Studying Swarms in the Field: The Next Step in an Ongoing Biophysics Project

A Proposal to the Research, Scholarship, and Creativity Fund

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Professor of Physics

Results of past RSC grant (Funded 2002)

The last RSC grant that I received was 10 years ago and provided partial support that enabled the PI (Saulnier) and an undergraduate student (Amit Bohara) to conduct biophysics research at Gustavus Adolphus College during the summer of 2002. The project undertaken was computational in form and consisted of developing analysis techniques and corresponding software to allow the study of collective animal behavior in nature. Specifically, analysis techniques and corresponding software were successfully developed and demonstrated using computer simulations. This analysis software permits researchers to study the swarming behavior of organisms using techniques borrowed from statistical physics. The 2002 RSC grant provided seed money to begin this new student-faculty research initiative. After the successful completion of the 2002 RSC grant, the newly developed analysis techniques and software were ready to be applied in a laboratory setting. In subsequent years, this next step was successfully accomplished by applying these analysis techniques and software to, first, inanimate objects resulting in a publication in a physics journal (***The American Journal of Physics***, Young, *et al.*, 2004) and, second, living organisms resulting in a publication in a biology journal (***Limnology and Oceanography Methods Journal***, Young, *et al.* 2006) (complete references below). Additionally, several presentations were made at national and regional conferences in both physics and biology. Hence, the 2002 RSC grant provide funds which directly led to a new research program that has been productive and beneficial for both the PI and undergraduate students (all presentations and publications involved undergraduates as co-authors, indeed many listing undergraduates as lead authors). The next step in this biophysics research program is to take this new technique and apply it in the field. This is the focus of this current RSC request and ideas behind this research are more fully developed below.

Description of Project

Introduction

Anyone who has observed a flock of birds swirl as a coordinated unit across the sky, or a school of fish flash in synchrony through the water, is aware of the behavioral aspects of animal aggregations. Nature is characterized by organisms that form aggregations. Sometimes these aggregations are temporary, such as birds congregating in a noisy flock on a birdfeeder and then scattering when the food has been depleted. Others are more long lasting, such as the herds of caribou that migrate across the Arctic. Some aggregations occur on scales of millimeters, such as the clusters of flagellated algae that form within the water column of a lake or ocean, while others occur on much larger spatial scales, such as schools of fish covering hundreds of meters. All of these aggregations, however, have one thing in common – the formation of the aggregation is the result of the collective behaviors of the individuals.

Zooplankton have traditionally been viewed as passive inhabitants of their environment, their movements controlled by the fluid environment in which they live. Their very name, plankton, derived from the Greek *planktos* (drifting), reflects this perception of animals moved by their environment, rather than moving within it. Consequently, the spatial and temporal patchiness, which characterizes the distribution of plankton, has been assumed to result from spatial and temporal variations in water movements and properties acting to concentrate or disperse organisms. However, it is now recognized that most zooplankton species possess an impressive repertoire of sophisticated behaviors, including directed swimming behaviors. Therefore, while the physical characteristics of the environment may play an important role in the location and nature of zooplankton aggregations, research suggests that both the formation and the maintenance of these aggregations also have strong behavioral components (Ohtsuka *et al.*, 1995; Ribes *et al.*, 1996; Waife & Frid 1996; Buskey 1998, 2000).

Purpose
The proposed research will utilize an analytical technique (recently applied for the first time to ecological problems by Saulnier and undergraduate co-investigators; Younge *et al.*, 2006) to describe the size, structure, and cohesiveness of zooplankton swarms and the influence of environmental factors on swarm dynamics. This research will build upon laboratory investigations conducted by Saulnier and his undergraduate assistants of the swarming behaviors of populations of *Brine shrimp* and *Ostracods*. These investigations indicate that swarming behavior is highly influenced by environmental cues. The dynamic nature of the swarms coupled with the behavioral characteristics of zooplankton species make them an excellent model organism for the application of the new analytical technique and for developing a behavioral model that may serve as a template for other swarming species. Because zooplankton swarms are structurally and behaviorally similar to schools of fish or flocks of birds, the results of this study are applicable to larger vertebrates. Thus, this project will contribute to the current state of understanding of the behavior of grouped organisms in general.

Here we propose to use the recently developed analytical technique to describe aggregations and aid in the development of descriptive behavioral models of the species being studied. The power of this technique lies in the fact that it does not require tracking each individual member of an aggregation; ***rather it provides a quantitative description of the structure of the aggregation (based solely on the pattern of the aggregation as a whole) from which the behavioral characteristics of the individual members may be inferred.*** Furthermore, as it provides information about all locations within an aggregation (and not just a single number used to describe the whole aggregation) it enables one to perceive, describe, and compare patterns or swarm sub-structures that are not immediately obvious visually.

The technique described here uses radial distribution and pair-correlation functions to quantitatively describe the structure and dynamics of an aggregation. Although these functions, and the associated analytical techniques, have traditionally been used by physicists to study inert particles, we will apply them to the study of grouped organisms. The radial distribution function provides information on how individuals are distributed across increasing distances from a central individual in an aggregation. It yields a local measure of how close the observed distribution is to a uniform one (i.e. a distribution where all positions are equally likely). The pair correlation function, on the other hand, provides a measure of the spatial variation of the influence that one group member exerts on others in terms of both the magnitude and direction (i.e. a positive or negative influence) of this spatially varying influence. Together these functions provide information about the average distance over which one swarm member may influence another, referred to as the correlation length.

As a concrete example of the information provided by these functions, consider a large room (e.g., a gymnasium) filled with people, all wearing blindfolds and walking in random directions throughout the room. Viewed from above, the people appear to be a dynamic two-dimensional swarm. This "swarm" could be photographed and analyzed using radial distribution and pair-correlation functions. These functions may be used to infer the behavioral characteristics of a typical swarm member as well as its influence on other members of the swarm. For example, in this case, because all members are blindfolded, they are able to sense and respond to the presence of another individual in the swarm only when they come in direct contact with each other, a fact that would be reflected in the resulting analyses. These analyses would also provide information on indirect interactions between swarm members. That is, when two group members collide, the collision affects not only their motion but also that of their neighbors, which will, in turn, influence the motion of more distant swarm members. The range, strength, and direction (positive or negative) of this indirect influence depends not only on the number of people in the "swarm" but also on their common behavioral characteristics (e.g., in this case, the fact that all of the people are blindfolded). The radial distribution and pair-correlation functions together provide a measure of how this influence or correlated behavior varies with position within the swarm. Locations within the swarm where the correlation values are negative indicate regions that are less likely to be occupied by a swarm member, while locations with positive correlation values are more likely to be occupied.

Now imagine how swarm structure and dynamics would change if we repeated this exercise using people who were not blindfolded. As in the example above, the group members are walking about the room in random directions. However, in this case, because they now have the benefit of sight, each group member will try to maintain a "personal space" by avoiding collisions before they take place. Whereas in the previous example an individual's effective space (the distance over which direct interactions take place) was equal to the individual's actual physical size, in this second scenario the effective size of an individual is greater than their actual physical size. The effect of this increased size will propagate outward from an individual through interactions with neighbors such that the range and strength of the influence of a single individual will be greatly enhanced. Thus, because of differences in the behavioral characteristics of the group members, a low density swarm whose members can perceive and react to the presence of other members from a distance may behave like a much higher density swarm whose members are blindfolded and can only perceive and interact with other members through direct contact. The exact shape of the radial distribution and pair-correlation functions for sighted swarms would depend on such factors as their visual acuity and their sense of acceptable "personal space", factors which may be influenced by environmental conditions. For example, if a fire suddenly broke out in one corner of the room, the people would rapidly move away from it and their notion of acceptable "personal space" would be greatly altered as they crowd around the exit. This would have a profound influence on the corresponding radial distribution and pair-correlation functions and the related swarm correlation length. Indeed, it is this influence that allows researchers to use ***global changes in group structure in response to external stimuli to infer the behavioral characteristics of the individuals comprising the aggregation (without tracking these individuals). This is the ultimate purpose of the proposed work.***

Radial distribution and pair-correlation functions may be computed for a variety of systems exhibiting group behavior by using videographic analysis. The basic procedure consists of recording a time-lapse video of the system under study (living or inanimate), extracting group member locations from each frame (without the need to track the specific motion of individuals from frame-to-frame), computing the radial distribution function for each frame, and finally averaging these results over many frames. For a more detailed description of the experimental procedure (should the committee wish) and some preliminary results (with cool videos and graphs) see, http://physics.gac.edu/~psaul/Swarm/ .

Project Design

Coral reef ecosystems are among the world's most complex, biologically diverse, and beautiful ecosystems. Although they occur only within a very restricted range, being limited to shallow marine waters between 30º N and 30º S of the equator, they have great economic as well as biological importance. They act as the spawning grounds for many commercial fish species, support a multi-billion dollar tourist industry, are a source of many new life-saving medicines, and function as a protective barrier to storms for islands and coastal areas. It is estimated that reef fish and mollusks feed 30-40 million people per year. In addition, they play an important role in sustaining biological diversity, global biogeochemical cycles, and the economies of many countries. Despite the recognized importance of these ecosystems, over 2/3 of the world's coral reefs are currently in decline or threatened. Human impacts to coral reefs include pollution by sewage and other contaminants, depletion of rare species to supply hobbyists, introduction and rapid spread of diseases, overfishing, harmful harvesting techniques (e.g. explosives, poisons), and accelerated sedimentation due to poor forestry, agricultural, and construction practices.

Human disturbances are not the only impacts to which coral reefs are subjected. The greatest natural impact on coral reefs is due to hurricanes. Although hurricanes can indeed cause major physical damage to the reef, reef ecosystems have evolved mechanisms to recover from such disturbances, much as plants have evolved mechanisms to survive in fire-prone regions. However, human disturbances have affected the ability of the reefs to recover from such damage. For example, Jamaican reefs suffered little long term damage from hurricanes until Hurricane Allen in 1980. After the hurricane, the staghorn coral (*Acropora cervicornis*) began to die off as white line disease spread through the population. Shortly after, the abundant sea urchin, *Diadema antillarum*, began to die off as a virus spread through that population. These combined impacts marked the initiation of a major deterioration of Jamaican coral reefs. The loss of the urchins, an herbivore, allowed algae to grow and spread over the reef, smothering the living corals and preventing new corals from settling.

The consequences of Hurricane Allen are a reflection of the complex interactions that exist among the organisms that inhabit the coral reef. Grazing fish and urchins keep algae from overrunning the corals, while other algae live symbiotically within corals. Like the relationship between coral and algae, there are undoubtedly innumerable intricate relationships that exist between a variety of reef organisms which are critical to the viability of the coral reef ecosystem, yet remain to be elucidated. One relationship that has recently come to light is the association between mysids and the longfin damselfish.

Mysids are small, crustacean zooplankton typically found in marine and freshwater environments. A unique aspect of their biology is their tendency to form schools that are strikingly similar in cohesiveness, precision of locomotion, and anti-predation responses to those formed by fish. Even more striking is the frequency with which mysid swarms are located within the territories of damselfish.

While there has been a number of publications that suggest the anti-predation advantages of schooling behavior and/or mathematically modeled the costs and benefits of schooling, there has been no work that has directly tested the advantages of schooling within a fish territory or the advantage to the fish of having a swarm in its territory. Damselfish are extremely territorial, aggressively defending their territories from egg predators, such as the bluehead wrasse and brittlestars. Because many egg predators are also planktivores, the damselfish territory may act as a refuge to the mysids, offering protection from these predators. There is also the possibility that the fish may gain an advantage by having a mysid swarm in its territory. Damselfish have an interesting social system in that the male establishes and defends a territory on which the eggs are laid and develop. Females visit the territories to lay their eggs, after which they disperse, leaving the males to guard the eggs from egg predators. One obvious measure of quality (both of the male and the territory) is the ability of the male to defend the eggs. A female would not want to risk depositing her eggs with a male who would be incapable of defending them from harm. It is possible that mysids give an indication of "quality" – if the male damselfish can keep other predators from eating the mysids, then he might also be able to successfully defend her eggs and offspring from predators. The mysids might also give another advantage to the damselfish and his offspring – the mysids might act as a distracter, drawing the attention of potential egg predators.

The proposed research will focus on this association between mysids and the longfin damselfish, investigating the adaptive value of schooling to the mysid (e.g. as an anti-predation strategy) and the adaptive value to the fish of having a swarm located in its territory (e.g. as an indication of habitat quality), using a combination of observation and experimentation under field conditions. Preliminary data suggest that there is a strong anti-predator benefit to swarming within a damselfish territory. Mysids presented to a damselfish on a territory that lacks a swarm are immediately ingested by that damselfish; however, swarms associated with damselfish territories are not attacked by the damselfish and potential predators that approach the territory are driven away by the damselfish. These observations also raise important questions about swarm formation (e.g. if damselfish that do not have a swarm in their territory eat mysids that enter their territory, how does a swarm get established in a territory without getting eaten?) Obviously, if the swarm is as beneficial to the fish as it is to the mysid, the process of swarm formation is also an important component to this relationship. ***Will the differences in swarms formed with and without the influence of damselfish exhibit the same spatial characteristics and individual mysid behavior? By applying the analytical techniques and software developed at Gustavus, to swarms observed in the field these questions may be able to be answered in a detailed way.***

The proposed field research will be conducted at the Discovery Bay Marine Laboratory, Jamaica (with Saulnier's long time biology co-investigator, Dr. Nancy Butler – see the feasibility section below), over a two week period during the summer of 2012. During the first week of the study, we will identify for study 10 damselfish territories associated with mysid swarms, 10 damselfish territories lacking mysids, and 10 mysid swarms not located in a damselfish territory. Each will be video-taped for a minimum of 30 minutes and the tapes reviewed to establish the behavioral patterns of the fish and/or mysids in each and to record the nature of predation events. Predation events will be scored as either unsuccessful or successful based upon whether eggs and/or mysids if are successfully taken by predatory fish. In addition, the type of predator will be noted. These observations will provide the baseline against which the experimental results will be compared. We will video and monitor one territory with a swarm and one swarm without a damselfish separately over a 24 hour cycle to establish the diurnal pattern of swarm dispersal and establishment. There are no data on diurnal patterns of swarm formation and behavior. Preliminary studies indicate that the swarms break up and disperse at night, but the process of swarm formation has yet to be established. The patterns of swarm formation and dispersal have profound implications with respect to inter-swarm dynamics and interactions and mysid-damselfish interactions. Any information that we can collect on these diurnal patterns will be novel and provide new insight into the dynamics of such swarms and their role in the coral reef trophic system.

During the second week of the study, a set of manipulation experiments will be conducted to test the association between swarm presence and predation risk to mysids and damselfish eggs and the behavior of the mysids when there is the risk of predation. All of these manipulations will be conducted on damselfish territories that have swarms associated with them and swarms lacking damselfish. A minimum of 10 replicates will be conducted for each manipulation and each will be recorded for 30 minutes. For the first manipulation, all mysids will be removed from a territory. This will test the benefit of the mysids to the fish in protecting his eggs from predators. For the second manipulation, the fish will be removed from its territory. This will test for the ability of the mysids to distract potential predators from the eggs when the male isn't present to defend his nest. In the third manipulation, both the fish and the mysids will be removed from the territory to estimate predation risk to the eggs in the absence of any protection or alternate prey. For the fourth manipulation, a predatory fish will be placed in a clear bottle and placed in the vicinity of a mysid swarm located in a damselfish territory. This will test the behavioral response of the swarm to the presence of a potential predator when the damselfish defender is present. For the fifth manipulation, a predatory fish will be placed in a clear bottle and placed in the vicinity of a mysid swarm that is not in a damselfish territory. This will test the response of the swarm to the presence of a potential predator when no defender is present. For each of these experiments, the predation attempts and success and behavioral responses of the fish and mysids will be recorded and the data compared to the pre-manipulation observations made during week one, as outlined above. The recorded videos will then be analyzed (mostly at Gustavus) using the previously developed software and techniques.

It is anticipated that the proposed experiments will increase our knowledge of the particular zooplankton species studied (mysids), serve as model study whose results may be applied to other animals that exhibit aggregated behavior, and illustrate the utility of a novel application to ecology of an analytical technique traditionally used by physicists to study inert particle dynamics. Other tangible anticipated outcomes include at least one presentation at an international meeting; the American Society of Limnology and Oceanography (despite the name it is indeed an international meeting and is often held outside of the U.S.) and at least one publication in a refereed journal (either the Journal of Limnology & Oceanography or the Journal of Plankton Ecology). The initial dissemination of results (both presentation and publication) will focus on describing the observed behavioral differences in swarming characteristics in response to various environmental cues and, using the analytical techniques, infer the behavioral characteristics of the individual organisms that are responsible for the observed global pattern change.

Feasibility

What qualifications do you bring to this project?

As the text above indicates, the PI has been working on this biophysics project for 10+ years. This is a long term project with tangible outcomes being produced along the way. The PI has the necessary analytical and computational skills and in experienced in collecting data in the laboratory setting. For this field work phase of the project, the PI will work closely with his long time biology co-investigator Dr. Nancy Butler (a former member of the Biology department at Gustavus who is now at University of Pennsylvania, Kutztown). Her expertise is critical and she will be involved in all aspects of the proposed field work. It should also be noted that Nancy has already secured funding to support her portion of the proposed field work.

What have you done to prepare for this project?
Analytical and computational tools have been developed and applied to inanimate and living systems resulting in publications and presentations as described above. We now have lots of experience at Gustavus in analyzing videographic data of swarms.

What is the time period?
The proposed field work will be conducted during June 2012. The resulting videographic data will be analyzed during the 2012/13 academic year. Additionally, some laboratory model systems may be investigated and that data analyzed (growing, filming, and analyzing swarms in a Gustavus lab).

Is the work's scope commensurate with the time period of the project?
Yes.

References

Buskey, E. J. 1998. Energetic cost of position-holding behavior in the planktonic mysid *Mysidium columbiae*. Mar. Ecol. Prog. Ser. 172: 139-147.

Buskey, E. J. 2000. Role of vision in the aggregative behavior of the planktonic mysid *Mysidium columbiae*. Mar. Biol. 137: 257-265.

Ohtsuka, S., H. Inagaki, T. Onbe, K. Gushima, and Y. H. Yoon. 1995. Direct observations of groups of mysids in shallow coastal waters of western Japan and southern Korea. Mar. Ecol. Prog. Ser. 123: 33-44.

Ribes, M., R. Coma, M. Zabala, and J.M. Gill. 1996. Small-scale spatial heterogeneity and seasonal variation in a population of a cave-dwelling Mediterranean mysid. J. Plankton Res. 18: 659-671.

Wiafe, G. and C.L.J. Frid. 1996. Sort-term temporal variation in coastal zooplankton communities: the relative importance of physical and biological mechanisms. J. Plankton Res. 18: 1485-1501.

Young, K., C. Christenson, A. Bohara, J. Crnkovic, and P. Saulnier. 2004. A Model System for Examining the Radial Distribution Function. Amer. J. of Physics, 72, # 9.

Younge, K., B. Johnston, C. Christenson, A. Bohara, J. Jacobson, N. Butler, and P. Saulnier. 2006. The use of radial distribution and pair-correlation functions to analyze and describe biological aggregations. J. Limnology and Oceanography Methods 4: 382-391.

Research, Scholarship, and Creativity Grant

Deadline February 10th

Please complete this checklist and attach it as the cover page of your grant application, whether you submit electronically or via hard copy.

Faculty Information

Name: **Paul Saulnier**

Dept: **Physics**

Email: PSAUL@GUSTAVUS.EDU

Rank: **Professor**

Checklist

X Description of previous projects (and outcomes) funded by RSC grants

X Complete project description, including separate statements of:

1. **Purpose.** What are the intellectual, conceptual, or artistic issues? How does your work fit into other endeavors being done in this field?

2. **Feasibility.** What qualifications do you bring to this project? What have you done/will you do to prepare for this project? What is the time period, i.e. summer, summer and academic year, academic year only? Is the work's scope commensurate with the time period of the project?

3. **Project Design.** This should include a specific description of the project design and activities, including location, staff, schedules or itineraries, and desired outcomes.

X RSC Budget Proposal Form

X If successful, my proposal can be used as an example to assist future faculty applications. This decision will not in any way influence the evaluation of my application. Check box to give permission.

Submission instructions

Electronic — Submit a single document containing the entire application to rsc-proposals@gustavus.edu.

Budget Justification

The research will be conducted over a ten day period during June 2012 at the Discovery Bay Marine Laboratory. The lab is operated by The University of the West Indies and provides all facilities required for this project, including wet and dry labs, boats, dive facilities, and housing. Funds are requested for the following:

Airfare to and from Jamaica for the PI: Estimated at $750 (est. provided by Expedia).

Rental car while in Jamaica: The research station is rather remote and will not be providing meal service. Further, the station does not provide transportation for visiting researchers. Therefore, a rental car will be needed for transport to/from the airport and for running errands to buy groceries and research supplies not transported from the states. Rental fee for a compact car for 10 days is estimated at $600 (est. provided by Montego Bay Airport Car Rental).

Housing, wet lab, and boat fees: Housing for PI staying on site in a bedsitting room is $38/day. Wet lab fees are $50/day for PI. Boat fees (for a 3 passenger run-about) are $10/day (this is the least expensive boat and more than adequate).
Housing and fee total = 10 x $98 = $980

Food allowance: $20 per day. Food total = 10 x $20 = $200

Field Supplies: Fish bottles (for introducing predatory fish to mysid swarms) – clear acrylic tubing (3in diameter), $70
Field books (water proof books for recording data in the field), $20
Fish nets (aquarium nets for catching and removing damselfish and mysids), $20
Fish nets (drop nets for capturing predatory fish), $50
Preservative (for preserving samples of mysids from swarms for species verification), $35
Supply total = $70 + $20 + $20 + $50 + $35 = $195

NAME: Paul Saulnier, Physics

STIPEND (Please check one box to indicate your distribution preference)
*Note: The RSC grant will fund up to 1,500 towards Project Costs***.** *If your project costs will exceed this amount, you may opt to apply a portion (or all) of your stipend to cover these additional costs. If this option is your preference, please select "Partial Amount".*

X **Full Amount (**$500-full professor)

Please Note:
Since the cost of the project exceeds $1500, I will use my stipend to pay for project costs beyond $1500. The remaining cost of the project will be supplemented with personal funds as necessary.

PROJECT COSTS: List each item individually with its cost. Attach additional sheets if necessary.	**Project Costs Amount**
I. Equipment (e.g. transcription machine, camera, digital recorder—but not computer hardware)	*I. Equipment*
1. None	1. $0
2.	2.
3.	3.
II. Materials (e.g. books, printing, software, lab supplies)	*II. Materials*
1. Field supplies (see page above)	1. $195
2.	2.
3.	3.
III. Personnel (e.g. typist, transcriptionist, student assistant)	*III. Personnel*
1. None	1. $0
2.	2.
3.	3.
IV. Travel (cannot include conference travel, see http://gustavus.edu/finance/travel.php for allowable expenses)	*IV. Travel*
1. Airfare	1. $750
2. Rental Car	2. $600
3. Lab fees, boat fees, housing, and food allowance	3. $1180

TOTAL PROJECT COSTS	**$2725**
TOTAL AMOUNT REQUESTED (Total Project Costs + Stipend)	**$2000**

(*Note: The RSC grant will fund up to an amount equal to your Full Stipend + 1,500 for Project Costs*)