID: 164627
Research output: Contribution to journal › Journal article – Annual report year: 1996 › Research › peer-review

LDA-study for modelling flows through screens

**General information**
Publication status: Published
Organisations: Department of Energy Engineering
Contributors: Ullum, U., Frederiksen, J., Akoh, E., Finderup Nielsen, N., Scheel Larsen, P.
Publication date: 1996

**Host publication information**
Title of host publication: Proceedings of the Eight International Symposium on Applications of Laser Techniques Place of publication: Lisbon
Source: orbit
Source-ID: 165862
Research output: Chapter in Book/Report/Conference proceeding › Article in proceedings – Annual report year: 1996 › Research › peer-review

Models for phytoplankton depletion above benthic filter-feeders

**General information**
Publication status: Published
Organisations: Department of Energy Engineering
Contributors: Larsen, P. S.
Publication date: 1996
Peer-reviewed: No

**Publication information**
Journal: Abstract of Workshop
Original language: English
On the striping phenomenon in ultrafiltration

General information
Publication status: Published
Organisations: Department of Energy Engineering
Contributors: Larsen, P. S.
Publication date: 1996
Peer-reviewed: No

Publication information
Journal: Abstracts, IUTAM Symposium Kyoto 1996
Original language: English
Source: orbit
Source-ID: 164629
Research output: Contribution to journal – Journal article – Annual report year: 1996 – Research

Particle capture in the mussel Mytilus edulis: role of latero-frontal cir

General information
Publication status: Published
Organisations: Department of Energy Engineering, University of Southern Denmark, Technical University of Denmark
Contributors: Riisgård, H. U., Nielsen, N. F., Larsen, P. S.
Pages: 259-266
Publication date: 1996
Peer-reviewed: Yes

Publication information
Journal: Marine Biology
Volume: 127
Original language: English
Source: orbit
Source-ID: 164628

Phytoplankton reduction in near-bottom water caused by filter-feeding Nereis diversicolor - Implications for worm growth and population grazing impact

Studies of vertical profiles of phytoplankton in the field combined with laboratory experiments demonstrated that reduction in phytoplankton concentrations in the near-bottom water layer, 5 to 10 cm in thickness on calm days, may play a significant role for the filter-feeding polychaete Nereis diversicolor in realizing its grazing capacity (estimated at 13.8 m3 m-2 d-1 in the shallow bay of Kertinge Nor, Denmark, in July 1994). Field-growth experiments were performed with worms transferred to U-shaped glass tubes placed at different heights (0, 4, 10 and 20 cm) above the seafloor. A considerably reduced specific growth rate of worms at the sea floor (0.2 ± 1.1% d-1), compared to worms elevated just 10 cm above the sediment surface (2.5 ± 0.8% d-1), indicates that extremely meagre food conditions may be prevailing at the bottom. Experimental laboratory data on the development of vertical algal cell profiles were compared with predicted values obtained by means of a simple diffusion model.

General information
Publication status: Published
Organisations: Fluid Mechanics, Department of Mechanical Engineering
Contributors: Larsen, P. S., Riisgård, H. U., Poulsen, L.
Pages: 47-54
Publication date: 1996
Peer-reviewed: Yes

Publication information
Journal: Marine Ecology - Progress Series
Volume: 141
ISSN (Print): 0171-8630
Original language: English
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Phytoplankton reduction in the bottom-near water caused by filter-feeding polychaete Nereis - implications for worm growth and population grazing impact

General information
Publication status: Published
Organisations: Department of Energy Engineering, University of Southern Denmark
Contributors: Riisgård, H. U., Poulsen, L., Larsen, P. S.
Pages: 47-54
Publication date: 1996
Peer-reviewed: Yes

Publication information
Volume: 141
Original language: English
Source: orbit
Source-ID: 164626

Progress report no.5 for period Jan.1 to Dec.31, 1996: STVF Framework Program: Computational and Experimental Fluid Mechanics

General information
Publication status: Published
Organisations: Department of Energy Engineering
Contributors: Larsen, P. S.
Publication date: 1996

Publication information
Original language: English
Source: orbit
Source-ID: 164631

Particle Motion in Unsteady Three-Dimensional Flow at Low Reynolds Numbers

General information
Publication status: Published
Organisations: Department of Mechanical Engineering, Fluid Mechanics
Contributors: Mayer, S., Larsen, P. S.
Publication date: Sep 1994

Publication information
Place of publication: Kgs. Lyngby, Denmark
Publisher: Technical University of Denmark (DTU)
Original language: English
(AFM; No. 94-04).
Electronic versions:
Mayer.PDF
Source: orbit
Source-ID: 275334
Surface Description Using Bicubic B-splines: Curvature Based Smoothing of Plane Cubic B-spline Curves

General information
Publication status: Published
Organisations: Fluid Mechanics, Department of Mechanical Engineering, Technical University of Denmark
Contributors: Hvid, S. L., Larsen, P. S., Sørensen, J. N.
Publication date: 1993

SUSPENSION-FEEDING IN MARINE SPONGES HALICHONDRIA-PANICEA AND HALICLONA-URCEOLUS - EFFECTS OF TEMPERATURE ON FILTRATION-RATE AND ENERGY-COST OF PUMPING

Filtration rate (measured as clearance of algal cells) was measured at different temperatures in the sponge Halichondria panicea. An increase in water temperature from 6 to 12-degrees-C caused the mean filtration rate to increase 4.3 +/- 2.3 times. This value was higher than previously found for other marine ciliary suspension-feeding animals. Filtration rate at 12-degrees-C was also measured in Haliclona urceolus by means of an indirect clearance method in addition to a direct technique for measuring pumping rate. It was found that the 2 sponge species had near-identical filtration rates, with maximum rates of approximately 60 ml min-1 (g dry weight)-1 at 12-degrees-C. The normal pump pressure, or operating point O(p), of a standard sponge (based on our own measurements and calculations from literature data for a 0.1 g dry weight Haliclona sp.) was estimated as the sum of main contributions to head losses along the flow path from entry (ostia) to exit (osculum). The head losses were as follows: ostia 0.0373 mm H2O; inhalant canal 0.1205 to 0.013 mm H2O; prosopyles 0.1153 to 0.02321 mm H2O; collar-filter 0.122 mm H2O; exhalant canals = inhalant canals; and osculum 0.1576 mm H2O. The (maximal) O(p) was found to be 0.673 mm H2O and the power output P(p) from the sponge pump was 0.677 μW. The pump work, defined as P(p)R-1 where R is the respiratory output, was 0.85 %. The low energy cost of filtration and the temperature effect are discussed and compared with recent data for other ciliary suspension feeders. It is argued that passive current-induced filtration may be of insignificant importance for sponges.

FILTER-NET STRUCTURE AND PUMPING ACTIVITY IN THE POLYCHAETE NEREIS-DIVERSICOLOR - EFFECTS OF TEMPERATURE AND PUMP-MODELING

General information
Publication status: Published
Organisations: Fluid Mechanics, Department of Mechanical Engineering
Pages: 177-188
Publication date: 1993
Peer-reviewed: Yes

Publication information
Journal: Marine Ecology - Progress Series
Volume: 96
Issue number: 2
ISSN (Print): 0171-8630
Original language: English
Electronic versions:
Larsen4.pdf

Bibliographical note
Copyright (1993) Inter-Research
Source: orbit
Source-ID: 251426
Electron micrographs of the filter-net structure in the facultatively suspension-feeding polychaete Nereis diversicolor O. F. Muller showed that the net is composed of an irregular mesh-work made up of long, relatively thick filaments (up to 300 nm) interconnected with a variety of shorter and thinner filaments. The thinner filaments range in diameter from 5 to >25 nm. The average size of the meshes, measured directly on the micrographs, lies between 0.5 and 1.0-μm, but due to shrinkage the values represent only about 75% of the actual dimension of the intact net. The effects of temperature on water processing were measured as clearance of suspended algal cells or measured directly. Pumping activity (undulating body movements of worms kept in glass tubes) was monitored using an infrared phototransducer technique. In the temperature interval from 5 to about 15-degrees-C there was a linear increase in clearance, and a doubling of the temperature was followed by a doubling in clearance. Direct measurements of pumping rate showed that high stroke frequency was correlated with high pumping rate. A doubling of temperature from 13 to 23-29-degrees-C led to a doubling of the stroke frequency and a halving of the net cycle length. At low temperatures a tendency towards an extended pause between pumping periods was noticed. The N. diversicolor pump was modelled as a positive displacement leaking unit, and earlier data on back pressure characteristics were examined in light of the proposed model. The pump model prediction of temperature dependence showed reasonably good agreement with experimental data. The consequences of leaving out the effect of viscosity or stroke frequency in the pump model were evaluated. Clearly, the temperature effect as related to viscosity is negligibly small in the N. diversicolor muscular positive displacement pump (unlike for viscous ciliary pumps).
Numerical Simulation of 3-Dimensional Flow in Straight and Curved Ducts of Rectangular Cross Section

General information
Publication status: Published
Organisations: Department of Energy Engineering, Fluid Mechanics, Department of Mechanical Engineering
Contributors: Gervang, B. G., Larsen, P. S.
Publication date: 1989

Publication information
Place of publication: Kgs. Lyngby, Denmark
Publisher: Technical University of Denmark (DTU)
Original language: English
(AFM; No. 89-09).
Electronic versions:
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Source: orbit
Source-ID: 275323

Three-Dimensional Electro-Fluid-Dynamics in Tuft Corona Wire-Plate Precipitations

General information
Publication status: Published
Organisations: Fluid Mechanics, Department of Mechanical Engineering, Technical University of Denmark
Contributors: Sørensen, L. S., Larsen, P. S.
Publication date: 1989

Publication information
Place of publication: Kgs. Lyngby, Denmark
Publisher: Technical University of Denmark (DTU)
Original language: English
(AFM; No. 89-03).
Electronic versions:
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Presentation of test cases TC-2A, TC-2B, TC-2C, TC-2D - Twodimensional, incompressible, wall flows with separation

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Organisations: Department of Energy Engineering
Contributors: Scheel Larsen, P.
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Three-Level, Viscous-Inviscid Interaction Technique for the Prediction of Separated Flow Past Rotating Wing

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Contributors: Sørensen, J. N., Larsen, P. S., Pedersen, B. M., Jensen, J. T.
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Velocity and Turbulence Distributions in Cyclone

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Organisations: Fluid Mechanics, Department of Mechanical Engineering, Technical University of Denmark
Contributors: Qing, X. H., Larsen, P. S.
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A non-Gaussian model of turbulence (soccer-ball integrals)
The statistics of the time evolution of a nonlinearly coupled system of first-order equations representing the Euler equations is studied. The probability distribution of functions is nearly Gaussian, while that of their time derivatives has exponential tails and moments of order 4, 6, and 8 that approach those of the exponential distributions. Physics of Fluids is copyrighted by The American Institute of Physics.

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