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## A mosaic of diverse ideas: The ecological legacy of J. Frederick Grassle

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## ABSTRACT

During the 40 years (and counting) of his scientific career, J. Frederick Grassle has made fundamental contributions to our understanding of marine ecosystems from coral reefs to deep-sea sediments. His advocacy and passion for marine biodiversity in the form of myriad groundbreaking studies and influential reviews, his generosity of ideas and capacity to catalyze and inspire those working with him as well as the science community in general, his breakthroughs in improved ocean observation, his marine science infrastructure initiatives, together with his tireless persistence, have helped lead to major shifts in approaches to marine science and the shape of modern ocean studies to one that favours multidisciplinary research, teamwork, continuous, long-term observation, in situ experimentation, recognition of the importance of marine biodiversity, and global cooperation on research and data sharing. In shallow-water ecology, he co-discovered sibling species of *Capitella* spp., important not only because it is a key pollution indicator but also because the work helped to pave the way for the discovery of numerous sibling species in other taxa with major ramifications for ecological understanding. He was also a key player in the West Falmouth oil spill study which, along with complementary mesocosm experiments, remains one of the most important and detailed studies of its kind. He was also a lead player in the first biological expedition to hydrothermal vents and wrote the seminal articles that helped to inspire the flurry of vent research that followed. He is perhaps best known for his deep-sea work, where he brought submersibles to the forefront as a sampling tool, brought experimental manipulative studies to the primarily descriptive discipline of deep-sea benthic ecology, and generated tremendous excitement, debate, and rekindled interest in marine biodiversity with the first quantitative estimate of global deep-sea diversity. His efforts to document marine biodiversity resulted in the international Census of Marine Life, and his emphasis on the need for continuous, long-term ocean observation has led to breakthroughs in international cooperation in cabled observatories such as LEO-15. These efforts have also enhanced efforts to integrate ocean data on a global scale in platforms such as the Ocean Biogeographic Information System (OBIS). The diversity of his contributions to marine science mirror the immense marine diversity he has recognized, documented, and championed so effectively over the last four decades.

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## 1. Introduction

Our appreciation of marine ecological diversity has changed dramatically in the last 40 years, not only in terms of our understanding of the oceans but in the way that we sample them in space and time (e.g. Levin et al., 2001; Snelgrove and Smith, 2002; National Research Council, 1995). Many of these new perspectives owe a great deal to the ideas and perseverance of J. Frederick (Fred) Grassle, for whom this special volume has

been organized. The papers that comprise this volume focus primarily on deep-sea ecosystems, where Fred's impact has been tremendous, but his legacy extends to all reaches of the ocean. His most influential and widely-cited papers focus on the diversity of shallow-water and deep-sea systems, but his tireless advocacy for expanded research in marine biodiversity, improved ocean observation, and metadata cooperation have led to major new programs that extend from microbes to leviathans, and from intertidal regions to the oceanic abyss (Table 1). Fred's vision has shaped marine ecology through his publications and has influenced the broader discipline of oceanography in multiple ways through the development of broad, international research initiatives and the establishment of a major research institute in

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**Table 1**  
Major contributions by J.F. Grassle to marine sciences.

| Contribution  | Ramifications   | Reference   |
|---|---|---|
| Patch Mosaic Model  | Major conceptual model for deep-sea diversity   | Grassle and Sanders (1973)  |
| Coral cryptofauna diversity   | Immense diversity of coral reef invertebrates documented  | Grassle and Grassle (1974)  |
| Deep-sea colonization studies   | Reduced rates in deep sea, experimental applications to deep-sea ecology, field tests of patch mosaic model                     | Grassle (1977); Grassle and Morse-Porteous (1987); Snelgrove et al. (1992, 1994, 1996)                        |
| <i>Capitella</i> sibling species  | Sibling species with different life history characteristics important for conservation, management and ecological understanding | Grassle and Grassle (1976, 1977, 1978)  |
| Methodological tools for deep-sea diversity studies                             | Best approaches and novel tools for deep-sea data analysis  | Grassle and Smith (1976); Smith and Grassle (1977)  |
| Buzzards Bay oil spill study  | Classic study on opportunists and oil spill response, using field sampling and mesocosms  | Sanders et al. (1980); Grassle et al. (1981); Oviatt et al. (1984); Grassle et al. (1985); Neff et al. (1989) |
| First biological study of hydrothermal vents                                    | Key reviews helped to spark scientific and public interest in hydrothermal vents  | Grassle (1985, 1986)  |
| Key review papers on deep-sea diversity   | Enhanced profile of deep-sea biodiversity   | Grassle (1988, 1989, 1991)  |
| Studies on effects of deep-ocean dumping  | Produced evidence of impacts of dumping that contributed to termination of sludge dumping in deep US waters                     | Van Dover et al. (1992); Bothner et al. (1994)  |
| Establishment of Institute of Marine and Coastal Sciences at Rutgers University | Major new research institute in ocean sciences with a particular focus on the mid-Atlantic Bight region                         | Many papers by many researchers at IMCS since ~1990 (see text)  |
| Global diversity estimates for the deep sea                                     | Stimulated excitement, debate and research on deep-sea diversity  | Grassle and Maciolek (1992)   |
| LEO-15 Ocean Observatory  | Helped to create global interest in ocean observatories as tool to provide critical real time and continuous data               | von Alt et al., 1997  |
| Ocean Biogeographic Information System  | Repository for global marine data sets allowing broad-scale analyses not previously possible                                    | Grassle and Stocks (1999); Grassle (2000)   |
| Census of Marine Life   | Major initiative to unite marine biodiversity researchers globally  | Ausubel (1999); Malakoff (2000)   |

marine and coastal sciences. He has been a tremendous catalyst and selfless team player for those who have had the opportunity to work directly with him as students, technicians, postdocs, and colleagues, as well as for the science community in general.

### 1.1. Deep-sea ecology

Our understanding of deep-sea ecosystems changed significantly in the early 1970s with the expanding use of submersibles as sampling and observational tools, and along with it the capacity for in situ manipulative experiments. An early summary of the potential and limitations of submersibles (Heitzler and Grassle, 1976) and a specific application (Grassle et al., 1975) helped to position submersibles as tools that are now widely used in deep-sea research. The terminology, methodology, and results from this work are still cited (e.g. Bailey et al., 2007; Ruhl, 2007), and the use of submersibles is now embraced at shallower depths in applications such as fisheries assessment (e.g. Lawson and Rose, 1999). Fred's methodological contributions extend to analytical approaches, such as the similarity measure normalized expected species shared (NESS, Grassle and Smith, 1976) and the relative merits of different diversity metrics for analysis of deep-sea data (Smith and Grassle, 1977; Grassle and Morse-Porteous, 1987; Grassle and Maciolek, 1992). These methods have been extended and are in common use today (e.g. Legendre and Gallagher, 2001).

One of Fred's most enduring methodological contributions is the development and successful demonstration of in situ experimental approaches (e.g. Grassle, 1977; Grassle and Morse-Porteous, 1987; Snelgrove et al., 1992) that have greatly influenced our understanding of factors that determine deep-sea diversity patterns and process. His groundbreaking study of deep-sea colonization demonstrated that colonization processes are dramatically slower in deep-sea sediments than in shallow water (Grassle, 1977). Though addition of organic material and adult migration are known to accelerate deep-sea colonization (e.g. review of Snelgrove and Smith, 2002) and exceptions have been

documented, the low rates found in this early work are widely accepted (e.g. Gage and Tyler, 1991). This experimental approach was particularly relevant in the context of Fred's patch mosaic model, which emphasized the importance of ephemeral patches as a mechanism to explain high deep-sea diversity (Grassle and Sanders, 1973). As one of the seminal papers in deep-sea ecology, the patch mosaic model has been widely cited over the last three decades, in venues ranging from textbooks to original new research papers. The patch mosaic model stimulated further studies in the Grassle laboratory, including in situ experimental approaches on the importance of patch type (Grassle and Morse-Porteous, 1987), patch composition (Snelgrove et al., 1992, 1994) and age (Snelgrove et al., 1996) and over large spatial scales (Etter and Grassle, 1992). Fred's lab also made discoveries that have influenced policy on deep-ocean waste disposal and the potential consequences of waste disposal in deep-sea communities (Van Dover et al., 1992; Bothner et al., 1994).

If only one of Fred's papers could be singled out, his *pièce de résistance* is the paper he published with Nancy Maciolek that provided a quantitative estimate of deep-sea diversity at a regional and global scale (Grassle and Maciolek, 1992). This paper was a major milestone, generating widespread interest and debate in deep-sea diversity (e.g. May 1992, 1994) outside the modest cadre of deep-sea biologists who had been discussing the subject since the publication of the Hessler and Sanders (1967) and Sanders (1968) papers. These papers had sparked a decades-long debate in which the Grassle and Sanders (1973) paper played a central role. The stimulating exchange that followed the 1992 Grassle and Maciolek paper on diversity in deep-sea sediments (May, 1992; Gage, 1996; Briggs, 1999; Snelgrove, 1999a, b; Lambshead and Boucher, 2003) and comparing it to shallow-water ecosystems (Gray 1994, 2001, 2002; Ugland et al., 2003.; Mackie et al., 2005; Sala and Knowlton, 2006) and land (Briggs, 1994; May, 1994; Benton, 2001) continues unresolved to this day (e.g. Coleman et al., 2007; Kaiser et al., 2007). Whether Fred's estimate of 10<sup>7</sup> species of macrofauna in the deep sea proves to be inflated, conservative, or just about right will likely take decades to fully

resolve. Experts remain divided, but the important contributions from this work are that the deep sea is species rich and that the broader research community and general public are now interested in deep-sea diversity and conservation. This debate also fuelled a broader discussion on methodological approaches to diversity analyses in ecology (e.g. Palmer and White, 1994; Smith et al., 2000; Gotelli and Colwell, 2001) and conservation (Neigel, 2003).

Fred's tireless efforts to promote the importance of deep-sea diversity over the years (Grassle, 1988, 1989, 1991) and those efforts he inspired in his past students (e.g. Carlton and Butman, 1995; National Research Council, 1995; Snelgrove and Grassle, 1995; Snelgrove et al., 1997; Snelgrove 1999a,b; Snelgrove and Smith, 2002) has greatly enhanced the profile of marine biodiversity and led to significant new research initiatives.

### 1.2. Hydrothermal vents

Fred's leadership in deep-sea ecology was well established by 1977, the year that geologists diving in *Alvin* on the Galapagos Spreading Center discovered biological communities at deep-sea hot springs. By 1979, Fred had organized a team of scientists with funding from the National Science Foundation to begin the studies that would help to elucidate the chemosynthetic nature of hydrothermal-vent ecosystems (Jannasch and Wirsén 1979, Karl et al., 1980), symbiotic associations between chemoautotrophic bacteria and marine invertebrates (Cavanaugh et al., 1981, Felbeck, 1981), community structure (Hessler and Smithey, 1983), taxonomic descriptions of endemic taxa (e.g., Boss and Turner, 1980, Jones, 1981), physiology of vent organisms (e.g., Arp and Childress, 1981), and other key topics. His major reviews (Grassle, 1985, 1986) of vent animal distribution and biology set the stage for an intense period of research activity on the biology and ecology of vent faunas that continues today. Fred and his Woods Hole laboratory went on to explore hydrothermal systems of 21° North on the East Pacific Rise, Guaymas Basin, Gorda Ridge, and the Mid-Atlantic Ridge. One major legacy for the vent community derives from Fred's wisdom in embracing interdisciplinary research across the boundaries of ocean sciences that flourishes today. A second legacy of this broad approach is the Census of Marine Life described below.

### 1.3. Shallow-water ecology

The causes and consequences of deep-sea species diversity – the nucleus of Fred's research program – were fundamentally influenced by parallel studies in shallow water. Early on, species diversity, both in predictable areas of coral reef communities (Heron Island, Australia) and in the deep sea, was attributed to specialization (Grassle, 1973; Grassle and Sanders, 1973). Less predictable reef regions were characterized by more opportunistic species with high degrees of genetic variability through increased effective population size. By far, the most widely cited of Fred's papers is on the life histories of opportunistic species following the West Falmouth oil spill (Grassle and Grassle, 1974). It proposed, for example, mortality as the best single measure of the degree of opportunism. This paper was the first (of many) that was co-authored by Fred and Judy Grassle. Their mutual interests and complementary expertise yielded priceless perspectives. Among this body of work was their documentation of sibling species in the pollution indicator *Capitella* spp. (Grassle and Grassle, 1976). Their documentation of sibling species was based on allozyme alleles, at a time before today's impressive array of molecular tools were available. This early work helped to alert ecologists to the possibility of sibling species with very different

life history characteristics, and significant ramifications for ecology, conservation, and management. Subsequent studies that expanded widely on this discovery have highlighted the widespread occurrence of this important phenomenon (Knowlton, 1993).

Fred's concern about stresses imposed on the fragile coastal benthos, together with his sustained interest in life histories of opportunists and genetic systems (Grassle and Grassle, 1976, 1977, 1978), motivated studies of benthic community responses to human assaults, including oil, pollutants, drilling muds, and organic enrichment (Sanders et al., 1980; Grassle et al., 1981, 1985, Oviatt et al., 1984; Neff et al., 1989). This work is still widely cited in textbooks almost 30 years later (e.g., Pinet, 2006). He readily embraced the idea of large, replicated, self-contained tanks such as the Marine Ecosystems Research Laboratories (MERL) for testing effects of experimental additions versus controls. MERL macrofaunal/meiofaunal communities were impressively similar to the natural benthos in Narragansett Bay (RI), allowing for extrapolation of experimental results to nature to a degree that few others have achieved.

Fred did not reveal a bias for deep-sea research. He showed great enthusiasm for his graduate students' diverse interests. Thus, he strongly supported shallow-water research on the relative importance of active and passive processes in larval settlement (Hannan, 1984; Butman, 1987, 1989), food consumption by yellowtail flounder (Collie, 1985, 1987a, b), hydrodynamics and enrichment effects on colonization of macrofauna (Snelgrove et al., 1993, 2001; Snelgrove, 1994), habitat selection (Snelgrove et al., 1999, 2001), and recolonization of salt marshes in response to food, microalgae and tidal exchange (Stocks and Grassle, 2001, 2003).

### 1.4. Census of Marine Life

In addition to the many studies of deep-sea diversity that have been inspired by Fred's research and passion, his leadership and vision led to the International Census of Marine Life, a major 10-year global research program that has engaged thousands of scientists from over 80 countries around the world in the study of marine biodiversity patterns and evolutionary relationships (Ausubel, 1999; Malakoff, 2000). This program has elevated marine biodiversity to a level of interest and support that only Fred could have dreamed of; it actually is his dream brought to life (literally and figuratively), and has done more to advance marine biodiversity research globally than any other initiative, past or present. Not surprisingly, Fred has nurtured a major profile for the deep sea within the Census, including the Census of Diversity of Abyssal Marine Life (CeDAMar), Continental Margin Ecosystems on a Worldwide Scale (COMARGE), Patterns and Processes of the Ecosystems on the North Atlantic (MARECO), Global Census of Marine Life on Seamounts (CenSeam), and Biogeography of Deep-Water Chemosynthetic Ecosystems (ChEss).

### 1.5. Ocean observation and LEO-15

One of Fred's enduring legacies is the Long-Term Ecosystem Observatory (LEO-15). Fred and his collaborator Chris von Alt, realized that by running permanent cables horizontally from the coast out to the shelf, scientists could obtain continuous, long-duration temporal coverage from sensors at a sampling frequency that could not be achieved through use of research vessels alone. In 1993, the first cabled ocean observatory was deployed: A buried electro-optical cable provided electricity from the New Jersey shore to a 15-m-deep sensor suite on the shelf and transmitted data back to shore in real time (von Alt et al., 1997). Coupled with

Earth-orbiting satellites and the emerging technology of autonomous underwater vehicles (AUVs) that were a key element in Fred's vision of the observatory approach, the LEO-15 observatory has facilitated investigation of coastal processes on new scales of time and space.

Over time, the LEO-15 system has grown to include gliders, HF-Radar, CODAR, and numerical models (Glenn and Schofield, 2003). It is now a component of the Mid-Atlantic Regional Coastal Ocean Observing System (MARCOOS), which spans from Cape Hatteras to Cape Cod. Research at LEO-15 and MARCOOS covers such diverse topics as benthic boundary layer conditions, impact of storms, ocean forecasting, upwelling effects on biogeochemistry, sediment transport, larval settlement, fishery dynamics, ecosystem modeling, improving search and rescue and hazard prediction (Traykovski et al., 1999; Gargett et al., 2004; Olson et al., 2003; Ma, 2004; Ma and Grassle, 2004; Glenn et al., 2004, 2008; Schofield et al., 2004, 2005; Moline et al., 2007). One of the less tangible outcomes has been the expansion of multidisciplinary science, where oceanographers from different disciplines working with engineers to study the same phenomena at the same place and time. Importantly, the LEO-15 concept has spread globally, and Fred has been instrumental in shaping the direction of the emerging US Ocean Observing Initiative (OOI) and related programs, both as a member of working groups and as a strong advocate in congressional testimony.

#### 1.6. The Ocean Biogeographic Information System (OBIS)

In 1997, Fred Grassle organized a workshop to bring together the world's pre-eminent marine benthic taxonomists, ecologists, and statisticians and asked them to identify a single strategy to advance the study of marine biogeography in a 5–10-year timeframe. The group unanimously endorsed the need to bring together existing information on species distributions, which was at the time spread among researchers, natural history museums, and governmental bodies, to create maps of the known range of species (Grassle, 1997).

Fred quickly grasped the full import of this idea. He identified the need for an online, constantly evolving database and GIS system for global marine species distribution data. This was at a time before Google, before the Global Biodiversity Information Facility, and when Internet Explorer was just 2 years old. Under Fred's leadership, this simple idea became the Ocean Biogeographic Information System (OBIS) (Grassle and Stocks, 1999; Grassle, 2000). OBIS is now a growing, international network of marine data providers with 14 regional nodes around the world—at the time of writing, the OBIS portal ([www.iobis.org](http://www.iobis.org)) was the largest marine biological data provider in the world, serving 16 million data records from 441 datasets.

As the lead of the OBIS Secretariat, Fred provided the leadership and principles that have guided OBIS's growth: the availability of data to all at no charge, an international scope that encompasses developing countries, and a tool to support management and education as well as research. He also recognized that the challenge of building a successful OBIS was not primarily technological but rather in changing the data culture in biological oceanography. He ensured that biologists with data and those looking to use shared data, were central in OBIS planning and advising, and the success of OBIS hinged on the trust researchers held for Fred at a time when data sharing was a new and uncomfortable idea.

#### 1.7. Institute of Marine and Coastal Sciences

The late 1980s was hardly an ideal period in which to launch a new oceanographic program given the weak economy at the time,

but Fred was lured from Woods Hole Oceanographic Institution to Rutgers University in 1989 to become founding Director of the new Institute of Marine and Coastal Sciences. Though Fred's career to that point had focused on science rather than administration, he was aggressively recruited for his stellar scientific background, his well-established leadership abilities, and his capacity to bring together, inspire, and work well with diverse groups of people.

With blueprints for a new \$13 million dollar state-of-the-art building, a budget to hire 11 new faculty lines and seven new staff, and a mandate to develop marine science in New Jersey, Fred launched an institute that is a spectacular addition to marine sciences. Responding to state, regional, national, and global issues, IMCS has achieved many successes, including establishment of the Mid-Atlantic Bight National Undersea Research Center, creation of LEO-15, OBIS, and CoML as summarized above, and development of a superb faculty who have worked to improve management of fisheries, water quality, and beaches, and develop successful new graduate and undergraduate marine science degree programs. These efforts have brought recognition to IMCS, which now boasts over 50 faculty and technical staff in 19 different research groups that are internationally recognized, and a marine science graduate program that is ranked among the top 10 in the United States.

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