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Silvia E. Ibarra-Obando

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DEDICATED SECTION

The Fifth International Seagrass Biology Workshop, 7–11 October 2002, Ensenada, Baja California, Mexico

Since 1996, seagrass experts have been meeting biennially to share knowledge of the biology of seagrasses and the animals associated with seagrass meadows. Previous workshops have taken place in Western Australia, Japan, the Philippines, and France. In 2002, the meeting was held in Mexico and four themes were chosen for the sessions: Ecophysiological Processes (Sven Beer, Chair), Plant–Animal Interactions (Kenneth L. Heck Jr., Chair), Genetics and Reproductive Biology (Gabriele Procaccini and Michelle Wycott, Co-Chairs), and Changes in Seagrass Beds at the Local and Regional Scale (Fred T. Short, Chair). An additional session on Traditional Knowledge and Wisdom (Sandy Wylie-Echeverria, Chair) provided an ethnobotanical perspective. Included here are abstracts accepted for the workshop, either as oral or poster presentations.

SILVIA E. IBARRA-OBANDO, WORKSHOP CHAIR

Session: Ecophysiological Processes

Seagrass Ecophysiology: Influence of Environmental Factors, Biogeography and Phylogeny

W. C. DENNISON AND T. J. CARRUTHERS, University of Maryland, Center for Environmental Science, P.O. Box 775, Cambridge, MD 21613.

Seagrasses, a functional rather than a systematic grouping, share many anatomical and ecophysiological features. This convergence relates to the selective pressures on the species of flowering plants that have successfully colonized the sea. Living partially or totally submerged presents several ecophysiological challenges: low, variable and unpredictable underwater light climates, competition for space and light by other marine flora, hydrodynamic stress as well as diffusion limitation due to boundary layers, sediment accretion and burial, and nutrient limitation or over-enrichment. The influence of environmental factors on seagrass species varies from strongly limiting due to the lack of an environmental factor (e.g., low light, low nutrients, diffusion boundary layers, sediment availability, missing grazers) through to strongly limiting due to the excess of an environmental factor (e.g., high light, high nutrient, hydrodynamic shear, sediment burial, intense grazing). The biogeographical setting of various seagrass species also influences ecophysiological responses; what is lethal in one part of a species range is relatively innocuous in another setting. The phylogeny of seagrass species, and the various morphological forms manifested, leads to another important influence on seagrass ecophysiology. Small, rapid turnover seagrass species have very different ecophysiology than large, slow turnover seagrass species. Species distributional patterns and ecological interactions are also profoundly influenced by the variability in growth form. Hence, generalizations regarding seagrass ecophysiology must be carefully scrutinized and rigorously tested in a variety of locations.

Variability in the Chronic PSII Pressure Along the Seagrass Leaves as a Tool to Examine Plant Performance

S. ENRÍQUEZ, Unidad Académica de Puerto Morelos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Apt. Postal 1152, 77500 Cancún, Quintana Roo, Mexico.

In a previous work, we described a permanent reduction in the quantum yield of photosystem II (Fv/Fm) along the second leaf of Thalassia testudinum, as a consequence of an accumulation of inactive reaction centers. We found that this variation was strongly associated with the number of hours that a particular leaf section is exposed to super-saturating irradiance. As we did not find any significant difference in the photosynthetic response, we conclude that this variation reflects a plant photoacclimative response to the variation in the photon flux density gradient within the canopy. An incomplete diurnal recovery of the light-dependent midday Fv/Fm reduction, it is probably the mechanism that

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explains the observed age-dependent Fv/Fm reduction. The variation in the photochemical signal registered along seagrass leaves integrates light environmental pressure as well as self-shading effects within the seagrass canopy. In this work, I examine the potential of studying this permanent Fv/Fm reduction to understand seagrass photoacclimation. Comparisons have been done to test differences in the pattern of Fv/Fm variation: (1) between leaves of two different species, *Zostera marina* and *T. testudinum*, growing under very contrasting light environments such as a Danish estuary and a coral reef lagoon in the Mexican Caribbean; (2) among *T. testudinum* leaves growing in six different meadows at different depths in a Puerto Morelos coral reef lagoon, strongly differing in their biomass density and in the light attenuation coefficient (Kd) within the seagrass canopy; and (3) among *T. testudinum* leaves growing within the same meadow but supporting different flowering effort. These comparisons highlight the potential of the permanent Fv/Fm reduction along seagrass leaves as a powerful tool to comprehend seagrass performance.

**Photosynthesis and Biochemical Characterization of Eelgrass Along the Pacific Coast of Baja California, Mexico**

A. CABELLO-PASINI, R. MUÑIZ-SALAZAR, AND D. H. WARD, (ACP; RM-S) Instituto de Investigaciones Oceanológicas, University of Baja California, Ensenada, Mexico; (DHW) U.S. Geological Survey, Alaska Science Center, 1011 E Tudor Road, Anchorage, AK 99503.

*Zostera marina* is the most abundant submerged aquatic macrophyte from coastal lagoons in Baja California, Mexico. In this study, we evaluated annual fluctuations of photosynthetic characteristics and biochemical composition of *Z. marina* inhabiting northern and southern lagoons of Baja California. In situ irradiance and water temperature were monitored throughout the year at San Quintín (northern lagoon) and at Ojo de Liebre and San Ignacio (southern lagoons). In situ irradiance was approximately twofold greater and water temperature was 5°C greater at the southern lagoons than at the northern one. Chlorophyll levels in the tissue of *Z. marina* were twofold greater at San Quintin, suggesting an acclimation to the lower irradiance levels at the northern lagoon than at the southern ones. Photosynthetic characteristics were relatively similar in shoots from all three sites. The hours of light saturated photosynthesis (Hsat), calculated from the photosynthetic characteristics and irradiance levels, suggest that *Z. marina* is light-limited during 20% of the year at the northern lagoon. Carbohydrate levels were twofold greater at the northern lagoon, suggesting that chlorophyll levels compensate for the lower light levels at this site relative to the southern lagoons. In contrast to carbohydrate levels, total protein levels were approximately 50% greater at the southern lagoons than the northern one. Fiber content and calories in the leaves of *Z. marina* were similar at all three sites. The distribution of *Z. marina* in the northern lagoon is approximately 1 m higher in the intertidal zone than meadows at the southern lagoons, suggesting that these populations are colonizing shallower areas as a response to lower light levels.

**The Effects of Long-Term Light Reduction on Carbon Allocation in Selected Seagrass Species Using the Stable Isotope 13C**

W. H. UY, M. A. HEMMINGA, AND J. E. VERMAAT, (WHU) Institute of Fisheries Research & Development, Mindanao State University at Naawan, 9023 Naawan, Misamis Oriental, Philippines; (MAH) Zeeuw Landschap, P.O. Box 25, 4450 AA Heikenszand, The Netherlands; (J EV) Institute for Environmental Studies, Vrije Universiteit, Amsterdam, The Netherlands.

In a 1-yr in situ shading experiment, carbon allocation was studied in four different experimental events. Two contrasting seagrass species were selected for the study: the short-lived, early successional *Halodule uninervis* and long-lived, late successional *Thalassia hemprichii*. The stable isotope 13C (NaH13CO3) was used to quantify carbon allocation to the different plant parts. Natural 13C/12C was lower in *H. uninervis* (−9.5 to −10.2‰) than in *T. hemprichii* (−5.9 to −6.6‰). The 813C values of the different plant parts were significantly different in both species, the leaves being more 13C-depleted than the roots and the rhizomes. In both species, tracer addition resulted in a significant enrichment compared to 13C natural abundance, in *H. uninervis* the enrichment representing twofold than in *T. hemprichii*. Shading up to 89% light reduction did not influence the enrichment in either species. However, significant differences were observed between experimental events or sampling periods and between species. The amount of 13C remaining in the plant 5 d after the 3-hr incubations was less...
than 5% the initial amount in the incubation bag. Most of this $^{13}$C remained in the leaves (up to 80% in *H. uninervis* and 88% in *T. hemprichii*). The rest of the incorporated carbon was exported to the non-photosynthetic organs (stems, rhizomes and roots). This translocation was significantly reduced by shading from 22% to 12% in *T. hemprichii* and from 34% to 20% in *H. uninervis*. Partitioning of $^{13}$C over non-photosynthetic tissue however, was not affected by shading in *T. hemprichii*, whilst in *H. uninervis*, a significant increase in the stem $^{13}$C content was observed.

The Importance of Tidal Emersion for Growth of *Zostera* sp. in New Zealand Estuaries

A. SCHWARZ, NIWA, P.O. Box 11-115, Hamilton, New Zealand.

Coastal biodiversity is currently an important area of research with substantial management implications for New Zealand. As one habitat component of estuaries, *Zostera* sp. can occupy up to 30% of the intertidal sand flat area, but its physiological characteristics are poorly studied. A better understanding of the growth requirements of this plant in New Zealand conditions is required, particularly as ongoing research suggests that the subtidal fringe is an important habitat for juvenile fish of commercially important species (Morrison, unpubl. data). The total area of seagrass habitat in New Zealand has declined over the last half of the 20th century with subtidal beds of *Zostera* sp. showing the greatest declines (Park 1999). While the physical action of tidal channels has a role in limiting extension to the subtidal in parts of estuaries (Turner et al. 1996), in other regions subtidal beds may have been depleted by a reduction in average water clarity due to increased sedimentation as a result of forest clearance and land development. The hypothesis for this study was that *Zostera* sp. is currently reliant on the period of emersion during low tide for net photosynthetic gains. In 2001, a study was initiated to evaluate the carbon balance of *Zostera* sp. in North Island, New Zealand estuaries. Photosynthesis and respiration characteristics of plants from different estuaries have been measured using both in situ and laboratory based techniques. Instantaneous measurements, as well as logged data under ambient light conditions, have been combined with measured in situ light at different spatial and temporal scales, and accounting for tidal variation. Data on photosynthesis and biomass of intertidal seagrass beds will be used in an attempt to hindcast the likely areal coverage of subtidal *Zostera* sp. under a different water clarity scenario, as well as to assess any likely water-clarity related risks to intertidal plants.

Can the Calcifying Macroalga *Halimeda opuntia* Increase CO$_2$ Availability and Enhance the Growth of *Thalassia testudinum*?

W. J. KENWORTHY AND J. P. REID, Center for Coastal Fisheries and Habitat Research, NCCOS, NOS, NOAA and Sirenia Project, Florida Caribbean Science Center, USGS, Gainesville, FL.

Seagrasses and calcareous macroalgae are important benthic primary producers in oligotrophic tropical waters worldwide. Throughout the Caribbean basins, *Thalassia testudinum* often forms dense productive meadows with a thick understory of *Halimeda* spp. In southeastern Puerto Rico, we observed manatees feeding in seagrass meadows with elevated “mounds” of *H. opuntia*. *Thalassia* short-shoots grow vertically up through the *H. opuntia* and in many areas the mounds occupy ≥50% of the leaf canopy. Manatees feed on the seagrasses by pushing aside the *Halimeda* and graze the seagrass leaves, rhizomes and roots. Within the mounding *Halimeda*, *Thalassia* short-shoot densities were significantly greater than outside the mounds, and leaves were significantly longer and wider, leading to much greater standing crop. Specific leaf productivity in the mounded *Halimeda* was higher, but not significantly greater than outside the mounds. However, because short-shoot densities were higher in the mounds, *Thalassia* areal leaf productivity was significantly greater in the thick understory of *H. opuntia*. The $^{13}$C values for *Thalassia* leaves growing in the mounds were more negative than leaves outside the mounds ($-8.69$ vs $-7.3$). We hypothesize that the lighter isotopic composition of the leaves growing in the *Halimeda* can be attributed to a greater availability of CO$_2$ in the microenvironment of interstitial water within the mounds. *Halimeda opuntia* is a calcifying algae capable of elevating CO$_2$ and other nutrient concentrations in the interstitial waters of the mounds by excreting protons and lowering pH. Slight acidification of the microenvironment surrounding the seagrass leaves could generate CO$_2$ concentrations well above ambient. Since CO$_2$ limits photosynthesis, *Thalassia* leaves bathed
in this water could be directly benefiting from the calcification process. The productivity of shallow carbonate mudbanks and shelves throughout the tropics is probably enhanced by this process.

Light Effects on the Circadian Evolution of Photosynthesis in Zostera noltii and Cymodocea nodosa Along a Vertical Gradient in Ria Formosa (South Portugal)

J. M. Silva and R. Santos, CCMAR, Universidade do Algarve, Campus de Gambelas, 8000-117 Faro, Portugal.

Ria Formosa is a coastal lagoon with an intertidal area of around 67 km². Most of this area is occupied by a monospecific population of Zostera noltii distributed along the channel slopes. Cymodocea nodosa occupies a vertically narrow band in the upper subtidal, confining with the lower extreme of the Z. noltii distribution. The light environment in this seagrass meadow changes continuously along the day, depending of the surface PAR and the tide schedule. The lower limit of the meadow receives an average daily PAR dose of 4 mol photons m⁻², while the upper limit receives around 15 mol photons m⁻². The aim of this work was to establish the relation between the circadian evolution of available PAR and the photosynthetic yield of PSII, measured by chlorophyll a fluorescence. Rapid light curves (RLCs) were obtained by PAM fluorometry, every 2–3 hr, for C. nodosa (subtidal) and for two zonation morphotypes of Z. noltii (lower and upper intertidal), from pre-dawn until sunset. The light reactions of photosynthesis were assessed by the parameters obtained directly by PAM fluorometry and by the fitting of P-I models to the RLCs. Both Z. noltii types and C. nodosa presented a similar pattern on the daily evolution of photosynthesis. The maximum electron transport rates (ETRₘ) followed the ambient PAR, whereas the photosynthetic efficiency, expressed by the initial slope of the RLCs, was higher during early morning, and then followed the inverse pattern of PAR. The two morphotypes of Z. noltii revealed a typical behavior of sun and shade plants. The initial slopes of all the RLCs were higher in the lower limit morphotype while the half-saturation irradiance was always higher on the upper limit morphotype. Cymodocea nodosa half-saturation irradiance lay between the two Zostera values, but the initial slopes of the RLCs revealed a very strong oscillatory tendency, peaking higher than Z. noltii in early morning and decaying to the lowest values at noon. This is the typical behavior of shade-type plants.

UV-Induced Changes in the Photophysiology and Photochemistry of Halophila johnsonii Eiseman

J. I. Kunzelman and M. J. Durako, University of North Carolina at Wilmington, Center for Marine Science, Wilmington, NC 28409.

Halophila johnsonii is currently listed as threatened on the U.S. endangered species list due to its rarity within an extremely limited range of distribution. This species tends only to establish from the mid-intertidal down to 3 m depth. Previous work has demonstrated that H. johnsonii, differing from its conspecific H. decipiens, exhibits high light-adapted photophysiology and contains a compound that absorbs maximally at 350 nm. Both of these characteristics were found to vary significantly following 4 d of acclimation during a reciprocal transplant experiment. Based on the plasticity of these photophysiological and photochemical responses, a controlled greenhouse experiment was performed using incident PAR with supplemental UV bulbs. Cut-off filters were used to measure the response of greenhouse acclimated plants to PAR + UVA + UVB and PAR + UVA, vs PAR alone. Changes in photosynthetic efficiency were measured by PAM fluorometry, and variations in pigment characteristics were monitored over the course of the experiment in order to quantify both short- and long-term acclimation to different UV treatments. These results may indicate whether high UV tolerance allows H. johnsonii to dominate in the intertidal while it appears to be competitively excluded subtidally.

Epiphytic Layers as UV-B Filters on Seagrass Leaves

E. W. Koch and L. A. Brandt, Horn Point Laboratory, University of Maryland Center for Environmental Science, P.O. Box 775, Cambridge, MD 21613; Gustavus Adolphus College, 800 W College Avenue, St. Peter, MN 56082.

Epiphytes are considered detrimental to seagrasses as they reduce the amount of light, i.e., photosynthetically available radiation (PAR) that reaches the plant surface. This study evaluated the possibility
that epiphytic layers can also be beneficial to seagrasses by reducing the amount of ultraviolet (UV)-B radiation that reaches seagrass leaves. Deposition of particles and growth of algae was allowed to occur on UV-B transparent artificial seagrass leaves at two sites: in a highly eutrophic estuarine area where seagrasses are at the limit of their existence and in a relatively pristine coastal lagoon where seagrasses are luxuriant. At pre-determined time intervals, the artificial leaves were collected and the transmittance of light through the epiphytic layer quantified in the UV and PAR ranges using a dual beam spectrophotometer equipped with an integrating sphere. The epiphytic layers that accumulated on the artificial leaves transmitted a significantly lower amount of radiation in the UV-B than in the PAR range. Therefore, epiphytic layers are effective UV-B filters on seagrass leaves. This benefit is lost when PAR transmission is reduced to levels below the compensation point.

Salinity Tolerance of Posidonia oceanica

Y. Fernández-Torquemada and J. L. Sánchez-Lizaso, Unidad de Biología Marina, Departamento de Ciencias Ambientales y Recursos Naturales, Universidad de Alicante, Alicante, Spain.

The effects of salinity changes on the leaf growth and survival of the Mediterranean seagrass Posidonia oceanica were investigated in short mesocosm experiments under constant conditions. Plants were placed in tanks of 300 liter and exposed to different salinity treatments (between 10 and 57 psu) during 2 wk. Posidonia oceanica was negatively influenced by increased salinity. Shoots showed a significant decrease in growth and survival whereas the biomass of its epiphytes did not show a clear response because of their high variability. Maximum leaf growth occurred between 30-39 psu. Plants suffered considerable mortality at salinities beyond 42 psu and below 29 psu, with 100% mortality at 50 psu. In salinities lower than 46 psu, surviving plants were able to recuperate their growth when returned to normal seawater salinity. These results suggest that P. oceanica is one of the seagrasses more sensitive to increased salinity and it is more tolerant to reduced salinity.

Role of Seagrass Flexibility on Surrounding Current Field

H. Tamura and K. Nadaoka, Graduate School of Information Science and Engineering, Tokyo Institute of Technology, Tokyo, Japan.

For proper understanding of hydrodynamic characteristics of seagrass bed canopy, it is of crucial importance to clarify the effects of flexibility of seagrass on the surrounding current field. For this purpose, we conducted both laboratory experiments and field measurements. In the former, we made detailed measurements of velocity field by using LDV (Laser-Doppler Velocimetry) and flow visualization techniques for flexible and non-flexible seagrass model bed installed in a wave flume. In the flexible seagrass model, Eulerian mean velocity and mass transport velocity were found to occur in the opposite direction of wave propagation near the top of the seagrass canopy. In the surface layer above the canopy, the mean velocities were in the direction of wave propagation. On the contrary, in the non-flexible seagrass model, the entirely opposite pattern was observed in the mean velocity profiles. To examine the mechanism of the appearance of the opposite pattern in the mean velocity profiles, the velocity data was decomposed into the mean, organized and turbulent components, and their interactive relationships were then investigated. It was also found that there arose a large-scale flow circulation around the seagrass bed canopy, with upwelling mean flow in and above the seagrass canopy, in the vertical section along the wave orbital motion. This circulation may have an important role in the suspension mechanism for particulate matters around a seagrass canopy.

Resource Allocation and Proteolytic Activity in the Seagrass Zostera noltii Hornem. Subjected to Light Reduction by Ulva Canopies


Plants of the Zostera noltii Hornem. were grown in laboratory under different light levels. Irradiance reduction was obtained by superposing Ulva canopies (2, 4 and 8 layers corresponding to 75%, 90% and 99% of light reduction). After 16 d of plant cultivation growth, mobilization of non-structural
levels of heavy metals in coastal lagoons, which could eventually accumulate in sediments and tissues of animals and plants. Consequently, the objective of this study was to evaluate the levels of Fe, Co, Cd, Zn, Ni, Mn, and Pb in the surface sediments, and the seagrass Zostera marina of coastal lagoons in Baja California and Alaska.

Seagrasses and Waves: Ecophysiological Traits and Rhizome Architecture of Species across Energetic Hydrodynamic Environments

M. L. CAMBRIDGE, School of Plant Biology, The University of Western Australia, Crawley, WA 6009, Australia.

In Western Australia, seagrasses (Halophyta) form meadows on wave-swept sandbanks as well as sheltered bays along some 2,000 km of temperate coasts. These seagrasses grow in wave-dominated environments from 1–30 m depth. In some cases, the habitats are extreme in terms of the force of oceanic swell waves and sand movement, compared to tidal estuaries where most seagrass research has been focused to date. As part of a study on the genesis and dynamics of these fast and diverse seagrass habitats, functional leaf anatomy and rhizome architecture are being investigated for species occurring at different levels of wave exposure. Depending on exposure to oceanic swell, storm wind direction and duration, there are different disturbance levels and frequencies ranging from local extinction to small gap formation. It is proposed that surviving the effects of exposure to ocean swell and associated sand movement is the predominant driver at one extreme of wave energy. This is reflected in suites of traits, including heavy fiber reinforcement to strengthen the aboveground stems or leaves, and deep vertical rhizome growth to cope with wave drag and large changes in sediment height. In physically less rigorous environments, mechanical destruction is less, and more species can survive. There is evidence for a range in flexibility to respond to change, and various options for occupying space in terms of rhizome architecture. These include patterns and rates of lateral growth, allocation to functional leaf anatomy showed varying proportions of photosynthetic tissues, aerenchyma and structural elements, which in turn affected patterns of dry matter and nutrient allocation, production of leaf area, and leaf turnover rates.

Heavy Metals in Sediments and Seagrasses from Coastal Lagoons in Baja California and Alaska

M. Morales-Ramírez, M. A. Huerta-Díaz, D. H. Ward, and Cabello-Pasini, (M-R, MAH-D, C-P) Instituto de Investigaciones Oceánológicas, Universidad Autónoma de Baja California, Ensenada, Mexico; (DHW) U.S. Geological Survey, Alaska Science Center, 1011 E Tudor Road, Anchorage, AK 99503.

Coastal lagoons are habitat for ecologically and economically important species. In the last three decades, however, these water bodies in Baja California have been impacted by industries, aquaculture, agriculture and human activities. The increment of these anthropogenic activities has increased the levels of heavy metals in coastal lagoons, which could eventually accumulate in sediments and tissues of animals and plants. Consequently, the objective of this study was to evaluate the levels of Fe, Cu, Co, Cd, Zn, Ni, Mn, and Pb in the surface sediments, and the seagrass Zostera marina of coastal lagoons.
from Baja California, Mexico (Punta Banda, San Quintin, San Ignacio, Ojo de Liebre) and Alaska (Izembek). In general, the levels of heavy metals in sediments were twofold greater at San Quintin and Alaska than in the rest of the lagoons. The most abundant metals in the sediments of these lagoons were Fe > Mn > Zn > Pb. The lowest levels of metals in sediments were found in geographically and anthropogenically isolated lagoons of Baja California (San Ignacio and Ojo de Liebre). Similarly to metals in sediments, the levels of metals were approximately twofold greater in Z. marina from San Quintin and Alaska than from the other lagoons. The levels of the most abundant metals in the tissue of Z. marina were Fe > Mn > Zn > Ni. There was a significant correlation between metals from the sediment and metals from the tissue of Z. marina at all sites, except at San Quintin. This suggests an active uptake of the metals from the sediment by Z. marina. In addition, there was a concentration structure of metals in the sediments and tissue of Z. marina in San Quintin Bay. This coastal lagoon has two arms with distinct flow patterns. The greatest levels of metals in the sediment and shoots of Z. marina were found in low energy areas and close to anthropogenically impacted areas of San Quintin Bay.

Nitrogen Budget of *Posidonia oceanica* as Determined by In Situ Uptake Experiments

G. LEPOINT AND J.-M. BOUQUEGNEAU, *Oceanology, B6, Life Department, University of Liège, B-4000 Liège, Belgium.*

Between Feb. 1997 and June 1999, we performed in situ experiments using the isotope 15 of nitrogen (15N) to measure the uptake of nitrate and ammonium by the roots and the leaves of *Posidonia oceanica*. Nitrate and ammonium leaf uptake fluxes (gN.m\(^{-2}\) y\(^{-1}\)) seem to have the same importance on an annual basis. We calculate that the N leaf uptake is insufficient to meet the annual N requirement of the plant. We observed very high *Posidonia* root biomass and measured higher specific uptake rates for this compartment. However, as in sediment, this uptake capacity is limited by the nutrient diffusion rate, root uptake is also insufficient to meet the N requirement. In fact, *P. oceanica* of the Revellata Bay (Corsica, France), as some other seagrasses, show a complex N budget in which uptake and recycling processes are involved. Such a complex budget allows *P. oceanica* to efficiently meet their N requirement in one of the most nutrient-poor areas of the northwestern Mediterranean Sea. We calculate that leaf and root would contribute respectively to 40% and 60% of the annual N uptake and to 60% of the annual N requirement of the plant.

Effect of High Irradiances on the Photoinhibition of Photosynthesis of *Zostera marina*

E. AGUIRRE-VON-WOBESER AND A. CABELLO-PASINI, *Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California, Ensenada, Mexico.*

Excessive irradiance can inhibit photosynthesis in a number of photosynthetic organisms including seagrasses. This phenomenon is known as photoinhibition of photosynthesis, and could cause an overestimation of the productivity of seagrass meadows. The objective of this study was to evaluate the regulation of photoinhibition in *Zostera marina* when exposed to elevated irradiances. Photosynthetic response of *Z. marina* to increasing irradiance was evaluated in the field, and in the laboratory, using pulse amplitude modulated (PAM) fluorescence and oxygen electrodes. A positive linear correlation between oxygenic photosynthesis and chlorophyll fluorescence was found, suggesting that fluorescence is an effective method for studying the effects of environmental parameters on photosynthesis of this species. Moreover, the slope of the relation between oxygen evolution and fluorescence was approximately 0.25, the theoretical value resulting of four electron transported per two water molecules split. Intertidal or subtidal shoots were incubated in outdoor tanks under 20%, 55% and 100% natural irradiance to evaluate acclimation of this species to different irradiance levels. Intertidal shoots kept for 7 d under 100% natural irradiance did not show a reduction of photosynthesis at noon. In contrast, subtidal shoots were photoinhibited even after 12 d under 100% natural irradiance. This suggests that subtidal shoots have a lower acclimation capacity to high irradiances than subtidal shoots.
A Computer Simulation Model of the Effects of Light and Nitrogen on the Growth Dynamics of Seagrass *Posidonia oceanica*

K. ELKALAY, C. FRANGOULIS, S. DJENIDI, AND J. H. HECQ, (KE, CF, JHH) Ecohydrodynamics, University of Liège, Sart Tilman, (B3), B-4000 Liège, Belgium; (SD) GHER, University of Liège, Sart Tilman, (B3), B-4000 Liège, Belgium.

A computer simulation model was developed to investigate nitrogen uptake kinetics for the endemic Mediterranean seagrass *Posidonia oceanica*. Goals were to evaluate the relative effects of light and nitrogen availability on nitrogen uptake, and partitioning between above- and below-ground biomass in the Bay of Calvi (Corsica, France). The model depicts a continuum of events, many of which have been observed in coastal waters. The model confirms that ammonium is more important source of nitrogen than nitrate for the whole plant. The simulations indicated also that below-ground biomass is slightly more important (57%) than above-ground biomass (43%) in overall nitrogen acquisition in most light and nitrogen environments encountered in the area. We calculated that minimum light requirements of *P. oceanica* growth are 15.7% of surface irradiance.

Effects of In Situ Sulfide Additions to the Sediment in Stands of the Tropical Seagrass *Cymodocea rotundata*

S. Z. B. HALUN, J. TERRADOS, J. BORUM, L. KAMP-NIELSEN, C. M. DUARTE, AND M. D. FORTES, (SZBH, MDF) Marine Science Institute, CS, University of the Philippines, Diliman, Quezon City, Philippines; (JT) Centro de Estudios Avanzados de Blanes, CSIC, Aces a la Cala Sant Francesc, 14 17300 Blanes, Spain; (JB, LKN) Freshwater Biological Laboratory, University of Copenhagen, Helsingørsgade 51, DK-3400 Hillerød, Denmark; (CMD) Instituto Mediterraneo de Estudios Avanzados, CSIC-Univ. Illes Balears, C/ Miquel Marques 21, 07190 Esporles (Islas Baleares), Spain.

This study investigated the effects of increased sulfide concentration in pore water on the seagrass, *Cymodocea rotundata*, which is considered one of the southeast Asian seagrass species most sensitive to siltation. The approach included the evaluation of the effects of in situ sulfide additions to the sediment on (1) the production of shoots, rhizome and roots, and the elongation rate of the horizontal rhizome of plants at the edge of the meadow, and (2) on leaf growth, mass allocation patterns and shoot density in a well-developed seagrass meadow. Pore water sulfide concentrations of 1 mM reduced by more than half the production of shoots, rhizome and roots, and the elongation rates of *C. rotundata* horizontal rhizomes of plants at the edge of the meadow, but had no effects on leaf growth and shoot density in a well-developed *C. rotundata* meadow.

Response of Turtlegrass to Natural and Reduced Light Regimes Under Conditions of Ramet Isolation

S. E. IBARRA-OBANDO AND K. L. HECK JR., (SEI-O) Centro de Investigación Científica y Educación Superior de Ensenada (CICSE), Km 107 Carretera Tijuana-Ensenada, Ensenada, Baja California, Mexico; (KLH) Marine Environmental Sciences Consortium, Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, AL 36528 and Department of Marine Science, University of South Alabama, Mobile, AL 36688.

Severing rhizomes was used to evaluate the influence of ramet isolation on the response of turtlegrass *Thalassia testudinum* to experimental light reduction. The experiment took place in Perdido Bay, Florida, from May to Oct. 2001. We used a factorial design with light (ambient and 40% reduction) and shoot physiological integration (severed and unsevered rhizomes and roots) as main factors. Each treatment was replicated in four plots. Light was reduced by a polyethylene mesh, and rhizomes along the border of the 0.5 m² experimental plots were severed with a knife at the beginning and middle of the experiment. Shading promoted a significant decrease in turtlegrass aboveground biomass, epiphyte biomass, and NAPP. Severed shoots showed a significant reduction in NAPP only in July, and no other response variable was affected by severing. These results indicate that if physiological integration is important in influencing susceptibility to shading, it occurs at a smaller scale than the selected in this study (0.5 m²).
Measuring Photosynthetic Characteristics of Seagrasses Using Pulse Amplitude Modulated (PAM) Fluorometry: Methodological and Scale-Based Considerations

M. J. Durako and J. I. Kunzelman, Center for Marine Science, The University of North Carolina at Wilmington, Wilmington, NC 28409.

Photosynthetic characteristics of the seagrasses Thalassia testudinum, Halophila johnsonii, and H. decipiens, as measured in situ, using a submersible pulse–amplitude modulated fluorometer (Diving-PAM) exhibit shoot-to-landscape scale variability. Shoot-scale variation has been assessed in Thalassia to develop a standard-methods protocol for this species. Significant within-shoot and among-shoot scale variation exists for several PAM-fluorescence parameters. The fraction of incident photosynthetically active radiation (PAR) absorbed by youngest leaves is significantly lower than the PAR absorbed by rank two and three leaves. Quantum yields (Y) and photosynthetic efficiency (Fv/Fm) exhibit greater variability and generally decrease with increasing leaf age. Maximum fluorescence of light-adapted leaves (Fm') decreases significantly from the bottom to the top of leaves. Quantum yields are significantly reduced when measured where leaf lesions are present, but this effect is very localized. Quantum yields exhibit relatively high variability for short-shoots within seagrass die-off patches and are significantly reduced for short-shoots exhibiting die-off symptoms. Quantum yields for both Halophila species generally increase with depth of occurrence and Y decreases within 4 d when deeper plants are transplanted into shallower waters, and vice versa. These patterns indicate rapid photoadaptation occurs in this genus. Regression analyses of Y and Fv/Fm, measured in Thalassia as part of a landscape-scale sampling program, revealed the presence of significant diurnal and light-field related variation. Response slopes for both characteristics are negative, as a function of time of day, and as a function of increasing photosynthetic photon flux density (PPFD) measured at the canopy; with more negative slopes for Y. These results indicate that the selection of leaf tissue, short-shoot location, and time of measurement need to be considered when determining photosynthetic rates for seagrasses in situ.

Application of Surveying Techniques to Assess the Effects of Sedimentation on Submersed Aquatic Vegetation in Potomac River Estuary


From June 1999 to May 2002, we used a total station and electronic level to measure changes in bathymetry at three sites in the Potomac River, a tributary of Chesapeake Bay. The sites are situated in a hydrodynamic location and are characterized by dense, mixed stands of Myriophyllum spicatum and Vallisneria americana, and a riverbank eroding at a rate of 1 foot/year. Consequently, terrestrial sediment is deposited into the river at a rapid pace and may have a negative effect on the plants’ general health (increased turbidity, shading of leaves) and distribution (burial of propagules). Every 2 mo, we sampled transects and quadrats at each site to evaluate large- and small-scale changes in bathymetry over time. We evaluated the prevailing transport dynamics of the area and discovered that much of the eroded sediment is deposited on top of the vegetation or is suspended in the water column. Also, we conducted laboratory experiments testing the effects of burial on plant survival and found that plants remained viable when covered by up to 5 cm of sediment, but did not survive deeper burials. In addition to quantifying the effects of sedimentation on plant viability, we quantified the surveying instruments’ accuracy and precision and discuss the efficacy of applying conventional, land-surveying techniques to measure changes in bathymetry in submersed aquatic vegetation habitats and the potential to employ these methods in other aquatic environments.

Interspecific Competition Between the Mediterranean Seagrass Posidonia oceanica and the Chlorophyceae Caulerpa taxifolia

G. Pergent, O. Dumay, and C. Pergent-Martini, ECL, University of Corsica, Faculty of Sciences, BP 52, 20250 Corte, France.

The interaction between the endemic Mediterranean seagrass Posidonia oceanica and the invasive tropical Chlorophyceae algae Caulerpa taxifolia was carried out in four sites from French Riviera. According to the season and the level of interaction, P. oceanica showed significant variations in term of phenology, epiphytic biomass, leaf renewal cycle, primary production, and tannin cell. So, the mean leaf length.
exhibited a significant reduction according to an increasing interaction (from 531.8 to 468.4 mm) and the mean leaf area index was reduced upper than 20%. Conversely, when the interaction became higher, there was an increase of the number of leaves produced per year according to the leaf renewal cycle, and of the mean foliar primary production (about 45%). The number of tannin cells increased significantly too. In the same time, C. taxifolia produced less secondary metabolites (e.g., Caulerpenyne—CYN), while the thalli length increased. In terms of energy allocation, it appears that P. oceanica experiences high energy costs to ensure leaf production. This increased primary production, which is brought on by interspecific competition with C. taxifolia, may, in the long term, lead to a shortage of nutrients necessary for plant growth. Indeed, although an increased allocation of photosynthetic products can, at least in the short term, lead to an energy surplus to the shoots of P. oceanica, such a mechanism must be studied over the long term. For C. taxifolia, the decrease in CYN concentration, with the concomitant increase in thalli length, appears to correspond to a classic strategy. So, the high energy allocated to the growth of thalli would be at the cost of another function (production of secondary metabolites).

Hydrosoluble Phenolic Compounds Production in a Mediterranean Seagrass According to Mercury Contamination


Today, early signs of modification of environmental conditions are increasingly useful for efficient monitoring. In marine environments, seagrasses would appear to be potentially valuable bioindicators of metallic pollution. Correlations have been found between the mercury levels accumulated in the plant tissue and its concentration in the water column. Moreover, in organisms, mercury undergoes a redox cycle, thus creating an oxidative stress. Secondary metabolites such as phenolic compounds may be considered as biochemical markers of antioxidant response to a stress. So, it would be of interest to verify, if in a seagrass exposed to mercury contamination, a modification of these compounds can be measured. In order to verify this hypothesis, hydrosoluble phenolic compounds were identified and quantified, over an annual cycle, in sheaths and blades of Posidonia oceanica (L.) Delile, a Mediterranean seagrass coming from a site contaminated by mercury and a pristine site of the Western basin. Total phenolic compounds were measured by spectrophotometry and simple phenolic compounds by GC/MS. The study revealed the involvement of cinnamic acid derivates (caffeic, p-coumaric, ferulic acids) and moreover flavonoids in quality of antioxidant, particularly in the sheaths coming from the contaminated site. The presence of phenolic glycoside, reducing the antioxidant power of the extracts, is also discussed. Indeed, the production of phenolic compounds mustn’t be studied only on a quantitative aspect, a complementary qualitative analysis is necessary to estimate the efficiency of the antioxidant response to a given stress.

Halophila stipulacea in the Gulf of Aqaba: Seasonal In Situ Allometry and Photosynthesis

T. Malm and S. Beer, Department of Plant Sciences, Tel Aviv University, Tel Aviv 69978, Israel and the Interuniversity Institute for Marine Sciences, P.O. Box 469, Eilat 88103, Israel.

Halophila stipulacea is the most common seagrass in the Gulf of Aqaba (Red Sea), extending from the intertidal to depths exceeding 70 m. Within the Israeli part of the Gulf, no plants are found growing shallower than 2 m, and both plant size and population density increase from 2–3 m to depths of 10–12 m. In an attempt to clarify this apparent anomaly, a combined demographic and ecophysiological study was carried out at the Northern Beach, Eilat, during the period Oct. 2001 to April 2002. It was found that 1) plants at 2–4 m depth a) covered only 10% of the bottom and b) had relatively small leaves (2–3 cm²); 2) plants at 5–10 m a) covered 75–100% of the bottom and b) had three times larger leaves than the shallower populations (8–10 cm²); 3) the growth rate was 0.1–0.2 nodes d⁻¹, and was slightly higher at 5 than at 2.5 m; 4) photosynthetic rates as well as the irradiances at which light saturation occurred (both measured by underwater PAM fluorometry) increased by some 100% between Feb. and April, and 5) the mortality of shallow growing plants was high during a southeastern storm event—otherwise the natural mortality of apical shoots was around 20% per month (some of this mortality was observed to be the result of grazing by sea urchins). During the spring 2002, the
following characteristics were to be investigated in outdoor mesocosms: the sensitivity of photosynthesis and growth to UV radiation, a possibility of nutrient limitation in shallow populations, and the potential of reproduction by seeds (by determining the number and germinability of seeds throughout seasons and depths). The results will be discussed with reference to the growth patterns found in the field and literature data.

Biogeochemical Variation on a Mesoscale in Tropical Australian Seagrasses

J. E. MELLORS, School of Tropical Environment Studies Geography, James Cook University, Townsville, Queensland, Australia and Queensland Fisheries Service, Queensland Department of Primary Industries, Cairns, Queensland, Australia.

Much of our knowledge on seagrass ecology has been through the study of the seagrasses Zostera marina, Posidonia oceanica and Thalassia testudinum of the northwest Atlantic, Mediterranean or Caribbean areas respectively. Consequently, much of the dogma regarding seagrass ecological processes and biological attributes/responses are based on the results of studies on a few structurally large species. In addition, often single parameters from one location/meadow have been used. This study investigates the validity of some of the seagrass paradigms for intertidal seagrass beds within the central region of the Great Barrier Reef World Heritage Area in northeastern Australia. A multivariate approach was taken to investigate nutrient status and sediment structure within eleven intertidal locations over a 556 km (meso-scale) stretch of coastline. Halophila spp. and Halodule uninervis (narrow form) characterized most of these locations. Consequently, in contrast to much of the literature, this study concentrated on species that are structurally small and that establish seasonally and interannually ephemeral beds. These seagrass beds also tend to be open systems with respect to nutrient cycling due to high grazing, low detritus and epiphyte production, and their reduced ability to baffle water currents. Whilst significant correlations indicated general relationships between biotic parameters and sediment nutrients and structure, MANOVA outcomes resoundingly showed that most of the variance in the chemical, physical, and biotic environments could be explained by the difference between individual locations. Even meadows colonized by the same species of seagrass, and in close geographical proximity, had significant differences in sediment nutrient status, sediment profile, and plant nutrient status. This study demonstrates that a research approach that takes into consideration fundamental habitat differences may be required to better understand and interpret ecological processes and biological attributes/responses of seagrasses.

Nitrogen Dynamics of the Surfgrass Phyllospadix iwatensis Makino

N. HASEGAWA, H. IIZUMI, AND H. MUKAI, (NH) Graduate School of Science, Hokkaido University, Sapporo, Japan; (HI) Japan Sea National Fisheries Research Institute, Niigata, Japan; (HM) Field Science Center for Northern Biosphere, Hokkaido University, Sapporo, Japan.

The nitrogen dynamics of the surfgrass Phyllospadix iwatensis were studied from estimations of nitrogen uptake and incorporation (nitrogen required for growth) in Akkeshi Bay, Hokkaido, Japan (43°00'N 144°50'E). Phyllospadix has been suggested to uptake nitrogen by leaves only from water column. This study showed P. iwatensis can uptake nitrogen not only from water column but also from sediments by leaves and roots, respectively, and the relative importance of each part was changed seasonally. Mainly, leaves of P. iwatensis contributed to total nitrogen uptake in fall and winter when dissolved inorganic nitrogen (DIN) in water column was high. Otherwise, the contribution of roots was higher than that of leaves in spring and summer when DIN in water column was very low. However, seasonal fluctuation of nitrogen uptake from external media did not sympathize with that of nitrogen incorporation. In summer, nitrogen uptake was not enough for increased nitrogen incorporation, but the excess of nitrogen uptake was occurred in winter. Nitrogen incorporation in summer might be supplied from internal nitrogen source, which was stored in winter, together with nitrogen uptake from external media.
Nitrate Reductase Activity Varies Along the Vertical Distribution of *Zostera noltii* (Hornem.)

A. Alexandre, J. Silva, and R. Santos, CCMAR, Universidade do Algarve, Campus de Gambelas, 8000–117 Faro, Portugal.

Nitrate reductase activity was measured using an in situ method, which determines the enzyme activity without cell disruption, in two *Zostera noltii* (Hornem.) morphotypes in Ria Formosa tidal lagoon, southern Portugal. The morphotypes are related to the vertical distribution of the species. They were collected in the upper and lower limits of an intertidal meadow, which correspond to a 2-m vertical gradient. The lower plants are only emerged for a 2-hr period in each tide contrasting to the 6 to 8 hr of emersion of the upper plants. In a first experiment, nitrate reductase (NR) activity was measured in whole leaves and in roots of *Z. noltii*. Nitrate reductase activity was 30- to 40-fold higher in leaves than in roots, which indicates that nitrate reduction is essentially made through the aerial part of the plant. The effects of temperature (5 C steps, from 5 C to 45 C), pH (7, 8 and 9) and elevation (upper and lower intertidal) on leaf NR activity were tested in a factorial design (n = 5). Temperature had a significant effect on NR activity. Nitrate reductase activity was always higher in the upper plants, at all temperatures. Activity peaks for upper and lower plants were, respectively, 6.38 Cmol NO\textsubscript{3} \textsuperscript{-} g\textsuperscript{-1} DW h\textsuperscript{-1} at 25 C, and 3.45 Cmol NO\textsubscript{3} \textsuperscript{-} g\textsuperscript{-1} DW h\textsuperscript{-1} at 35 C. There was no significant effect of pH on enzymatic activity. A significant interaction between pH and temperature was found only at 30 C and pH 8. The higher NR activity of upper plants may be an adaptation to the reduced immersion time when nitrate of the water column is available to plants.

Effects of Light Availability on Growth and Architecture of *Zostera noltii* Hornem.

G. Peralta, J. L. Pérez-Lloréns, I. Hernández, and J. J. Vergara, (GP, JLP-L, IH, JJV) Department of Biology, University of Cádiz, 11510 Puerto Real (Cádiz), Spain; (GP) Spatial Ecology, NIOO-CEME, P.O. Box 140, 4400 AC Yerseke, The Netherlands.

The growth-irradiance curve of *Zostera noltii* was characterized for entire plants collected from Cadiz Bay Natural Park (southwestern Spain). Using an outdoor mesocosm, over a period of 2 wk, plants were exposed to 1%, 7%, 42% and 100% SI. Maximum growth was observed in plants under 42% SI (2.4 mg DW plant\superscript{-1} d\superscript{-1}). Lower growth values (1.6 mg DW plant\superscript{-1} d\superscript{-1}) were observed at 100% SI, suggesting negative effects of photoinhibition on the growth of this species. Light availability affected the overall growth, but also the pattern of the plant development. The contribution of the apical shoots to the leaf production was nearly constant (ca. 1.13 cm plant\superscript{-1} d\superscript{-1}) regardless of the light level (except at 1% SI). Differences in growth among the light treatments were due to differences in recruitment and growth of lateral shoots. Rhizome branching was only observed at 42% SI. We discuss the possibility of a branching light threshold and its ecophysiological relevance for the recruitment and density gradients of shoots within seagrass meadows.

Does *Thalassia testudinum* Suffer from Photoinhibition in a Reef Environment? An Experimental Study into Interactive Effects of Irradiance and Nutrients.

G. Reyes-Zaivala, Unidad Académica Puerto Morelos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Q. R., Mexico.

The interactions of nutrient availability and light on the seagrass *Thalassia testudinum* were evaluated in a tropical reef lagoon, where oligotrophic conditions and supersaturating levels of irradiance prevail. The hypothesis was, that excess of irradiance foments photodamage, which is enhanced by the oligotrophic conditions, since nutrients are required for repair of the photosystems in the dark. To evaluate this hypothesis, 24 plots (1.20 \times 1.50 m) were placed at two times of the year (summer and winter) in a back-reef area of the lagoon. Treatments were: shading (cage with neutral mesh), fertilization (injection of fertilizer into the sediment), combined shading and fertilization, control (no treatment), procedural control of shading (cage without mesh), and procedural control of fertilization (puncture the sediment). Parameters of growth (LER, PI), production (P, P/B, SGR), plant morphometrics (LAR, SLA, LWL, SWR, RWL, leaves per shoot, leaf length and width, biomass per shoot), and photobiology [ETR vs irradiance, Fv/Fm, absorptance, (Chla), (Chlb), (carotenes)] were mea-
The interactive effects of light, nutrients and herbivory on the structure and functioning of a subtropical turtlegrass meadow were studied. The variables included light at ambient and 40% reduction; nutrients at ambient and 2X ambient concentrations; and herbivory with no herbivory. The simulated effects of a density of 15 sea urchins/m², a three-way ANOVA showed that nutrient additions resulted in significant decreases in turtlegrass aboveground biomass, epiphyte biomass, and NAPP, while belowground biomass increased significantly during the peak of the growing season. Shoot density, average number of leaves per shoot, and leaf length showed a generally increasing trend. In enriched plots, the contribution of seagrass material to the food web. The implications of these results will be discussed to evaluate whether seagrass detritus is indeed trash or treasure in this environment.
As with terrestrial plants, seagrasses seem to respond more significantly to light and nutrients levels, than to herbivory.

**Plant–Animal Interactions in Seagrass-Dominated Ecosystems: A Review and a Prospectus**

K. L. Heck Jr., J. F. Valentine, and P. M. Spitzer, Dauphin Island Sea Lab, University of South Alabama, 101 Bienville Boulevard, Dauphin Island, AL 36528.

Two of the best-known generalizations about seagrass-dominated ecosystems are: (1) that seagrasses are “nurseries” that provide abundant shelter from predators and enhanced food supplies for juvenile finfish and shellfish; and (2) that direct grazing of seagrasses is of little importance in coastal food webs. These familiar paradigms concerning plant-animal interactions in seagrass meadows have recently been reassessed, and we begin by reviewing them. The seagrass “nursery hypothesis” has recently been confirmed by a meta-analysis of data on survival and growth of juveniles in seagrass meadows vs other shallow water habitats. There are a few notable exceptions, however, and we consider them. Regarding grazing of seagrasses, it has become clear that its trophic importance has been significantly underestimated, owing primarily to methodological problems and idiosyncrasies of study sites. We also have learned that herbivores can, and sometimes do, consume the bulk of aboveground production, especially in lower latitudes, and that intermediate levels of herbivory can stimulate new shoot production. In less studied areas, there is new and increasing evidence that both epifaunal and infaunal animals produce positive effects on seagrasses. Best understood are the beneficial effects of epiphyte consumption by mesograzers, such as crustaceans and mollusks, which can prevent seagrasses from being shaded by epiphytes, even in the face of high nutrient loading. There is also growing evidence that semi-infaunal bivalves can often produce positive effects on seagrasses by fertilizing porewaters and by providing additional shelter for mesograzers. Fertile areas for future plant-animal research are manifold, and a sampling includes: the effects of herbivory on seagrass demography and flowering rates; the magnitude of seed predations; the role of mesograzers in determining epiphyte composition and abundance; and the biogeochemical effects of infaunal feeding and burrowing activities as they influence on the metabolism of roots and rhizomes.

**Proximate Constituents of *Halodule wrightii*: Food for Captive Manatees along the Northeastern Coast of Brazil**

K. M. Magalhães, S. J. Macedo, G. Taraki, E. Eskinazi Leça, and F. de O. Magalhães, (KMM) Rural University of Pernambuco, Recife, Brazil; (SJM, GT, EEL) University of Pernambuco; (FOM) Catholic University of Pernambuco, Recife, Brazil.

*Halodule wrightii* Ascherson is a common food for captive manatees (*Trichechus manatus* L.) in the northeastern region of Brazil. In Pernambuco, they are fed exclusively seagrass leaves collected from Pilar Beach, eastern end of Itamaracá Island (7°43’S 34°49’W). Our study aimed at determining seasonal and spatial variations in the proximate constituents of this important local food source. Seagrasses were collected from Pilar Beach, at three different depths (exposed lower intertidal to subtidal areas) during 3 mo of the dry season (Jan.–March 1998) and 3 mo of the rainy season (June–Aug. 1998). The plants were divided into leaf, leaf sheath, rhizome and root. The levels of ash, protein, carbohydrate, lipid, cellulose, lignin, hemicellulose and caloric content were determined for each plant fraction. The results showed that the leaves had high protein levels, carbohydrates and caloric content throughout the year, showing no significant differences between the rainy and dry seasons, suggesting continuous growth throughout the year. No significant differences were found between depths. The high levels of cellulose in *H. wrightii*’s leaves indicate that the plants are adapted to the strong hydrodynamics conditions in the area. In the roots, we can also find high levels of proteins possibly due to the conversion of fixed nitrogen into organic compounds. The low levels of soluble carbohydrates in the rhizomes suggest the rhizomes are not used as storage organ in this tropical region and, as the leaves have high levels of protein during both seasons, the species seems to be opportunistic or “r” strategist. This study shows that the nutritional value of *Halodule* leaves fed to manatees is relatively constant between seasons and depths.
How does Seagrass Diversity Influence Faunal Diversity and Is the Influence Consistent Across Different Assemblages of Organisms?

P. S. LAVERY, G. HYNDGES, AND A. BREARLEY, (PSL, GH) Centre for Ecosystem Management, Edith Cowan University, Joondalup, Western Australia, Australia; (AB) Botany Department, The University of Western Australia, Nedlands, Western Australia, Australia.

We examined the influence of seagrass composition on the composition and spatial and temporal patterns in the faunal biodiversity of seagrass meadows. While spatial heterogeneity in seagrass ecosystem biodiversity has been described for faunal assemblages, it rarely done simultaneously for different types of biota and different seagrass habitats. We examined fish, macroinvertebrates and macroalgal assemblages in four habitats on Success Bank, Western Australia: Posidonia coriacea and Amphibolis griffithii habitat, and deep and shallow unvegetated habitats. Each assemblage was examined separately to describe diversity between and within habitats and between seasons. These patterns were then compared to those revealed when the datasets were combined. Multivariate analyses confirmed that each assemblage varied significantly between habitats, sites and seasons. Assemblages in different seagrass habitats were different to each other and to that in sand habitats. Assemblages in sand were also different to each other, but less so that between seagrass habitats (e.g., Clarke’s R values (ANOSIM) for differences in fish assemblages between the seagrass habitats were 0.608 ($P < 0.001$) compared with 0.242 ($P = 0.019$) between the sand habitats. Amphibolis griffithii forms dense meadows whereas $P$. coriacea forms patchy meadows with areas of sand within the habitat. The diversity of $P$. coriacea was more similar to that of shallow sand ($R = 0.212$ and $P = 0.021$) than was the case for $A$. griffithii habitats ($R = 0.563$ and $P < 0.001$). These differences were maintained in the combined data set (macroinvertebrates, fish and macroalgae), indicating that no one assemblage was driving the patterns. The results revealed a strong influence of seagrass habitat on biodiversity. Generally, the influence of habitat was stronger than any spatial or temporal variability within habitats. The relative similarity of diversity in $P$. coriacea and shallow unvegetated habitats suggests that these patterns are largely driven by habitat structure.

Does Increased Habitat Structure Provide Increased Refuge from Predation?

J. MATTILA AND K. L. HECK JR., Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, AL 35628, (JM) Present address: Huso Biological Station and Department of Biology, Environmental and Marine Biology, Abo Akademi University, Emabiliryvagen 713, FI-22220 Emkirby, Finland.

Submerged aquatic vegetation (SAV) usually hosts higher numbers of both invertebrates and fish than unvegetated substrates. Predation risk is thought to decrease with increasing SAV biomass or shoot density, resulting in higher abundance and diversity of potential prey species in complex areas (i.e., in dense vegetation). We hypothesized that predation pressure might remain unchanged in SAV habitats if the ratio between predators, prey and surface area was kept constant. This hypothesis was tested with aquarium experiments where pinfish (Lagodon rhomboides) were used as predators and grass shrimp (Palaemonetes pugio) as prey. Predation effects were studied on an unvegetated substrate and at three different densities (400, 2,000 and 4,000 leaves m$^{-2}$) of artificial SAV (mimicking turtlegrass Thalassia testudinum). Our results showed that SAV provided significantly more shelter than unvegetated substrate, but no significant differences were found among the different SAV densities. These results conflict with results from most previous experiments that tested the sheltering role of SAV, where increasing leaf density was associated with increased prey survival. However, our experimental design differs from all previous experiments in that we increased both the numbers of prey and predators with increasing seagrass density thereby mimicking what is observed in nature, whereas previous experiments were conducted with constant numbers of prey and predators at differing densities of SAV. Our results indicate that it is not safe to assume that increasing vegetation density will consistently lead to proportionally higher prey survival, and may help explain why small invertebrates frequently leave the shelter of seagrass and move out onto unvegetated bottoms.
Detritus Consumption in Polychaete Borers of *Posidonia oceanica* Sheaths in the Mediterranean Sea: Implications for the System

M. C. Gambi and M. Cigliano, Laboratorio di Ecologia del Benthos—Stazione Zoologica “Anton Dohrn”, 80077 Ischia, Napoli, Italy.

Polychaete borers of the Mediterranean seagrass *Posidonia oceanica* dig sinuous burrows into the sheaths, which are widely distributed and abundant in beds with different typology, shoot density and depths, and occur all year around. Gut content analysis of the two most abundant species, *Lysidice ninetta* and *L. collaris*, showed the prevalence of both dead and live seagrass tissues. In order to evaluate the ecological implications of these organisms for the system, laboratory experiments on detritus consumption were performed with both species. Specimens of *L. ninetta* and *L. collaris* were grouped into three size classes; five individuals of each class were separately reared and with intact scales offered. The amount of tissue removed by worm feeding was estimated at regular intervals (2–3 d) for each sheath by means of an image analysis technique. Two experiments were performed lasting for 40 and 85 d, respectively. For both *L. ninetta* and *L. collaris*, significant differences were found between the three size classes examined. Mean tissue consumption at the end of the 40 d experiments ranged for both species between 1.3 (small individuals) and 3.8 (large individuals) mg dry weight per sheath, corresponding to 6.8% and 11.8% of the sheath mass, while for the 85 d experiment values ranged between 1.7 (small individuals) and 5.5 (large individuals) mg dry weight per sheath, corresponding to 8.8% and 15.5% of the sheath mass. These data correlated with those on shoot density and sheath production in selected *P. oceanica* stands, lead to estimate that, according to borer abundance, the sheath mass removed by these organisms ranged from 1.7 g d.w/m²/y to 6.5 g d.w/m²/y. These values represent approximately from 3.5% to 9.8% of the sheaths mass produced each year. Considering that sheath decay in *P. oceanica* is very slow, and that sheaths represent a sink for the organic carbon, these consumption values, although relatively low, have an important ecological significance.

Macroalgae Associated to *Halodule wrightii* Beds on the Coast of Pernambuco, Northeastern Brazil

K. M. Magalhães, S. M. B. Pereira, N. C. L. Guimarães, and L. B. Amorim, Biology Department, Rural University of Pernambuco, Brazil, Recife, Brazil.

Benthic, drift and epiphytic macroalgae associated to two populations of *Halodule wrightii* (Pilar Beach at 7°43' S 54°49' W and Campos Beach at 8°44' S 35°06' W) were studied in Northeastern Brazil. The monthly collections between July 2001 and April 2002 were done along transects ranging from exposed intertidal areas to areas 4.5 m deep. Thirty-seven taxa were identified. The most representative Division was Rhodophyta (with 47% of the species), followed by Phaeophyta (29%) and Chlorophyta (24%). The flora from the two areas was quite different with only four species in common: *Hypnea musciformis*, *H. spinella*, *Dictyopteris delicatula* and *Spatoglossum Schroederi* which is expected as the macroalgal flora not associated to seagrasses is also different in these two areas. The Campos' seagrass meadow is characterized by the common occurrence of *Caulerpa cupressoides* var. *lycopodioides*, *L. disticha* and *Halimeda incrassata*. *H. incrassata* was observed to be competing with the seagrass for space. In contrast, in Pilar's seagrass meadow, *Dictyota menstrualis* e *Spatoglossum Schroederi* were the most common species. Most of the macroalgae (58%) were found growing in the sediment and on rocks within the seagrass meadow while only 26% were epiphytic on the seagrass leaves and 12% were drift algae which were not identified as benthic or epiphytic in any sample. The low number of epiphytic species is likely to be due to the dominance of certain species such as *H. musciformis* known for their rapid growth and potential to shade other photosynthetic organisms.

Nutrients, Gastropod Grazers, and Seagrass Leaf Turnover Rate as Controls of Epiphyte Loading on *Thalassia testudinum*

T. A. Frankovich, J. C. Zieman, B. J. Peterson, and J. W. Fourquarean, (TAF, JCZ) Department of Environmental Sciences, University of Virginia, Charlottesville, VA; (BJP, JWF) Department of Biological Sciences and Southeast Environmental Research Center, Florida International University, Miami, FL.

Within seagrass ecosystems, epiphyte biomass provides a necessary food source supporting higher trophic levels, but excessive epiphyte loading can lead to seagrass loss. The amount and nature of
epiphyte loading is the result of various controlling factors. Nutrient availability allows for the growth of algal epiphyte biomass, while grazing organisms control epiphyte accumulation. Seagrasses themselves may ameliorate or exacerbate epiphyte fouling by their leaf turnover rates. Our studies of Thalassia testudinum in Florida Bay indicate that the regional distribution of epiphyte loads is strongly influenced by nutrient availability, particularly phosphorus. Correlational studies also suggest that snail grazer abundance may be an important temporal control on epiphyte loading. Variability in Thalassia seagrass leaf turnover rate in this subtropical ecosystem is small relative to epiphyte loading and snail grazer abundance. The relative importance of these controlling factors is discussed in the form of a theoretical model of seagrass epiphyte loading. This model is based upon current literature consensus and presented correlational and experimental evidence.

Waterfowl Grazing on Zostera: Exclosure Experiments

J. O. Albertsen and H. Mukai, Akkeshi Marine Biological Station, Hokkaido University, Akkeshi-gun, Hokkaido, Japan.

The whooper swan is a major seagrass herbivore in the Akkeshi Estuary, northeast Japan. The large number of swans wintering in the estuary has a serious impact on the standing biomass of eelgrass. Four waterfowl exclosures were erected in a Zostera marina bed, and six exclosures were placed in a gradient of different densities in a mixed bed of Z. marina and Z. japonica. Seagrass parameters were collected when the migrating swans arrived in the autumn and after the birds had been observed grazing in the seagrass beds for 1 mo. We discuss these parameters according to grazing pressure and seasonal factors.

Caridean Shrimp Associated to Seagrass Meadows in the Gulf of Mexico and Caribbean Sea: Composition, Diversity and Density


Extensive seagrass meadows grow in shallow waters of the Gulf of Mexico and Caribbean Sea. This habitat provides a complex physical array for a great diversity of fauna. Between this fauna, caridean shrimps are density dominant associated. Invertebrates were caught with a Renfro’s beam trawl. Some water and sediment parameters were examined. A total of 26,947 specimens, 20 species belonged to families Palaemonidae, Alpheidae and Hippolytidae were collected in 13 localities in the Gulf of Mexico and Caribbean Sea. Hippolytidae family was diversity and density dominant. Dominant species were Thor dobcki (45.9%), Hippolyte zostericola (23.4%), and Toseuma carolinense (12.9%).

Outwelling of Zostera noltii Detritus from the Western Sector of Ria Formosa Tidal Lagoon (Southern Portugal) to the Ocean


The import/export fluxes of Zostera noltii detritus through the Ancão inlet, which links the western sector of Ria Formosa tidal lagoon (southern Portugal) to the ocean, were assessed both by harvesting plant detritus with nets along tidal cycles, and by estimating fluxes of detritus for a range of tidal cycles with a hydrodynamic model. The total amount of leaf material release from the sector was estimated using available data on the Z. noltii leaf release. Aerial photographs were used to map the species meadows and a geographical information system was used to calculate the area covered by Z. noltii. Model estimates of the transport dynamics of vegetation detritus, which included the influence of the wind regimes at the time of net sampling, were compared with sampled data. Simulations of Z. noltii transport supported the observations that the transport of vegetation detritus floating at the surface was not a continuous process, but in pulses (very high values in some tides). The simulated Z. noltii transport through the Barra inlet was of the same order of magnitude than the measured values. There was a significant effect of flow on Z. noltii transport, with averages of 52.9 g m⁻¹ h⁻¹.
exported in ebb flows and 34.3 m$^{-1}$ h$^{-1}$ imported in flood flows. A total of 61.1 tons of dry weight of Z. noltii leaves were exported during 1 yr and 39.6 tons were re-imported. There is a net yearly export of 21.5 tons of dry weight of Z. noltii leaves from the western sector of Ria Formosa to the adjacent coastal area or about 9.7 tons of carbon, 817 kg of nitrogen and 84 kg of phosphorous. The total organic carbon released by Z. noltii meadows of the western sector of Ria Formosa in 1 yr was about 162 tons of C. Consequently, the percentage of the production that is exported is about 4%. This organic matter may play an important role in the food web of the adjacent coastal system, as there is no attached vegetation in this area. This flux is maintained throughout the year probably fueling the important local fisheries of bivalves, octopus and fish.

**Intertidal Zostera noltii Beds: Are the Last Seagrass Remains in the Wadden Sea Important Nurseries for North Sea Fish?**

P. Polte, Wadden Sea Station Sylt, Alfred Wegener Institute Foundation for Polar and Marine Research, Bremerhaven, Germany.

Worldwide subtidal seagrass beds are known as important nursery areas and breeding grounds of various fish species. Within the whole Wadden Sea area from the Netherlands up to Denmark, subtidal seagrass beds are completely extinct since the “Wasting Disease” in the 1950s. Nowadays the occurrence of exhaustive seagrass meadows is exclusively bounded to the intertidal. This investigation deals with the question if those remaining intertidal seagrass beds have positive impacts on species richness and breeding success of North Sea fish, although this biotope is only temporary available during high tide and requires an intensive tidal migration. The results of drop trap and beach seine sampling showed that numbers of fish species and individuals were consequently higher within seagrass beds compared to adjacent sand flats. By using light traps in tidal areas with different emersion it could be shown that habitat structure affects the migration behavior of fish. On vegetated tidal flats, juvenile whiting (Merlangius merlangus, L.) immigrate into the shallower parts of the intertidal close to the shore, whereas on unvegetated sand flats whiting stayed close to the deeper gulleys. The complex structure of the seagrass bed increases the density of prey by attracting a variety of epibenthic crustaceans. On the other hand the plants shelter juvenile fish from predation by seabirds. Experiments pointed out that intertidal Zostera noltii meadows act as spawning grounds for pelagic fish species as garfish (Belone belone, L.) and herring (Clupea harengus, L.). Both species immigrate to the intertidal area to attach their spawn to the seagrass leaves. These studies suggest that intertidal Z. noltii-beds are able to increase the diversity and abundance of fishes, although no explicit seagrass specialists could be found.

**Microhabitat Distribution, Population Dynamics and Fitness of an Infaunal Amphipod (Corophium volutator Pallas) in a Patchy Seagrass Landscape**

C. Boström, M. Lastuniemi, and E. Bonsdorff, Åbo Akademi University, Environmental and Marine Biology, Akademigatan, 20500 Åbo, Finland.

There is an important relationship between spatial habitat patterns and many ecological processes, such as dispersal, recruitment, access to mates, predator–prey interactions and diversity. However, few studies have addressed how spatial patterns of seagrass landscapes affect the life cycle and fitness of individual species. We investigated how Corophium volutator, a common and widely distributed infaunal amphipod, utilize a sub-tidal seagrass landscape in the northern Baltic Sea, Finland. In 1998–99, five different types of micro-habitats were sampled by scuba-diving: (1) bare sand, (2) patches of Ruppia maritima, (3) the unvegetated eroding edge relief of Z. marina patches, (4) the sheltered interior parts of Z. marina patches and (5) discrete, unvegetated patches of clay embedded in a sand matrix. A pilot sampling program was carried out in 1998, while the sampling effort (1–2 times/mo) in 1999 spanned over the reproduction period (4 mo: June–Sep.) of C. volutator in the study area. Population structure was studied in terms of total abundance, individual biomass, size distribution, number of gravid females, sex ratios and fitness (number of eggs per female, egg size and juvenile growth). In 1998, the interior parts of Z. marina patches were male-dominated, while females were found in equal numbers in interior parts and along patch edges. The share of gravid females and the total number of eggs per female was significantly higher at patch edges compared to the interior parts. By contrast, in 1999 no significant differences in population structure and fitness components were found among the...
habitats sampled, and the population dynamics was spatially and temporally synchronized in all habitats sampled. The only habitat patches clearly differing were the clay patches, supporting amphipod densities exceeding the highest recorded in the literature. Possible reasons and consequences of the surprisingly similar ecological functions provided by the physically different habitats within patchy seagrass beds are discussed.

Assessment of a Trophic Cascade Model in a Temperate Seagrass System under a Natural Nitrogen Gradient

P. JORGENSEN AND S. E. IBARRA-OBANDO, Centro de Investigación Científica y Educación Superior de Ensenada (CICESE), Ensenada, Baja California, Mexico.

The decline of seagrass systems was traditionally conceived under physico-chemical control. The importance of top-down processes was recently recognized. In order to test a trophic cascade model which postulates that an increase of small fish predators control the abundance of mesoherbivores leading to epiphyte algal overgrowth and seagrass loss, we assessed the effect of a small fish on the growth of Zostera marina. The experiment took place in San Quintin Bay, a “Y” shape coastal lagoon in Baja California (Mexico), in July 2001 during upwelling conditions. We selected three seagrass meadows representing a fertilization gradient: base Y, BY (maximum), west arm, BF (intermediate), and east arm, SQ (least). To corroborate spatial differences of inorganic nutrient concentrations we carried out three semidiurnal time series at 3 hr intervals in each meadow. Samples for nitrates + nitrites, ammonium, phosphates and silicates concentrations, among other variables, were considered.

After 30 d, the growth of Z. marina leaves inside cages with 40 individuals m⁻² of the pipefish Syngnathus leptorhynchos (inclusion treatment, I) was compared with the one in cages without the fish (exclusion treatment, E; n = 4). Nitrates + nitrites mean concentration was significant higher in BY (1.55 μM) than in BF (0.80 μM, P < 0.02) and SQ (0.51 μM, P < 0.01; n = 14). Seagrass growth differed both between meadows (BF > BY, P = 0.03) and treatments. At BY, inclusion of the fish resulted in reduced seagrass growth (P = 0.02): 1.4 cm d⁻¹ shoot⁻¹, compared to 2.9 cm d⁻¹ shoot⁻¹ in E treatment. At BF and SQ the inclusion of the fish did not have effect on seagrass growth (P > 0.05), I: 2.9 and 2.8 cm d⁻¹ shoot⁻¹ vs E: 3.8 and 2.3 cm.d⁻¹ shoot⁻¹, respectively. These results suggest that top-down control of Z. marina growth varies as a function of nutrient status in San Quintin Bay meadows. To evaluate this hypothesis we are, at present, repeating the experiment under low nutrient conditions, winter months.

Structural Characteristics of Two Different Bed Types of Posidonia oceanica (L.) Delile

J. A. BORG, M. J. ATTRILL, A. A. ROWDEN, P. J. SCHEMBRI, AND M. B. JONES, (JAB, MJ/A, MBJ) School of Biological Sciences, University of Plymouth, Drake Circus, Plymouth, U.K.; (JAB, PJS) Department of Biology, University of Malta, Msida, Malta; (AAR) National Institute of Water & Atmospheric Research, P.O. Box 14-901, Kilbirnie, Wellington, New Zealand.

Seagrass beds occur in various structural forms, ranging from small patches to continuous beds. Such variability has identified seagrass habitats as ideal models for the study of marine landscapes. Understanding the ecology of different seagrass landscapes enables an assessment of changes in the diversity of associated fauna and flora that may result from habitat fragmentation and forms a basis for the implementation of successful conservation and management strategies. The endemic Mediterranean seagrass Posidonia oceanica forms dense and extensive monospecific meadows that occur in several different morphotypes, including reticulate (seagrass interspersed with bare sand) and continuous beds. This study examined whether nearshore reticulate and farshore continuous P. oceanica beds, located adjacent to each other and at similar depths, had different meadow structural characteristics. Bed structural descriptors, including shoot density, number of leaves per shoot, mean leaf length and shoot dry weight, were estimated from P. oceanica shoots collected from adjacent reticulate and continuous beds at three different spatial scales: (i) tens of meters; (ii) hundreds of meters; and (iii) a few kilometers. Results of 2-factor ANOVA (factor 1 = bed form; factor 2 = sampling locations) carried out at the three spatial scales indicated a significant interaction for shoot density (P < 0.05) but not for the other bed descriptors. Overall, the study suggests that continuous and reticulate P. oceanica beds have similar bed structural characteristics and that habitat structural complexity of the foliar
stratum does not differ appreciably between the two different bed types. The findings are discussed in the light of available data on _P. oceanica_ landscapes and the relevance of the obtained results for conservation and management of this seagrass are highlighted.

**Distribution Pattern of Fish in Seagrass Beds Along the Swedish West Coast**

M. Gullström, A. Svenson, S. Baden, and L. Pihl, Kristineberg Marine Research Station, Department of Marine Ecology, Goteborg University, Goteborg, Sweden.

The diversity and richness of the fish fauna in seagrass beds may be of considerable importance throughout the world. Besides the many stationary species, temporary and transient fish may utilize seagrass habitats as spawning and nursery grounds, foraging areas as well as predation refuges. In the present study, we examined the distribution patterns of fish in eelgrass (_Zostera marina_, L.) beds along the Swedish Skagerrak coast. Spatial variation in abundance of fish was investigated on local scales (20 km) in three fjord systems, and on a regional scale (200 km) in three areas along the coast. Temporal variation was studied in the three fjord systems from June through Oct.. Species composition was shown to differ between regions, the three fjord systems, and inner and outer parts of those fjord systems. Generally, there was a trend showing an increase in fish density over time during the recruitment period, while the species diversity and individual sizes was relatively stable. The fish density ranged on the local scale from 0.19 to 15.13 fishes/m² and the mean for the three regions were 2.88, 7.94 and 11.42 fishes/m², respectively. For all areas and sampling occasions, 41 species were identified belonging to principally gasterosteidae (53%), gobidae (39%), syngnathidae (2.4%), labridae (2.2%) and gadidae (1.8%). In addition, gut content of five important fish species was analyzed in order to classify them into trophic categories and ascertain their functional role in the seagrass ecosystem. The result indicates that different feeding niches were exploited for the most abundant fish species associated to eelgrass beds along the Swedish Skagerrak coast.

**A Portable Drop Net: A New Sampling Gear of Fauna in Water Column at Seagrass Beds**


To quantitatively collect fish and invertebrates at seagrass beds, a portable drop net system was modified. The net is 3 × 3 m and 1.1 m in height with steel chain attached at the bottom edge of skirt net. The net has a ceiling net that enables to capture some fauna escaping from the top at seagrass beds deeper than 1 m. Two people on a small boat can handle the net. Capture efficiency, which was estimated by a maximum likelihood method, was high for pelagic fish such as _Myoxocephalus brandti_, and _Hexagrammon octogrammus_. Efficiencies for demersal fish such as _Pleuronectes obscures_ and _P. pinnifasciatus_, and for fish that inhabit near the bottom such as _Pholis crassispina_ and _Opisthocentrus dybowskii_ were relatively low, due to escape at the bottom of skirt net. Similarly, _Pandalus hesselrei_ which is closely associated with seagrass leaves showed high capture efficiency and _Crangon spp._ which resides near the bottom showed low efficiency. By using the capture efficiencies, faunal biomass at a seagrass bed in northern Japan was estimated. In May 2000, _Pandalopsis pacifica_ was the most abundant in number followed by _P. crassispina_, _Crangon spp._, _M. brandti_. As biomass basis, _Zoarces elongates_ was the highest and _M. brandti_ followed. Biomass we obtained was higher than those estimated by a trawl sampling, suggesting that the drop net is a more suitable gear to know faunal biomass at seagrass beds.

**Seagrass Biomass and Faunal Abundance in Laguna de Alvarado, Mexico**

A. Raz-Guzman and A. Corona, (AR-G) Instituto de Investigaciones sobre los Recursos Naturales, UMSNH, Morelia C. P. 58330 Mich., Mexico; (AC) Instituto de Ciencias del Mar y Limnología, UNAM, Cancun, Mexico.

The relationship between habitat and fauna has been of long-standing interest in a variety of aquatic environments including seagrass beds. The coastal lagoon of Alvarado is small, oligo-mesohaline and
has only one species of seagrass, *Ruppia maritima*. Four samples were collected from two sides of a spit bar with contrasting environmental conditions. A quadrant fitted with plastic walls to insure collection of fauna was used to determine the relationship between seagrass biomass and macroepibenthic fauna in a sheltered and a non-sheltered site. Biomass was recorded as dry weight and fauna was identified with the appropriate taxonomic keys. The two windward localities contrast with the two leeward ones with respect to turbidity, currents, type of substrate and seagrass biomass, and leaf length. A direct relationship was recorded between seagrass biomass and faunal abundance with an increase along the environmental gradient from the non-sheltered area to the sheltered one. Peracarid and gastropod abundance followed this trend. In the case of small mesograzers, such as amphipods and isopods, this abundance increase is directly associated with the habitat value of the meadow given by its greater biomass, whereas the snails are common inhabitants of the seagrass blades. An indirect relationship was recorded for caridean and penaeid shrimp, as the denser seagrass leaves in the two sheltered localities cause a reduction in the abundance of shrimp. Tanaidaceans are found at the bottom-water interface and are more abundant where seagrass biomass is lower, as they prefer muddy habitats. Bivalves are poorly represented, as they are mostly infaunal. Xanthid crabs are few in general, and fish most probably escaped collection thanks to their mobility. Thus, the relationship between biomass and abundance depends on the species both of seagrass and of associated fauna.

**Approach for Construction of the Closed Hydrosphere Ecosystem Modeled after Eelgrass Beds**

Y. Nishino, Y. Ishikawa, and K. Suzuki, (YN, YI) Institute for Environmental Science, Japan; (KS) Seikai National Fisheries Research Institute, Nagasaki, Japan.

Construction of the Hydrosphere Ecosystem in the Closed-System of Geo-Hydrosphere Experiment Facility as a part of the Closed-System of Ecology Experiment Facilities (CEEF) is currently under way. The material circulation mechanism and the effect of environmental changes on the ecosystem are to be studied after forming a stable ecosystem in the CHEF. The eelgrass ecosystem on the shore near Rokkasho Village is chosen as a model for constructing the closed hydrosphere ecosystem. In order to develop a stable ecosystem, preliminary two investigations such as sampling of epifauna at eelgrass beds in Mutsu Bay and culture of eelgrass *Zostera marina* were done. The sampling was attempted on a monthly basis, from Aug. 2001 with the improved NORPAC net (diameter, 440 mm; mesh size, 0.334 mm). The cultivation test of eelgrass was done in the small closed system, which has a 2-m³ aquarium from June 2001 to March 2002. Eelgrasses were transplanted into the closed system from Mutsu Bay for the test. From the results of the two investigations, we discuss the possibility of construction of the Closed Hydrosphere Ecosystem modeled after eelgrass beds based.

**Predation on Seeds of the Seagrass *Posidonia australis* in Western Australia**

R. J. Orth, K. L. Heck Jr., and D. J. Tunbridge, (RJO) Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Williamsburg, VA; (KLL) Dauphin Island Sea Lab, University of South Alabama, Dauphin Island, AL; (DJT) Marine and Freshwater Research Laboratory School of Environmental Science, Murdoch University, Perth, Australia.

While predation often governs seed abundance, and ultimately seedling and adult plant distribution and abundance in terrestrial ecosystems, there is a dearth of information for seagrass dominated ecosystems. We report here on the first study to examine predation rates on seeds of *Posidonia australis* measured during a field tethering experiment at five locations in Western Australia. Seeds were tethered in seagrass and adjacent unvegetated sand for 24 hr and then assessed for damage. Seed predation was noted at all sites and ranged from partially to completely eaten seeds. Higher proportional damage was observed in seagrass than on unvegetated sand but was only significantly greater at three of the five sites. We did not observe direct predation on the seeds but losses may be due to small fishes or invertebrates living within the canopy. Our results add to the growing body of evidence that seagrass seed predation does occur and that this predation has the potential to affect recruitment. Our data also presents an interesting contrast to the paradigm for faunal studies, which has shown higher proportional mortality in bare sand compared to seagrass.
Effects of Nitrogen Content of Turtlegrass (*Thalassia testudinum*) on Rates of Herbivory by the Bucktooth Parrotfish (*Sparisoma radians*)

M. E. Goeker, K. L. Heck Jr., and J. F. Valentine, Dauphin Island Sea Lab, University of South Alabama, Dauphin Island AL 36528.

Some vertebrate herbivores selectively feed on plans rich in nitrogen, while some invertebrates have shown no such preference. We tested the ability of the bucktooth parrotfish (*Sparisoma radians*) to selectively consume nitrogen-rich turtlegrass (*Thalassia testudinum*) leaves in both laboratory and field choice experiments. Lab results showed a fivefold greater consumption of high nitrogen *T. testudinum* leaves. At two field sites, we found more than a 10-fold greater consumption of high nitrogen *T. testudinum*, while a third site showed a sixfold greater consumption. To eliminate morphological cues, an agar mixture containing ground up leaves of either high or low nitrogen *T. testudinum* was offered to the fish, and almost twice as much high nitrogen agar was consumed. The mechanisms underlying the preference of *S. radians* for plants rich in nitrogen remain unknown but may be related to differences in chemical defenses. Selective feeding on plants rich in nitrogen, over evolutionary time, may have resulted in competitive interactions that selected for dominance by plants low in nitrogen.

Organisms as Resource Providers: A Tale of two Suspension Feeders in Seagrass Communities

B. J. Peterson, K. L. Heck Jr., and J. W. Fourquarean, (BJP, JWF) Florida International University, Department of Biological Sciences, University Park, Miami, FL 33199; (KLH) Dauphin Island Sea Lab, Dauphin Island, AL 36528.

Two field experiments were conducted to examine the potential positive interactions between suspension feeding organisms and seagrass assemblages. In St. Joseph Bay, Florida, mussel density manipulations resulted in the doubling of the total phosphorus levels of sediments, the significant reduction of leaf tissue C:P ratios; demonstrating that the mussels increased the sediment nutrient content and that these increased nutrients were biologically available to the plant. *Thalassia testudinum* responded to the presence of mussels by significantly increasing leaf lengths and productivity. Another response to the presence of mussels included a significantly reduced epiphytic load on the seagrass leaves. Secondly, utilizing mussel mimics and sediment nutrient enrichment, the separate factors of increased habitat structure and increased nutrient enrichment resulting from the mussels was tested. In Florida Bay, Florida, persistent and widespread cyanobacteria blooms have coincided with the large-scale decimation of sponge communities. One hypothesis is that the large-scale loss of suspension feeding sponges has rendered the ecosystem susceptible to these recurring blooms. A stratified random sampling design was used to identify 207 sites throughout the extent of Florida Bay. Sponge biomass estimates from these sites in conjunction with laboratory grazing rates of the dominant sponge species in Florida Bay were determined and used to assess the impact of the sponge mortality event. If the presence of sponges is able to control these phytoplankton blooms and consequently increase light availability to the benthic plant communities, then sponges may play an important role in reducing the shading effects of phytoplankton blooms, and the loss of this organism may have cascading effects on the associated seagrass community. These studies suggest that seagrass meadows may exist as a mosaic of nutrient and productivity “hotspots” when suspension-feeding organisms are present. These positive interactions may have important consequences in the development, structure and organization of seagrass communities.

Seagrass Density and Abundance of Epibenthic Crustaceans: Implications for Outmigrating Juvenile Salmon in the Northeast Pacific

S. Wyllie-Echeverria, J. R. Cordell, J. R. Skalski, T. Klinger, M. Stamey, C. Young, K. L. Fresh, and T. Wyllie-Echeverria, (SW-E, JRC, JRS, TK, MS, CY,) College of Ocean and Fishery Sciences, University of Washington, Seattle, WA; (KLF) NOAA/NMFS, NWFS, Seattle, WA; (TW-E)Department of Zoology, Brigham Young University, Provo, UT;

Epibenthic crustaceans are a valuable prey resource for outmigrating juvenile salmon (*Oncorhynchus* spp.) in estuaries of the northeast Pacific. Because four species of salmon are listed under the U.S.
Endangered Species Act as either Threatened or Endangered, protection of juvenile habitat is a high priority. Previous research has established the link between Zostera marina and the presence of epibenthic prey items, but no studies document the relationship between varying seagrass densities or leaf metrics and epibenthic crustacean abundance. The goal of this pilot study was to determine if the abundance of epibenthic salmonid prey was linked to variation in either Z. marina leaf metrics or shoot densities. In the summer of 2001, we randomly selected 11 stations along a 2,400-m transect through a shallow subtidal Z. marina meadow (~1.1 m MLLW) in northern Puget Sound, WA. At each station we sampled epibenthic crustaceans using a suction quantitative pump. We returned to the station and harvested all Z. marina within a 0.25-m³ area to obtain shoot density, leaf area and a leaf area index (LAI). While there was no relationship between leaf area or LAI and salmonid prey resources, we found a significant relationship (P = 0.0459) with shoot density. We discuss the implication of our findings specifically for Z. marina conservation in the northeast Pacific and generally for future studies designed to establish linkages between seagrass density and epibenthic crustaceans.

To Bore or not to Bore, that’s the Question: New Record of Polychaete Borers in Thalassia testudinum (Banks ex König) Leaf-sheaths in the Mexican Caribbean

B. I. Van Tussenbroek and M. C. Gambi, (BIVT) Unidad Académica Puerto Morelos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Cancún, Mexico; (MCG) Laboratorio di Ecologia del Benthos—Stazione Zoologica 'A. Dohrn' Napoli, Italy.

Borers in seagrasses have achieved a certain degree of niche differentiation in exploiting tissues of their host species, and known species, belong to Isopoda and Polychaeta. Isopods bored mainly living leaf tissue, and seemed quite specialized, occurring exclusively in their associated seagrass species, whereas polychaetes bored principally dead sheaths persisting along the rhizome, and had been found also in other substrata (algae, sediment). Polychaetes had only been registered in the seagrass Posidonia oceanica of the Mediterranean; this work deals with a new record of polychaete borers in dead sheaths of Thalassia testudinum off the Mexican Caribbean. The two species found were classified as Nematoceranis cf unicornis and Lysidice cf ninetta (Eunicidae), and they were slightly different from the same taxa reported in P. oceanica. At some sites, polychaete borers were very abundant, occupying almost all seagrass shoots. Based on their burrowing habit they were classified as small (0.20–0.50-mm width) and large (0.50–0.96 mm width) borers. Burrows of small borers were restricted to one sheath (sheath age between 2 and 5 mo), while large borers burrowed through many sheaths (age of sheath between 3 mo and 3 yr). This new record suggests that polychaete borers in seagrasses are more widespread than previously thought, and that the number of records might increase as observations are made in other seagrass species with persisting sheath remnants.

The Quality of Seagrass as a Dugong Food Resource: The Importance of the Effects of Season and Water Depth

J. Bité, S. H. Marsh, and I. Lawler, James Cook University, Townsville, Qld 4811, Australia, R. Coles Northern Fisheries Centre, Department of Primary Industries, 38-40 Tingira St Portsmith, Cairns, 4870 Australia.

Dugongs (Dugong dugon) have high biodiversity value as the only extant member of the Family Dugongidae and one of only four members of the Order Sirenia (seacows). They are listed internationally by the IUCN as vulnerable to extinction. Dugongs have declined substantially through most of their Indo-Pacific range. Dugong populations in Australian waters are now believed to support most of the world’s dugongs. Hervey Bay is a large embayment situated immediately south of the Great Barrier Reef Marine Park, approximately 350 km north of Brisbane, Australia. The dugong population in the Hervey Bay region was estimated to be approximately 2,200 in 1988 and 600 in 1993. This dramatic decrease in dugong numbers followed widespread destruction of seagrass beds after a cyclone and repeated flooding in early 1992. Dugongs feed almost exclusively on seagrasses. Evidence of dugongs feeding on sub-tidal seagrasses is increasingly reported. Previous studies have shown that the nutritional content and recovery after grazing of intertidal seagrasses varies considerably. Presently, little is known about the nutritional value of sub-tidal seagrasses grazed by dugongs. This project, based in Hervey Bay, aims to determine the effects of season and water depth on the nutritional value (N, water soluble carbohydrates, digestibility, fiber and lignin) of heavily and low grazed seagrasses, and the recovery rates of sub-tidal seagrasses after grazing. The impact of flooding on seagrasses will also
While it is widely recognized that herbivory can control the abundance, and influence the life histories of many marine plants, herbivores are thought to consume only limited amounts of seagrass production within months. The mechanism for recolonization is primarily through rapid rhizome extension, 2 to 3 times faster than recorded previously. Intense branching also results in a high density of growing apices. Large numbers of fruits are present which can recolonize a disturbed patch.

**Active Recruitment by Posidonia**

D. I. Walker and G. A. Kendrick, Botany, School of Plant Biology, University of Western Australia, 35 Stirling Highway, Crawley, 6009, Australia.

Some seagrasses actively recruit through sexual reproduction, especially the Zosteraceae and Cymodoceaceae and particularly in the tropics. For Posidoniaceae, seedling recruitment has been observed rarely in Mediterranean environments. A demonstrated exception is in Posidonia coriacea, which has been observed to establish new meadows in both siliceous and carbonate sediments through annual seedling establishment in Two Peoples Bay and on Success Bank, Western Australia. The population structure and age of seedlings of *Posidonia coriacea* has been characterized for these two locations. Recruitment and growth of these seedlings is rapid for a *Posidonia*, doubling to quadrupling the number of shoots for each successive year. These seedlings have been observed to persist and grow in situ for up to 9 yr, although rates of persistence varied between the two locations studied. There were higher numbers of older cohorts in populations from Success Bank, on the temperate west coast, than from Two Peoples Bay, on the temperate south coast of Western Australia. The annual recruitment events and rapid growth rate observed in this study supports the view that *P. coriacea* is a colonizing species. These observations challenge the present view that species of *Posidonia* rarely colonize from seedlings, suggesting that seedling recruitment is important for meadow maintenance in *P. coriacea*, and we urge a re-evaluation of seedling recruitment in other species of *Posidonia*.

**Population dynamics of Halophila ovalis after dugong grazing in a dynamic sub-tropical ecosystem**

K. McMahon, Marine Botany Group, Centre for Marine Studies, University of Queensland, Brisbane, Australia.

Seagrass meadows exposed to regular disturbance are expected to be dominated by species with rapid turnover, open nutrient cycling and the ability to reproduce quickly from seed. In Moreton Bay, Queensland, large herds of dugongs (20 to 150 individuals) consume vast quantities of seagrass. *Halophila ovalis* is the preferred forage species. *Halophila ovalis* growth dynamics were investigated by rhizome tagging and estimating flowering and fruiting densities. Two grazed seagrass sites were studied, one intertidal (−0 ms) and one sub-tidal (−1.5 ms). Intertidally, *H. ovalis* rhizomes grew 20 ± 3 mm apex−1 d−1 and 1 ± 0.1 new leaf apex−1 d−1 was produced. These rates were halved at the sub-tidal site where rhizomes grew at 6 ± 1 mm apex−1 d−1 and 0.5 ± 0.05 new leaf apex−1 was produced every day. The density of apices was 1,000 m−2 giving the potential of lateral rhizome extension of 6 to 20 mm2−1 d−1. Total productivity for these meadows was 1.5–8 g dw m−2 d−1 or 0.6–3.0 g C m−2 d−1. Preliminary estimates of flowering and fruiting found high densities of fruits in *H. ovalis* meadows, 570 m−2 between Oct. and Dec. 2001 with an average of 15 ± 4 seeds fruit−1 (8,550 seeds m−2). Fruits were not detected in Jan. 2002. *Halophila ovalis* meadows in Moreton Bay demonstrate that they respond quickly to dugong grazing based disturbance, returning to pre-grazing biomass within months. The mechanism for recolonization is primarily through rapid rhizome extension, 2 to 7 times faster than recorded previously. Intense branching also results in a high density of growing apices. Large numbers of fruits are present which can recolonize a disturbed patch.

**Seagrass Herbivory: New Evidence of Dynamical Interactions Between Seagrasses and Their Consumers**

J. F. Valentine, Dauphin Island Sea Lab, University of South Alabama, 101 Bienville Boulevard, Dauphin Island AL 36528.

While it is widely recognized that herbivory can control the abundance, and influence the life histories of many marine plants, herbivores are thought to consume only limited amounts of seagrass produc-
tion and have little effect on their biology. Emerging evidence suggests that this view is incorrect and that marine herbivores consume substantial quantities of seagrass in many coastal areas. The apparent contradiction between high estimates of consumption, and the persistence of extensive seagrass meadows, indicates that many dynamic, unstudied interactions exist between these plants and their consumers, and that our current understanding of seagrass herbivory is overly simplified. Among the new findings to be presented are that herbivores can trigger shifts in seagrass species composition (from vulnerable to less vulnerable species), growth rates, and possibly reproduction. Recent evidence also indicates that some seagrasses produce chemical defenses that may deter repeated attacks by grazers. Additionally, we will address the hypothesis that intense harvesting of piscivorous fishes has led to anomalously high densities of marine herbivores and seagrass grazing in modern-day food webs. Using the marine reserves of the Florida Keys, we have found that while the presence of piscivorous fishes can reduce the density of smaller seagrass herbivores they have little impact on overall grazing rates. When taken together, this new evidence strongly suggests that we have underestimated the importance of seagrass herbivory in many coastal ecosystems.

Session: Traditional Seagrass Knowledge

Report from the Traditional Seagrass Knowledge Working Group

S. WYLLIE-ECHEVERRIA, M. MATEO, AND J. BORG, (SWE) University of Washington, Seattle, WA; (MM) Universitat de Barcelona, Barcelona, Spain; (JB) University of Malta, Msida MSD 06, Malta.

During and after ISBW-4 scientists from Iceland, Spain, France, Malta, United Kingdom, Sweden, Germany, Australia, Japan and the United States formed the traditional seagrass knowledge (TSK) Working Group to advance the notion that traditional ecological knowledge and wisdom (TEKW) may strengthen regional efforts to protect the seagrass biome. This effort was guided by studies that demonstrated seagrass flora had both cultural and socio-economic value for coastal dwellers in the north Atlantic and northeast Pacific for many generations. For the last 2 yr the TSK Working Group has compiled information and data now archived at the School of Marine Affairs, University of Washington. The objectives of this working session are to (1) submit a synthesis report; (2) engage in dialogue with others wishing to contribute to the project and (3) discuss the future of the TSK.

Using the Concept of Ecological Services to Promote Management and Conservation of Seagrasses

M. DE LA TORRE CASTRO, Department of Systems Ecology, Stockholm University, Stockholm, Sweden.

The concept of ecological services has been developed in the last decades to highlight the links between natural ecological functions and human welfare. Ecological services are the benefits that humans derive, directly or indirectly, from ecological functions. The use of this concept has provided a framework to analyze the interface between economics and ecology as well as to communicate the importance of nature for human activities and survival. The concept has been applied to other ecosystems but it has been scarcely used for seagrasses. While most ecological functions are well identified for seagrass ecosystems, the links between them and benefits for humans are still not obvious for many decision makers. The objective of the presentation is to broaden the application of the concept of ecological services to seagrasses and to discuss possible methods of analysis and valuation. A classification of ecological services for seagrasses will be presented based on previous classifications and the concept of total economic value. Primary and secondary productivity from seagrasses will be specially highlighted as the principal ecological functions providing welfare to humans. The practical applications of the concept will be shown with an example of valuation of seagrasses in a rural tropical context.

Session: Genetics, Taxonomy and Reproductive Biology

Anthesis Effects on the Biometry and on the C, N, P Contents of Flowering Shoots

S. GOBERT AND J. M. BOUGUENEAUX, Oceanology, University of Liège, B66, Sart Tilman B-4000 Liège, Belgium.

The oligotrophic Bay of Calvi (Corse-France) is characterized by a well-developed Posidonia oceanica (L.) Delille meadow. From 1977 to 1993, flowers were scarce and seedlings rarely observed. However,
from 1994 to 2001, the meadow has blossomed each year, especially in 1994, in 1998 (flowering index of 36 ± 25% and 10 ± 9% respectively). We have compared the biometry and the C, N, P contents of flowering and nonflowering shoots. The anthesis induces a decrease in the number of juvenile leaves resulting in a significant reduction in the number of leaves on the flowering shoots. All the leaves of the flowering shoots are narrower than the leaves of nonflowering shoots. A modification of the leaf growth also appears in flowering shoots; the oldest leaves are longer and the leaves induced during or after anthesis are shorter. At 10-m depth, we have estimated that the anthesis lasts roughly 3 mo and that the flowering is induced 7 mo before anthesis. The flower formation causes a modification of C and N concentration in intermediate and adult leaves. The percent of C has significantly increased in leaves of flowering shoots. However, the percentage of N has significantly decreased in these leaves. These changes suggest metabolic modifications for blossoming. A minimum daily requirement (mg shoot⁻¹ d⁻¹) of 3.4 and 4.8 mg of C, 0.09 and 0.09 mg of N, 0.01 and 0.02 mg of P for nonflowering and flowering shoots respectively shows that additional quantities of C and P are required for the peduncle floral elaboration. The unchanged quantity of N required for the peduncle elaboration suggests that N is limited in the environment and that a process of resorption from leaves to floral peduncle occurs.

Taxonomy in the Family Zosteraceae

J. Kuo, Centre for Microscopy and Microanalysis, The University of Western Australia, 35 Stirling Highway, Crawley, Western Australia 6009, Australia.

Taxonomy of the Zosteraceae is reviewed based on the vegetative and reproductive morphology and anatomy, chromosome number as well as fossil records. The vegetative morphology of the Zosteraceae is similar to most of other seagrass families by having creeping herbaceous rhizomes bearing a shoot of several ribbon-like leaves and a few roots at each rhizome node. On the other hand, the reproductive structure of the Zosteraceae is the most unique among the angiosperms. Flowers are formed on one side of flattened spike-like axes (spadices), which is enclosed within a specialized sheath of the leaf (spathe). Currently, the family has been classified into three or four genera depending on different schools of opinion. The genus Phyllospadix (up to six species in two subgenera) can be easily distinguished from other genera in the family by having dioecious plants with chromosome number 2n = 18, 20; enlarged retinacula; peculiar seed morphology; as well as with their restricted habitat and distributional preference. The remaining genera have monoecious plants bearing ellipsoid seeds. Both Heterozostera (4 species with 2n = 36) and Nanozostera (up to 9 species, with 2n = 12 or 24, depending on the species) have small retinacula and an open leaf sheath. It has been proposed to combine these two genera, however, Heterozostera has 4–10 cortical vascular bundles in rhizome internodes, while other genera have only two. The genus Zostera (about 4 to 6 species, with 2n = 12) lacks retinacula but has a close leaf sheath. Zostera marina is the only species in the genus that has a diverse morphology with a wide distribution and adaptation. A re-examination of fossil materials of Archaeozostera (with four species) from Japan and Heterozostera tamarica from central Peru concluded that these fossil materials might not be related to the Zosteraceae. A phylogenetical relationship in the family will be discussed.

Parameterization of Sexual Reproductive Capacities of the Seagrasses Enhalus acoroides and Thalassia hemprichii in Unsilted and Heavily Silted Sites in Cape Bolinao, Northwest Philippines

C. D. A. LaCap, J. E. Vermaat, C. M. Duarte, M. D. Fortes, R. N. Rollon, F. Alberto, E. Serrao, and C. Billot, (CDAL, MDF) The Marine Science Institute, College of Science, University of the Philippines, Diliman, Quezon City 1101 Philippines; (JEV, RNR) Department of Environmental Science & Water Resources, International Institute for Infrastructural, Hydraulic & Environmental Engineering, P.O. Box 3015, 2601 DA Delft, The Netherlands; Present address: Institute for Environmental Studies, Vrije Universiteit, De Boelelaan 1115, 1081 HV Amsterdam, The Netherlands; (CMD, FA) Instituto Mediterraneo de Estudios Avanzados, CSIC-Universitat Illes Balears, Carretera de Valldemossa km 7.5, 07071 Palma de Mallorca (Islas Baleares), Spain; (RNR) Environmental Science Program, College of Science, University of the Philippines, Diliman, Quezon City, 1101 Philippines; (ES, CB) Centro de Ciencias do Mar, Universidade do Algarve, Campus de Gambelas, 8000–810 Faro, Portugal.

The main difficulty in deriving similar estimates for sexual reproduction is the low frequency of flowering of most seagrass species and high seedling mortality often leading to conclusions that sexual
reproduction of seagrasses is insignificant especially in shorter time scales. Flowering frequency of *Thalassia hemprichii* is low, similar to most seagrass species, but *Enhalus acoroides* can produce up to 9 flowers/yr, suggesting that sexual reproduction for this species may be significant. We estimated that *E. acoroides*, in unsilted meadows, have the capacity to attain pre-disturbance shoot densities within a year although inclusive of seedlings which are not as resilient as fully-grown shoots. Yet, in instances wherein there is no nearby seagrass patch to facilitate clonal growth, sexual reproduction may be able to sustain this species. *Thalassia hemprichii* in unsilted meadows are able to attain considerable shoot densities within the first year but may take as much as a decade, or as little as several years to fully recover depending on the size of the contributing population and the density of remaining patches. *Thalassia hemprichii* is mainly dependent on vegetative reproduction whereas the converse may be true for *E. acoroides*, which receives high recruits from sexual reproduction. Finally, we argue that for heavily silted sites with almost no chances at all of being pollinated, developing sexual reproductive structures is a high waste of resources with very low expected returns.

**Genetic Variability of Zostera marina Populations from Baja California and the Gulf of California**

R. Muñiz-Salazar, S. L. Talbot, D. H. Ward, G. K. Sage, and A. Cabello-Pasini, (RM-S, AC-P) Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California, Km. 107, Carretera Tijuana-Ensenada, Baja California, México; (SLT, DHW) U.S. Geological Survey, Alaska Science Center-Biological Science Office, 1011 East Tudor Road, Anchorage, AK.

Zostera marina is an important component of the ecology of coastal lagoons of Baja California and Sonora. Despite the ecological importance of the *Z. marina* populations, nothing is known about their genetic structure in Mexico. Consequently, we determined levels of genetic variation within and among populations of *Z. marina* in coastal lagoons of Baja California and Gulf of California. Populations of *Z. marina* at Estero Punta Banda, Bahía San Quintín, Laguna Ojo de Liebre, Laguna San Ignacio, Bahía Magdalena along the Pacific coast of Baja California; and Isla Tiburón, Punta Chueca, Bahía Agiabampo, Bahía Santa María and Bahía Concepcion in the Gulf of California were studied using eight microsatellite loci. Expected heterozygosities ranged from 0.5 to 0.6 among all populations. The significant overall Fst and Rst values (0.25 and 0.35, respectively; *P* < 0.006) suggest a substantial structure genetic among Pacific coast populations. Genetic differentiation was not correlated with geographic distance as expected by the isolation-by-distance model. In contrast to the populations from the Pacific coast of Baja California, little or no genetic differentiation was detected within populations from the Gulf of California, indicating high gene flow among these populations probably facilitated by strong local currents or a recent separation.

**Genetic Characterization of Eelgrass (Zostera marina L.) of Izembek Lagoon, Alaska**


Izembek Lagoon in southwestern Alaska contains one of the largest beds of eelgrass (*Zostera marina L.*) in the world, which provides important nutrients for a variety of wildlife species. Despite the value of the eelgrass populations in Izembek Lagoon, little is known about the level of genetic diversity and population structuring. We therefore characterized populations of eelgrass in Izembek Lagoon, using autosomally-inherited microsatellite loci, and compared them with similar data gathered from populations elsewhere in Alaska, including a population derived from individuals translocated from Izembek Lagoon to Adak Island of the central Aleutian Island chain. Comparisons are also made with population of eelgrass elsewhere along the Pacific Coast. We found decreased levels of heterozygosity in northern Pacific populations, as well as increased incidence of inbreeding and levels of clonality, relative to populations at lower latitudes. Among all populations examined, the overall Fst value was high and significantly different from zero, indicating substantial genetic differentiation. In some cases, population differentiation was positively correlated with geographic distance between populations, as expected under a model of isolation by distance. For other populations, however, there was little
correlation between geographic distance and levels of differentiation. Our data suggest more than one model of dispersal accounts for observed patterns of differentiation among these populations.

Seagrass Evolution: New Insights from Generic Molecular Phylogenetic Studies

M. Waycott, School of Tropical Biology, James Cook University, Townsville, 4811 Queensland, Australia.

The marine angiosperms ('seagrasses') represent a series of three or four adaptive radiations to a submerged marine habit from freshwater and saline origins. The majority of seagrass genera show a bi-ocean split in their species distributions: tropical genera such as Halodule, Syringodium, and Thalassia occur in the Caribbean and the Indo-Pacific; Posidonia occurs in the Mediterranean and the Australian Indo-Pacific. Based on historical biogeographic analysis, these radiations may have occurred either prior to the breakup of the Tethys Sea during the late Cretaceous or following the closure of the Panamanian Isthmus in the Eocene. Additional information has been generated on the longer term evolutionary trends among the marine angiosperms for five seagrass genera belonging to two of the three major seagrass lineages—the Cymodoceaceae complex: Posidonia, Halodule, and Syringodium and the marine Hydrocharitaceae: Thalassia, and Halophila. All genera show a clear signal of significant genetic divergence between their respective ocean systems except for Halophila decipiens, which occurs across both ocean systems showing little genetic divergence supporting the idea of very recent long-distance dispersal. Thalassia and Syringodium contain only the one species and each ocean system are remarkably homogeneous within each ocean system but significantly different between ocean systems supporting the notion of vicariant speciation. The more speciose Halophila and Halodule present more complicated evolutionary relationships among species however both contain clear evidence of vicariance. Posidonia again supports vicariance between ocean systems with the Australian radiation reflecting the more complex and persistent environment that occurs there. The rates of genetic divergence between ocean systems observed indicates a more recent radiation than the Cretaceous based on comparable studies of terrestrial angiosperms however, the role that clonality and its associated longevity of individuals, may represent a significant factor in suppressing the accumulation of genetic variability and thus a cretaceous origin cannot be discounted.

Reproductive Effort of Cymodocea rotundata, C. serrulata, and Halodule uninervis in Seagrass Beds Along the Coasts of Eastern Philippines

N. M. Cayabyab, R. N. Rollon, C. C. Ragos, H. M. E. Nacorda, and M. D. Fortes, Marine Science Institute, University of the Philippines, Diliman, Quezon City, 1101 Philippines.

The reproductive effort of seagrasses Cymodocea rotundata, C. serrulata, and Halodule uninervis was quantified over a wide latitudinal range (10–18°N) along the unexplored Philippine Pacific coasts. A combination of conventional methods and age reconstruction technique was utilized in determining the (1) intensity and frequency of flowering and fruiting and (2) seasonality of such efforts. A total of 35 sites were surveyed covering coves, bays, and fringing and offshore reef system. Cymodocea rotundata, C. serrulata, and H. uninervis occurred in 71%, 51%, 71% of the total number of sites, respectively, and these constituted up to 79%, 76%, and 52% of the total number of shoots. Flowering of C. rotundata occurred all throughout the year with peaks around Dec.–Feb, and some apparent flowering flushes during March–April in some sites. Overall data showed that 21% of this species produced flowers at least once in its lifetime, however, spatial variation was observed, i.e., flowering shoots was high (up to 50%) in San Miguel Bay, Bicobian Cove, and Andis Island. Reproductive output of this species was also high; reaching up to 17% (equivalent to ca. 280 fruits m⁻²) of the shoots collected from Andis Island (Samar) had fruits. For C. serrulata and H. uninervis, shoots with flower were considerably low. Less than 5% of all C. serrulata shoots sampled had flower marks while flowering shoots of H. uninervis found to be localized in two 'regions', Calagua and Polillo Islands. Although the pattern was less clear compared to C. rotundata, peaks of flowering for C. serrulata and H. uninervis appeared also in summer months, March–April. Particularly in Calagua Islands, shoots of both species were found to be fruiting intensely. The results might indicate that flowering and fruiting events of these seagrass species may not be rare temporally and spatially as previously believed.

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Microsporogenesis in *Thalassia testudinum* Banks ex Köning

J. G. Ricardo-Wong, B. I. Van Tus森broek, and J. M. Guzmán, (JGR-W, JMG) Laboratorio del Desarrollo en Plantas, Facultad de Ciencias, UNAM, Mexico; (Blot) Instituto de Ciencias del Mar y Limnología, Estación de Biología Puerto Morelos, UNAM, Mexico.

The (sub-)tropical seagrass *Thalassia testudinum* invests considerable amounts of its resources into sexual reproduction. Nevertheless, virtually nothing is known concerning the development of the reproductive structures of this dioecious species. Present work is part of a larger study into the embryology of the male and female reproductive structures, and presents the microgametogenesis and the microstructure of the pollen grains. Floral buds in different development stages and flowers in anthesis were collected during the spring of 2001 and 2002 in Puerto Morelos Biology Station (Mexico). Part of this material was fixed in FAA (alcohol, formaldehyde and acetic acid) and it was processed for paraffin inclusion. Serial 5 to 10 µ thick sections were obtained and stained with the safranin-fast green technique. The rest of material was fixed in glutaraldehyde-paraformaldehyde-s-collidine buffer, included in LRwhite and cut with a glass knife to obtain 1 µ thick sections in ultramicrotome for observations under an optical microscope. These preparations served to describe the development of the wall of the anther, the arquesporial cells, the meiosis of microspores mothers cells with the consequent formation of tetrads, the structure and function of the tapetum. The scanning electron microscope was used for the description of the micromorphology of the pollen grains.

Chloroplast DNA Phylogeography of Indo-Pacific Seagrasses

K. G. Araño, J. N. Ouborg, and E. de Ruyter van Steveninck, (KGA, ERS) International Institute of Infrastructural, Hydraulic and Environmental Engineering, P.O. Box 3015, 2601 DA Delft, The Netherlands; (KGA, JNO) Department of Aquatic Ecology and Environmental Biology, Toernooiveld 1, University of Nijmegen, 6525 Ed Nijmegen, The Netherlands; (KGA) Marine Science Institute, University of the Philippines, Diliman, Quezon City 1101, Philippines.

Restriction fragment length polymorphism (RFLP) technique was applied on non-coding regions of the chloroplast genome of *Enhalus acoroides*, *Thalassia hemprichii*, *Cymodocea rotundata*, *Cymodocea serrulata*, *Syringodium isoetifolium*, *Halodule uninervis* and *Halophila ovalis* to determine phylogeographic relationships. Representative samples from various parts of the Indo-Pacific Region such as the Philippines, Vietnam, Malaysia, Indonesia and Kenya were included in the analysis. Seventeen pairs of universal chloroplast primers in combination with ten restriction enzymes were used. No variation was found within each species from different sites on the primer-enzyme combinations (170) tested. Sequencing of some the chloroplast DNA regions was also done in which very few polymorphisms were identified.

Contribution of Sexual Reproduction to the Growth and Development of a New England Eelgrass (Zostera marina L.) Bed

L. A. Harris, S. W. Nixon, S. Granger, M. Traber, and B. Buckley, Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882-1197.

Current eelgrass restoration techniques have focused on transplanting adult plants from donor beds to other sites using various techniques. As an alternative, several efforts are underway to use seeds to create restored eelgrass beds. The probability that transplanted eelgrass or seeds will survive to grow and reproduce, sexually or vegetatively, is related to environmental variables that affect both individuals and the population dynamics of the restored bed as a whole. As a first step in integrating these population characteristics with individual success, we have examined the relative contribution of sexual reproduction in New England eelgrass beds. Rates of flowering shoot, spadix, fruit, and seed production were determined in three eelgrass meadows located in Rhode Island. In addition, the viability of these seeds was determined by subsampling a large seed stock collected for restoration purposes, and staining this subsample with tetrazolium chloride. To estimate dispersal rates and the contribution of seeds to existing beds, cores were taken from within the study sites in late summer, sieved and the number of seeds counted. Using these data, an estimate of sexual reproduction will be presented and compared with existing data describing vegetative reproduction.
Population Genetic Diversity in Seagrasses

G. PROCACCINI, Laboratory of Benthic Ecology, Stazione Zoologica 'A. Dohrn', Ischia (Na), Italy.

Population genetic studies in seagrasses have received significant inputs from development of new variable molecular markers in the last 10 yr. Meadows or patches of different size can be represented by a variable number of genotypes, and the assessment of population boundaries is often difficult. In different species, population genetic diversity resulted differently than theoretically hypothesized and was not always related to reproductive system and dispersal potential. Putative factors determining population genetic structure in this group of marine organisms are the following: 1) local environmental conditions and historical patterns of species dispersal. Different populations of the same species, in fact, can go from being uniclonal to be extremely genetically diverse, in relation to recent and past patch colonization and dynamics in different geographical areas; and 2) balance between sexual reproduction and vegetative propagation, whose reciprocal importance varies among species and localities. Meadow structure, at the end, is the result of a range of different factors modulating seedling recruitment, extent of clonal propagation and habitat physical features. In this presentation I will review the existing knowledge on population genetics of different seagrass species in relation to reproductive system, habitat characteristics and sensitivity of the molecular markers utilized.

Phylogenetic and Population Genetic Analyses of Zostera Species Based on rbcL and matK Nucleotide Sequences

Y. KATO, K. AIOI, Y. OMORI, N. TARAHATA, AND Y. SATTA, (YK, NT, YS) Department of Biosystems Science, Graduate University for Advanced Studies, Hayama, 240-0193 Kanagawa, Japan; (KA) Aoyama Gakuin Women’s Junior College, Tokyo, Japan; (YO) Yokosuka City Museum, Yokosuka, Japan.

Nucleotide differences within and between two seagrass species, cosmopolitan Zostera marina and Z. caulescens endemic to Japan, were examined in rbcL and matK gene regions in the chloroplast genome. The total length of nucleotides compared for these regions is approximately 3.5 kb. Based on phylogenetic and population genetic analyses, the following observations and inferences were made. 1) In the inclusion of some other Alismatidae species available in the phylogenetic analysis, Z. marina and Z. caulescens are shown to form two distinct monophyletic groups and are most closely related to each other among the Alismatidae species. 2) The divergence time between the two Zostera species and their closest relative, Potamogetonaceae, is estimated as approximately 100 myr ago. This estimate is consistent with the time of origin for seagrasses inferred from fossil records in the Cretaceous. 3) The divergence time between Z. marina and Z. caulescens is estimated as about 7 myr ago, suggesting that the emergence of Z. caulescens endemic to Japan might be related with the latest reformation of Japan Archipelago. 4) The synonymous nucleotide diversity within endemic Z. caulescens is larger than that in cosmopolitan Z. marina. This suggests that the difference in their current geographic distribution has little or no effect on the different extent of synonymous nucleotide diversity. Rather, the differences in mating system and/or evolutionary history might have played important roles. In order to confirm these and clarify the evolutionary mechanism in these relatively closely related seagrass species, it is necessary to examine more rapidly evolving nuclear DNA than chloroplast DNA. Some preliminary results on nuclear genes, phyA and phyC, are also discussed.

Vegetative and Generative Biomass Allocation in Zostera marina from Bahía San Quintín, Mexico

A. E. MELING-López AND S. E. IBARRA-ObANDO, (AEM-L) Departamento de Investigaciones Científicas y Tecnológicas de la Universidad de Sonora (DICTUS), Rosales y Niños Héroes S/N 82000, Hermosillo, Sonora, México; (SEI-O) Centro de Investigación Científica y Educación Superior de Ensenada (CICESE) Km 107 Carretera Tijuana-Ensenada, 22830, Ensenada, Baja California, México.

Biomass allocation in eelgrass, Z. marina, is mostly to vegetative reiteration by lateral shoots. Only a small part of this allocated energy is to sexual reproduction. Our hypothesis indicates that the rates of vegetative and generative biomass vary from stable (subtidal, SBT) to stressed (intertidal, INT) environment, being the last one the most properly to sexual reproduction. We took monthly samples from June 1996 to Nov. 1997 using 3 frames of 0.04 m² in both intertidal and subtidal environments
in each of the four selected localities in order to obtain both vegetative and reproductive shoots density (shoot m⁻²) and biomass (gDWm⁻²). Biomass was separated in above- and belowground, and vegetative and reproductive components. Reproductive shoots were studied in order to describe and to compare sexual reproduction cycles using phenological characteristics, and to determine the reproductive effort and seedling growth. The results showed differences between vegetative and generative shoots from SBT and INT, indicating that density was higher in intertidal but shoot length was higher in subtidal. Average total biomass was higher in subtidal (349.9 gDWm⁻² vs 198.7 gDWm⁻²). Above biomass was higher than underground and reproductive biomass. The reproductive effort was higher in the INT than in SBT, because the reproductive effort in a population is shoot density dependent. Sexual reproduction was higher in intertidal than subtidal indicating that the generative biomass allocation is more important in a stressed environment than in a stable one. This variation represents an allocated biomass cost for sexual reproduction in both seedling production and recruitment. Beside in intertidal and subtidal sexual reproduction was succeed and represent genetic variation, the vegetative production of lateral shoot is however, in most cases the best strategy of eelgrass bed maintain.

Seasonality of Tropical Australian Seagrasses

J. E. MELLORS, School of Tropical Environment Studies and Geography, James Cook University, Townsville, Queensland, Australia and Queensland Fisheries Service, Queensland Department of Primary Industries, Cairns, Queensland, Australia.

Little has been published on the seasonality of inshore seagrasses in tropical Australia other than seasonal changes in standing crop. The dominant seagrasses that occur in these seagrass meadows are Halophila spp and the narrow form of Halodule wissevorfis. This study investigated the differences in growth rates, sediment nutrient status, plant nutrient status and biomass accumulation that existed between summer (termed the growing season) and winter (the senescent season) for an intertidal seagrass at two locations in tropical eastern Australia. This study found that even though the meadows investigated were colonized by the same species of seagrass (Halophila minor), and were in close geographical proximity to each other, significant differences in sediment nutrient state, sediment profile, and plant nutrient status existed between the two locations. Despite this, seasonal differences were consistent at each location. This study also found that growth parameters differed significantly between locations and also seasonally within location. However, the locational and seasonal differences of each growth parameter were not consistent across locations. It is hypothesized that this result is due to the two seagrass beds being at different stages of development, as one of the seagrass beds was in a state of recovery after a dramatic decline in seagrass biomass and cover the year previous to this study. This study supports the notion that seasonality is an important component of tropical seagrass habitats and is contrary to expectation that seasonality is negligible in tropical seagrass meadows.

Vegetative Dynamics and Sexual Reproductive Effort of Thalassia hemprichii and Cymodocea rotundata along the Coasts of Eastern Philippines

R. N. ROLLON, N. M. CAYABAY, M. Y. ROLEDA, C. C. RAGOS, H. M. E. NACORDA, and M. D. FORTES, Environmental Science Program, College of Science, University of the Philippines, Diliman, Quezon City 1101, Philippines.

The study quantified vegetative dynamics and reproductive effort of seagrasses, Thalassia hemprichii and Cymodocea rotundata, occurring more frequently along the coasts of eastern Philippines. We surveyed a total of 35 seagrass beds covering ~2,000 km of coastline (10–18°N latitudinal range) and employed in situ and reconstruction techniques to derive vegetative and reproductive parameters. Although considerable differences between sites were detected, there was no correlation found between latitudinal and any of the indices measured. For T. hemprichii populations, the overall mean net recruitment (Rnet) was slightly higher than zero (0.036 ln units/yr) indicating that the general condition was at equilibrium. However, this may be seriously declining in some meadows. Vertical and horizontal growth rates of T. hemprichii were 2–5 cm sht⁻¹ yr⁻¹ and 20–80 cm apex⁻¹ yr⁻¹, respectively. The Rnet, vertical and horizontal elongation rates of C. rotundata were quantitatively faster compared to T. hemprichii and its temporal variation in vertical internodal length was more pronounced. Both species, however, showed similar trends with time and had generally low vertical elongation rates during Dec.–Feb.. Strong variability signal between different sites within coves (e.g., Bicobian Cove,
Relative Importance of Vegetative Growth and Seed Production on Population Growth of Zostera spp. in Northern Japan

M. Nakaoka, K. Aioi, N. Kouchi, H. Mukai, Y. Omori, and M. Watanabe, (MN) Graduate School of Science and Technology, Chiba University, Chiba 263-8522, Japan; (KA) Aoyama Gakuin Women’s Junior College, Tokyo, Japan; (NK, HM, MW) Akeshi Marine Laboratory, Hokkaido University, Akeshi-gun, Japan; (YO) Yokosuka City Museum, Yokosuka, Hokkaido, Japan.

Multispecific seagrass beds in northern Japan are characterized by the co-occurrence of endemic and threatened species of Zostera (Z. asiatica, Z. caulescens and Z. caespitosa) with the cosmopolitan eelgrass (Z. marina). These endemic species generally occur in deeper parts of the beds. To understand factors responsible for their co-occurrence pattern, we carried out comparative analyses on vegetative growth and seed production of Z. asiatica, Z. caulescens and Z. marina at several sites in northern Japan. Leaf and rhizome growth rates, as well as annual net primary production of Z. asiatica and Z. caulescens were similar to, or even higher than, coexisting Z. marina. In contrast, seed production was much smaller for these endemic species. Notably, considerable amounts of predispersal seeds were consumed by a seed predator (a tanaid crustacean) for Z. caulescens. Accordingly, the density of seedling was much lower for the endemic species. These findings showed that Z. asiatica and Z. caulescens allocate more resources to vegetative growth than seed production in comparison with Z. marina. Clonal propagation is thus considered more responsible for population growth of these two species. Possible factors causing lower resource allocation to seed predation include: (1) requirement for larger investment to vegetative growth (enlargement) to account for low light conditions, and (2) more stable environmental condition in the deeper parts of the beds where seagrasses are less subjected to strong and frequent disturbance regime.

Life Strategies of Subtropical Eelgrass Zostera marina L. Populations in Southern Baja California: its Southern Limit Distribution along East Pacific

N. A. Santamaría-Gallegos, J. L. Sánchez-Lizaso, R. Rosmenera-Rodríguez, (NAS-G, JLS-L) Unidad de Biología Marina, Universidad de Alicante, Alicante, España; (RR-R) Herbario Ficológico, Universidad Autónoma de Baja California Sur México, Ensenada, Mexico.

In Southern Baja California (SBC), there exist several Coastal Lagoons which shelter eelgrass Z. marina populations: Guerrero Negro (GN), Ojo de Liebre (OL), San Ignacio (SI), and Bahía Magdalena (BM). This is the southern distribution limit of eelgrass in the eastern Pacific. Information about eelgrass in SBC is scarce. It is important to understand the adaptive responses of eelgrass, a temperate species, to a restricting subtropical environment. We hypothesize that southern populations, confronting higher summer temperatures, will show higher generative effort and, in extreme ambient conditions they will display an annual life pattern. In order to test our hypothesis, differences in life form, generative and branching effort, and biomass allocation among populations in GN, OL, SI and BM were analyzed, and compared with the only eelgrass population over the east coast of SBC, in the Gulf of California. A time during the known eelgrass flowering season was randomly selected for sampling. Fifteen sites were included: 9 subtidal and 6 intertidal. All eelgrass populations, both intertidal and subtidal, along the western coast of SBC were perennials and on the eastern SBC coast, all eelgrass plants were annuals. High variability on flowering effort was observed among perennial populations and did not show any latitudinal gradient. Flowering effort was higher in intertidal sites. However, El Cuervo, a subtidal site in BM showed the highest flowering effort and coincides with a very low influence of the California Current and summer temperatures up to 29 C. Local ambient temperature in each site had more influence on plant morphology and flowering effort than latitu
dinal gradient. Differences among eelgrass populations and the environmental conditions they confront in SBC are discussed in terms of ambient stress and predictability.

Population Genetic Structure in *Cymodocea nodosa*

M. V. Ruggiero and G. Procaccini, Laboratory of Benthic Ecology, Stazione Zoologica 'A. Dohrn', Ischia (Na), Italy.

*Cymodocea nodosa* is a dioecious seagrass species, with male flowers reduced to only one stamen and female flowers bearing two ovaries. The ability of seeds to disperse is quite limited, fruits remaining buried into the sediment until germination nearby the mother plant. A trend toward a limited dispersal of sexual propagules and subsequent maintenance in situ of new genotypes can markedly influence the genetic structure of *C. nodosa* populations. On the other side, studies on clonal propagation showed that *C. nodosa* presents a high vegetative growth and consequently, a high potential for space occupation. Four polymorphic microsatellite loci were used to describe the genetic structure of a *C. nodosa* meadow on a fine scale, adopting a grid-like sampling scheme, in order to assess the differential contribution of clonal and sexual reproduction to the propagation and persistence of the population. The studied population is located at the Castello Aragonese in Ischia (Italy). It extends continuously at 4-6 m depth over an area of about 1,800 m². Data on distribution of different genotypes and meadow genetic structure are interpreted in light of different demographic features of the meadow such as density of shoots, seeds and flowers, and distribution of age classes.

Genetic Variation and Population Biology of Tropical Seagrasses

M. Waycott, School of Tropical Biology, James Cook University, Townsville, 4811 Queensland, Australia.

The study of how seagrass populations are formed and maintained is critical not only to better understand the biology of these interesting and unique marine organisms, but also to develop adequate management strategies in environments that are increasingly subjected to unnatural disturbances. Significant insights can be made by combining information on the population structure of a species as assessed using population genetic information and data on the reproductive strategies of the plants in those populations along with information on longer term historical processes such as their evolutionary history as assessed using molecular phylogeny. This study presents data from four species of seagrass in the two major tropical ocean systems that are being surveyed for population genetic variation using DNA fingerprinting markers: *Thalassia testudinum*, *Syringodium filiforme* from the Caribbean and *Halophila ovalis* and *Halodule uninervis* from the Indo-Pacific. These seagrass species represent a wide range of reproductive and life history strategies and we would expect their population genetic structure to reflect these differences. However, all species demonstrate differing scales of clonal diversity within and between populations from evidence of local clones to widely dispersed clones. The implications of these patterns to processes of local and species-wide dispersal are discussed and the paradigm that seagrasses cannot disperse over long distances is questioned. These data represent the baseline for the study of tropical seagrass population dynamics and when coupled with robust ecological data being collected on sexual reproduction, vegetative growth rates and colonization rates will provide information on the relative importance of sexual vs vegetative population processes in tropical seagrasses.

Rhizome Morphology and Reproductive Shoot Formation in the Japanese *Zostera*

Y. Omori, Yokosuka City Museum, Yokosuka, Japan.

The four Japanese *Zostera* species have diverse characteristics in the rhizome morphology and the formation of erect reproductive shoots. *Zostera caespitosa*, in particular, has the most peculiar morphology. It has compressed rhizomes that grow sub-erectly and have a series of 6-7 or more congested short internodes (1.4-1.7 mm in length) as well as the sparse but long ones (5-35 mm in length). Each series of short internodes tends to be arranged alternately with every 2-3 long internodes. On the other hand, the other three species have slightly compressed cylindrical rhizomes that creep horizontally and always have regular long internodes. All four *Zostera* species are flowering from late
spring to summer. However, the differentiation of the erect reproductive shoot in *Z. caulescens* occurs in early winter that is at least 4 mo earlier than that of other three species. This different initiation timing may have some direct association with the extremely long erect reproductive shoot, 6–8 m in length, in *Z. caulescens* comparing with usually less than 1.5 m in the other three species. It seems that the reproductive shoots of *Z. caespitosa* and *Z. asiatica* are differentiated from the apex of the newest lateral shoot of normal rhizome branching while those of *Z. caulescens* and *Z. marina* develop from the rhizome apex. The diversity of the rhizome morphology and the differentiation timing for the erect reproductive shoots in *Zostera* may have important ecological and biological implication.

Physiological and Genetic Characterization of *Zostera marina* in San Quintin Bay, Mexico

R. Muñiz-Salazar, S. L. Talbot, D. H. Ward, G. K. Sage, and A. Cabello-Pasini, (RMS, AC-P) Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California, Km. 107, Carretera Tijuana-Ensenada, Baja California, México; (SLT, DHW, GKS) U.S. Geological Survey, Alaska Science Center-Biological Science Office, 1011 E. Tudor Road, Anchorage, AK.

Perennial meadows of *Zostera marina* inhabit both arms of San Quintin Bay, but are exposed to different current patterns, salinity, temperature and nutrients levels. Consequently, we conducted studies to determine if *Z. marina* meadows within subtidal and intertidal populations differed physiologically (photosynthetic rates) and genetically (DNA microsatellite loci) between both arms of San Quintin Bay. Two distinct morphotypes of *Z. marina* were observed throughout the year. Subtidal populations were twofold longer and wider than intertidal populations. There was no significant genetic difference between subtidal and intertidal populations using eight microsatellite DNA markers, but there was a significant response of photosynthesis as a function of irradiance, suggesting that the variation between populations is a physiological response to environmental conditions. Between meadows from both arms, the overall Fst value was low but significantly different from zero (0.02, \( P < 0.05 \)) indicating reduced gene flow and possible genetic structuring within San Quintin Bay. Both meadows showed heterozygotes deficiency as consequence genetic structure (Wahlund Effect) and high clonality. Reasons for the genetic differences are unclear, but are likely influenced by the different patterns of circulation in each arm.

Session: Changes in Seagrass Beds at Local and Global Scales

Changes in Abundance and Distribution of Seagrass Beds in the Bay of Cartagena and Neighboring Areas (Colombian Caribbean)

J. M. Díaz-Merlano and D. I. Gómez-López, Instituto de Investigaciones Marinas y Costeras, José Benito Vives de Andrés—INVEMAR A.A. 1016 Santa Marta, Colombia.

The spatial distribution of seagrass beds within the Cartagena Bay and neighboring areas was reconstructed through comparative analyses of maps, aerial photographs and satellite imagery, as well as observations in the field for five time periods within the last six decades. From slightly more than 1,000 hectares of seagrass beds existing in 1935–45, only 76 remained in 2001, which is less than 8%. The loss rate of seagrass within the bay showed an inverse exponential pattern, whereas outside of the bay the tendency was linear. The almost disappearance of this community was probably raged by the reopening of the Canal del Dique early in the 1930s, causing the introduction of important amounts of turbid freshwater and sediments into the bay, and subsequently accelerated by the rapid development of the industrial zone, spilling of polluted industrial and domestic waters, dredging, and coastal development. The reduction of seagrass areas has been seemingly accompanied by changes in the structure of the animal community, becoming apparent through the evident disappearance of suspension feeding invertebrates, which were so far dominant elements three decades earlier. The loss of seagrass beds in the bay during the 20th century seems likely to be part of the long lasting human transformation process of this ecosystem, which started three centuries before.
Do Increasing Hydrodynamics Contribute to Losses of Seagrass Beds in the Wadden Sea?

A. Schanz, H. Asmus, and R. Asmus, Alfred Wegener Institute for Polar and Marine Research, Wadden Sea Station, Sylt, Germany.

Seagrass beds in the Sylt-Rømø Bay, a tidal system at the east coast of the North Sea, declined by more than the half from 1924 until now. Long-term observations within the bay gave evidence that these losses of epibenthic communities may be a consequence of both, natural development and man-made changes. Especially the construction of causeways and dikes, as well as enhanced fishery activities altered environmental conditions and habitat structures, and incrementally led to increasing erosion processes. In addition, extensive land use increased nutrient availability and altered the trophic state during the last decades. A comparison of a sheltered and a hydrodynamically exposed seagrass bed from 1997–99 provided evidence that hydrodynamics, in particular currents and waves, have strong impact on seagrass communities. Experience with an in situ “three-current-flume,” modifying the entire current velocity, and cross transplantation experiments between sheltered and exposed seagrass beds demonstrated that stronger currents directly affect seagrass bed development by reducing seagrass density and shoot morphology, as well as the expansion of seagrass beds. In addition, stronger water dynamics amplify eutrophication effects in intertidal areas by controlling grazing processes, thereby indirectly impacting seagrass development, by inducing a higher vulnerability due to enhanced fouling. Further, stronger currents may limit the complexity of seagrass habitats at exposed areas, for example for the colonization by macrofaunal species. Since changes in environmental conditions are ongoing (e.g., increase of nutrients and rise in sea level), the results of this study show that considering hydrodynamics gains new insights into the thresholds of environmental conditions in order to conserve seagrass communities as a part of ecosystem.

Assessing Change in Seagrass Ecosystems on a Regional Scale: The Relative Merits of Fixed Stations and Systematic Random Sampling

J. W. Fourquarean, L. M. Ruten, M. J. Durako, J. C. Ziemann, and T. A. Frankovich, (JWF, LMR) Department of Biological Sciences and Southeast Environmental Research Center, Florida International University, Miami, FL; (MJD) Center for Marine Science, University of North Carolina at Wilmington, Wilmington, NC; (JCZ, TAF) Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22904-4123.

Because of their sensitivity to human-induced changes in the coastal zone, seagrasses have fared poorly worldwide over the last century and are the targets of many monitoring programs designed to measure trends in seagrass communities. Two general monitoring strategies are commonly applied in seagrass ecosystems: repeated observations of fixed sites and repeated systematic random sampling of study areas. Fixed-station monitoring generally provides the most sensitive measure of temporal pattern, but it is often difficult extrapolate from fixed stations to the surrounding ecosystem. In contrast, repeated systematic random sampling captures spatial pattern, but spatial heterogeneity can mask gradual trends through time. In the extensive seagrass ecosystems of south Florida (over 15,000 km²), we employ a mixture of fixed sites and random sampling to assess the quality and trends in seagrass ecosystems. Aspects of seagrass status measured in this program include: species composition, density, biomass, biomass allocation, elemental content, stable isotopic content, population age structure, leaf growth rate and epiphyte loads. All measured parameters are directly related to our conceptual model of the relationships between nutrient availability and seagrass communities. Monitoring of fixed stations, in some instances for over 15 yr, has defined the intra- and interannual patterns inherent in seagrass beds in the region. Repeated systematic random sampling has allowed a description of the regional status of seagrass beds. In Florida Bay, repeated surveys have been successful in tracking the ecosystem-scale changes that have occurred in the wake of the seagrass die off that occurred in the late 1980s. On a broader regional scale, the systematic sampling has provided a detailed baseline against which to measure change. It is imperative that the designs of monitoring programs be created with an understanding of the important management issues so that proper weight can be given to these two general monitoring approaches.
Climate Change and Seagrasses: Climate-Linked Dynamics, Carbon Limitation and Carbon Sequestration

R. M. Thom, A. B. Borde, G. D. Williams, D. L. Woodruff, and J. A. Southard, Battelle Marine Sciences Laboratory, Sequim, WA.

Seagrass systems are vulnerable to climate variability and change, and may play an important role in carbon cycling and storage in some areas. Climate-related factors relevant to eelgrass include the following:

Temperature—In our studies of eelgrass (Zostera marina L.) in Pacific Northwest (USA) systems, shoot density, biomass and flowering increased two- to sixfold between 1998 and 2001. This corresponded with a change in water temperature and climate factors related to a transition between a strong El Niño and La Niña event. As confirmation of our findings, recently published studies have shown global increases in ocean primary productivity during this period. This remarkable change is consistent with regional shifts in climate regimes now referred to as the Pacific Decadal Oscillation (PDO). Carbon dioxide—research is also showing that eelgrass can be CO₂-limited. Hence, in theory, increases in atmospheric CO₂ could enhance eelgrass production. Sea level rise—storm surge—Sea level rise poses a threat to eelgrass through increased water depths. However, the threat to eelgrass distribution needs further evaluation by region. Carbon storage—Because of their high productivity rates and storage and export processes, seagrass systems can potentially sequester large amounts of carbon through loss to below-ground systems and export of detritus to deeper areas where burial occurs. Estimates of the significance of carbon sequestration to local, regional, or global carbon management have not been made. Because of the importance of seagrass systems to fisheries resources, the threats posed by climate change on seagrass systems, and their potential importance as a carbon sink, seagrass systems should be made part of the national and global climate change programs.

Changes in Seagrass Beds at Talibong Island, Andaman Sea, Thailand

S. Poovachiranon, Phuket Marine Biological Center, P.O. Box 60, Phuket 83000, Thailand.

A permanent line transect of 2,000 m in length was set up on a seagrass bed at the eastern part of Talibong Island in the Andaman Sea, southern Thailand. Species composition and percentage cover of seagrasses were monitored in 1982, 1992, and 2001. A total number of 10 species of seagrasses, namely Halophila ovalis, Enhalus acoroides, Thalassia hemprichii, Cymodocea serrulata, C. rotundata, Syringodium isoetifolium, Halodule uninervis, Halodule pinifolia, H. minor, and H. beccarii, were recorded at various distances from shoreline. Monitoring conducted in 1982, 1992, and 2001 showed clearly that the seagrass bed were diminished in terms of percentage cover from 80% to 50% between the distance of 900-1,300 m of the line transect. High rate of sedimentation on the seagrass bed was observed during the last decade. Silt was recently deposited on top of very fine sand, which used to be the characteristic substratum of the seagrass bed in 1982. It is suspected that silt from coastal development and construction areas was transported to seagrass beds via the adjacent river mouths. It is suggested that strict preventive measures should be proposed to curtail the land-derived sedimentation on seagrass beds.

Seagrasses Monitoring Program in Yucatan Peninsula (southeast Mexico)


The seagrasses community has been recognized as a biological indicator of different kinds of impacts in coastal ecosystems. The economic activities in the coastal zone of Yucatan Peninsula are growing; and the impacts on the marine resources are present. In order to establish a baseline of the seagrasses community condition, and support management decisions in protected marine areas in the Gulf of Mexico and Caribbean Sea zones through a multicriteria decision analysis, an extensive quarterly sampling program was conducted in six localities of Yucatan Peninsula in 2001, conducting measurements of composition, coverage, biomass, leaf dynamics and hydrology. The community is composed by Thalassia testudinum, Syringodium filiforme, Halodule wrightii, Halophila decipiens, and Ruppia maritima. The results indicate high variability in the community and heterogeneity in response to freshwater
Seagrasses of Abu Dhabi, United Arab Emirates, Arabian Gulf

R. C. Phillips, R. A. Loughland, and Y. Yousef, (RCP, RAL) Commission of Environmental Research, Emirates Heritage Club, Abu Dhabi, United Arab Emirates; (YF) Faculty of Science, Department of Botany, Abbasia, Ain Shams University, Cairo, Egypt.

Fieldwork was conducted in the Arabian Gulf on the seagrasses of Abu Dhabi from 1997 through 2000. The work included aerial inspection from a helicopter and extensive fieldwork from boats using snorkel and scuba diving. Three species of seagrasses were found, e.g., Halodule uninervis, Halophila ovalis, and H. stipulacea. Overall, a total of 5,500 hectare of seagrass coverage was found inshore and offshore in the Abu Dhabi Emirate. These plants are judged to constitute a nursery and habitat of inestimable value. Dugongs and turtles were observed grazing on these plants during the work.

A 5m-Thick Posidonia oceanica Core

M. A. Mateo, P. Renom, J. Romero, I. Martínez, C. Guallar, D. Garrido, R. Julià, and R. Michener, (MAM, PR, JR, IM, CG, DG) Departament d’Ecologia, Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain; (RJ) Instituto de Ciencias de la Tierra Jaume Almera (CSIC), Lluís Solé i Sibaris s/n, Ajdu. 30102, 08028 Barcelona, Spain; (RM) Boston University Stable Isotope Laboratory, Department of Biology, Cummington Street, Boston, MA 02215.

Seagrass palaeoecological studies are very scarce due to the paucity of the fossil and sedimentary records left by these marine macrophytes. A notable exception occurs in the Mediterranean Sea. Posidonia oceanica (L.) Delile accumulates massive organic deposits as a consequence of the persistence of its dead belowground organs (leaf sheaths, rhizomes and roots). We cored a P. oceanica meadow at 9-m depth in the Port Lligat Bay (Girona, Spain) using a light, floating drilling platform that combines penetration and rotating actions. A 5-m thick, 9-cm diameter core was obtained in four sections of ca. 1.25 m each. Abundant coarse organic matter derived from P. oceanica was observed all along the core without interruptions. The first sections have been investigated in more detail. Accelerator mass spectrometry 14C dating was used at five levels of this first section to establish the age of the material. Radiocarbon age of P. oceanica detritus at 120 cm from the top of this core section was of 1,600 yr BP. From the 14C ages and the relative position in the core, a linear accretion rate of 0.88 mm yr⁻¹ was estimated for the P. oceanica deposits. From this information, a ca. 6,000 yr of maximum antiquity can be inferred for the 5-m core. Changes along the first section of the core in (1) relative abundance of sheath, rhizome and root necromass, (2) total P. oceanica material density, (3) accretion rates, (4) elementary composition (C, N), (5) isotopic composition of sheath material (delta-14C and delta-15N), (6) content of fine organic matter (<1 mm), and (7) granulometric composition, have been investigated. Other features of the P. oceanica deposits such as residence time, role as biogeochemical sinks, frequency of perturbations occurring in the system, or the phenomena potentially hindering a correct interpretation of the information recorded are discussed.

Spatial Distribution of Epiphytic Coralline Algae on Halodule wrightii Ascherson in the Archipelago of Abrolhos, Brazil


Crustose coralline algae (Rhodophyta—Corallinales) are frequently found as epiphytes on seagrasses but little is known about their distribution and abundance on Halodule wrightii Ascherson. The aim of this study was to compare the distribution of coralline crusts on natural plants and on plastic mimics, in order to verify possible seasonal variation and distribution patterns on the hosts’ leaves and between sites at the Abrolhos Archipelago, Brazil. Two sites were investigated.
on the northern sides of Santa Bárbara and Siriba Islands. In order to quantify algal colonization, groups of 12-15 plastic mimics were placed at each site for 24-d periods in winter and summer. A random collection of ‘natural’ leaves was also carried out. Epiphytes were quantified using point counts to estimate their cover on basal, middle and apical portions of the leaves and mimics. Two species of crustose algae were distinguished, of which the most abundant epiphyte was *Titanoderma pustulatum* (Lamouroux) Nägeli. Epiphytes covered more seagrass at Santa Barbara than at Siriba in winter, although in summer the pattern was reversed (ANOVA, *P* < 0.001) a fact that may be related to differing water movement at the two sites at these times of year. The maximum value of *T. pustulatum* was 82% cover at Santa Barbara (winter) and 58% at Siriba (summer). A negative correlation was found between the two species of calcareous algal epiphytes at Santa Barbara in winter (*n* = 15, *r* = −0.91, *P* < 0.001), a time when there was less substratum available for colonization. Filamentous algae were only found in winter at Siriba, when more free space became available, indicating that these algae are opportunistic. Epiphytes were concentrated at the apex on ‘natural’ leaves, which could be related to age of the leaf part, considering that mimics carried heavier epiphyte loads on the middle portion of their leaves.

**Distributional Patterns of an Annual Eelgrass, Zostera marina, Population in the Gulf of California**

J. Torre-Cosío, L. Bourillón-Moreno, A. E. Meling-López, and P. Ramírez-García, (JFC, LB-M) Comunidad y Biodiversidad A.C., Guaymas, Sonora and School of Renewable Natural Resources, University of Arizona, Tucson, AZ; (AEM-L) Depto. Investigaciones Científicas y Tecnológicas de la Universidad de Sonora, Hermosillo, Sonora, Mexico; (PR-G) Instituto de Biología, UNAM, Mexico D.F., Mexico.

We estimated and described the extent, distributional patterns and stability of the annual eelgrass, *Zostera marina*, in the Infiernillo Channel, Gulf of California. These are the most extensive annual eelgrass beds in northwestern Mexico, presenting distinctive physiological characteristics (i.e., high seed production and germination, and changes in the temperature trigger the germination) as other populations in the Gulf. Total coverage of the eelgrass beds was estimated using oblique and vertical aerial color photography and video from a blimp and an aircraft from 1999 to 2001. Differential GPS was used to map eelgrass bed contours and inspection of beds was done from the boat or by diving. Information on depth and eelgrass characteristics (i.e., continuous, patchy, short, tall) was collected to characterize the beds. In addition, traditional ecological knowledge of the Seri (Comcáac) Indians was used to locate them. The continuous eelgrass beds cover 12% (3,642 hectare) of the Channel and patchy eelgrass covers another 10% (3,045 hectare). Four types of eelgrass beds were observed in terms of their location: (1) isolated beds near estuary mouths, (2) beds along mainland and Tíburon Island coasts, (3) deep central beds, and (4) beds occurring inside large, shallow, protected bays. Eelgrass beds were sub tidal (1-8-m depth) ranging in size from 4 to 243 hectare; the majority (67%) had an area of less than 50 hectare. Eelgrass beds regrew in the same areas during the 3-yr study, maintaining the same shapes and sizes. Distributional patterns and stability of the beds are due to the accumulation of large seed banks in specific areas of the Channel. We discuss the eelgrass beds importance in the productivity of the Channel, the local fisheries and the Seri culture. Finally, we present long term monitoring research recommendations and conservation measurements of this unique eelgrass population.

**Annual Changes on Seagrass Species Composition and the Size of Seagrass Beds at Nagura Bay, Ishigaki Island, Okinawa, Japan**

Z. Kanamoto, Center for Marine Environmental Studies, Ehime University, Matsuyama 790-8577, Japan.

Annual changes on seagrass species composition and the size of seagrass beds at Nagura Bay, Ishigaki Island, Okinawa, Japan, were assessed during the period of 1998–2001, and compared with the data obtained in 1977–78 and 1997. Assessments of seagrass beds in the bay were conducted using transect lines along seagrass beds between 150 m in the outer bay and over 1,000 m in the inner bay. Seagrass beds were narrower in the outer bay than the inner bay due to a lack of mud flats. Seagrass composition in the bay consisted of eight species. *Cymodocea rotundata* and *Thalassia hemprichii* were the most common and abundant species in the bay while *Halodule uninervis*, *H. pinifolia*, *C. serrulata*, and *Halophila ovalis* were common but not abundant. *Syringodium isoetifolium* was restricted to certain areas in
the outer bay in 1977, but found in the wider areas of the entire bay in 1997–2001. *Zostera japonica* was found only in the mouth of Nagura River in 1978, but now occurred commonly in tidal flats of the inner and middle bay, and also a few in the outer bay. Seagrass beds expanded in some areas of both inner and outer bay in years 1998–2001 in comparison with those in 1977–78. However, no statistically significant seasonal change has been found. Seagrass coverage is dependent on the sandy substratum in the bay, which changed by the influences of typhoon and westerly winds. Furthermore, the size of seagrass bed seemed to be influenced by the submersible construction and drainage of aquaculture ponds. The seagrass beds decreased at northern middle part of the bay in 1999 due to the construction of prawn farming ponds during 1998 and 1999. Small changes in seagrass beds were caused by substrate conditions and water pollution, which were the result of natural or man-made disasters.

**Impact of a Sewage Treatment Station on Zostera noltii Meadows at Ria Formosa Lagoon, Southern Portugal**

S. CABAÇO, R. MACHÀS, AND R. SANTOS, CCMAR, Universidade do Algarve, Campus de Gambelas, 8000-117 Faro, Portugal.

The impact of a sewage treatment station on *Zostera noltii* of Ria Formosa, southern Portugal, was assessed by characterizing four meadows distributed along the environmental gradient, from the effluent discharge to a main channel of Ria Formosa. The biomass, density, epiphyte load and morphometry (leaf length and width, internode length and diameter, and root length) of *Z. noltii* were evaluated. Environmental variables of water column and sediment such as salinity, inorganic nutrients and redox potential were also quantified. At low tide there was an evident decrease of ammonium, nitrate, phosphate and salinity in the water column from the effluent source to the main channel. At high tide, nitrites were the most available nutrient in the water column while ammonium concentration was low, except in the main channel where nitrate concentration was very low. Sediment porewater showed high levels of ammonium and phosphate in all meadows while nitrites were very low. Redox potential was more negative (anoxic) in the disturbed meadows (around $-300$ mV) than in the main channel ($-100$ mV). Shoot density was lower near the effluent source (about 6,000 shoots m$^{-2}$) than in the main channel ($>13,000$ shoots m$^{-2}$). In general, total biomass and percentage of epiphytes were higher at disturbed sites, decreasing along the nutrient gradient. Disturbance appears to increase the morphometric features of leaves and internodes and to decrease the maximum root length. The root length and root biomass showed lower values where nutrient concentrations were higher. Results suggest that sewage effluent disturbance may have an inhibitory effect on shoot density and both root length and biomass, but stimulate the total biomass and the morphometric features of the leaves and internodes of *Z. noltii*.

**Direct Evidence of Imbalanced Posidonia oceanica Population Dynamics in the Spanish Mediterranean**

N. MARBA, C. M. DUARTE, E. DÍAZ-ALMELA, AND J. TERRADOS, (NM, CMD, ED-A) IMEDEA (CSIC-UIB) Institut Mediterrani d'Estudis Avançats, C/ Miquel Marquès 21, 07190 Es porles (Illes Balears), Spain; (JT) Centre d’Estudis Avançats de Blanes (CSIC), Accès a la Cala Sant Francesc 14, 17300 Blanes, Spain.

Seagrass beds have experienced important declines in many areas around the world since 1970. Monitoring efforts to assess the status of seagrass meadows in order to detect future losses at early stages are increasing. Seagrass shoot demography is a useful early warning indicator of large-scale seagrass loss, particularly in slow growing species as *Posidonia oceanica*. We examined shoot recruitment and shoot mortality rates of *P. oceanica* in 15 Spanish Mediterranean meadows between 2000 and 2001 through the direct census of tagged shoots in permanent plots. From summer to winter 2000, three 0.12-m$^{2}$ to 0.25-m$^{2}$ permanent plots were established in each meadow and all the shoots within it were tagged with plastic cable tie around its vertical rhizome. Plots were visited 1 yr later and, then, the number of surviving shoots and the number of new shoots produced between consecutive visits was counted. Shoot mortality rates ranged from $0.027 \pm 0.033$ yr$^{-1}$ to $0.327 \pm 0.012$ yr$^{-1}$, whereas shoots recruited at rates ranging from $<0.017$ yr$^{-1}$ to $0.163 \pm 0.014$ yr$^{-1}$. In most of the meadows examined, shoot mortality exceeded shoot recruitment rates, being shoot mortality rates, on average, 6.4-fold higher than those of shoot recruitment. The net pop-
ulation growth rates during 2000–01 experienced by the *P. oceanica* at the meadows studied ranged from 0.002 yr$^{-1}$ to -0.303 yr$^{-1}$. If the net population growth rates were maintained, shoot density could thin to half within 2.2 to 12 yr in those populations where population dynamics was unbalanced. However, the large mortality rates experienced by the *P. oceanica* during 2000–01 are probably due to unusual high water temperature, and in some meadows, the passage of unusual severe strong storms.

**Simulating Effects of a Hurricane: Experimental Manipulations of a Tropical Seagrass Community in the Mexican Caribbean**

V. CRUZ-PALACIOS AND B. I. VAN TUSSENBROEK, (VC-P) El Colegio de la Frontera Sur, Unidad Chetumal, Chetumal, México; (BlT) Unidad Académica, Puerto Morelos, Instituto de Ciencias del Mar y Limnología, UNAM, Cancún, México.

Seagrass beds in the Caribbean Sea are exposed to major meteorological events such as hurricanes and tropical storms, which are accompanied by high water movement, and resuspension and deposition of sediments. Experiments about the effect of these disturbances on seagrasses have mainly been accomplished from an autoecological perspective, not from a community one. Seagrass communities in reef lagoons from the Mexican Caribbean are generally composed of 1 to 3 species of seagrasses and 3 to 20 species of psammophytic macroalgae. Experimental treatments (one-time application with different levels) of high water movement, sediment burial and sediment removal are applied into 60 vegetation plots located in a reef lagoon site. The aim of this study is to test the hypothesis that these events cause shifts in the community structure (species composition and abundance), and that these shifts are due to differential susceptibility of the species to be (partially) removed by a major meteorological event. This susceptibility of a species to be removed, is thought to depend on the plant’s architecture, specially in terms of above and below-ground distribution patterns of plant tissues, such as proportion above- and below-ground biomass, depth of rooting, and surface area of above-ground tissue.

**Landscape Analyses of Zostera noltii in Response to Barrier-Islands Dynamics**

A. CUNHA, R. SANTOS, A. GASPAR, AND M. BAIRROS, CCMAR Centre for Marine Sciences, Universidade do Algarve, Campus de Gambelas, 8000 Faro, Portugal.

The western sector of Ria Formosa lagoon (south of Portugal) communicates with the ocean by the Ancão Inlet, which shows a typical 40-yr cycle of eastward migration and westward reopening. This induces a cyclic sediment disturbance on the seagrass environment. The spatial changes of *Zostera noltii* was analyzed with aerial photography in 1980, 1989 and 1996, and again in 1997 just after a new inlet was opened. Changes in total area, number of patches, mean patch area, mean patch coefficient of variation, and landscape fractal dimension were analyzed. The stability of patches over time using both the fractal dimension ($D$) and the stability coefficient ($H$) were also assessed. Between 1980 and 1989, the total area and the mean patch area increased while the number of patches decreased, indicating patch coalescence and growth. The coefficient of variation increased during this period indicating that coalescence was more frequent in larger patches. Between 1989 and 1996, there was a conspicuous increase in total area, patch number and coefficient of variation indicating a period of high recruitment. The fractal dimension decreased between 1980 and 1996, indicating that landscape complexity decreased when patches become bigger and with patch recruitment. After the inlet opening, the seagrass area, number of patches, patch mean area and coefficient of variation decreased. The fractal dimension of the seagrass landscape increased by 50%, showing that besides a decrease in total area, number of patches and patch mean area, patch fragmentation was an important consequence of anthropogenic disturbance. The coefficient of stability $H$ increased between 1980 and 1996 and decreased after the inlet was opened. This coefficient was always higher then 0.5 suggesting a landscape under stable processes.
Recent Trends in Eelgrass, *Zostera marina*, Distribution and Abundance along the West Coast of Baja California, Mexico


Seagrasses are critically important components of marine coastal and estuarine ecosystems, but are declining worldwide. As part of an ongoing program to inventory and monitor seagrass beds along the Pacific coast of Baja California, we assessed trends in the distribution and abundance of eelgrass at San Quintin Bay. Change in spatial extent of eelgrass was evaluated through a map-to-map comparison of a 1987 Satellite Pour l' Observation de la Terre (SPOT) multispectral scene and a 2000 Landsat Thematic Mapping 7 (TM) satellite. Eelgrass comprised 49% and 43% of the spatial extent of San Quintin Bay in 1987 and 2000, respectively. We detected a 14% (−322 hectare) decline in spatial extent of eelgrass over the 13-yr interval, and losses were most evident in subtidal areas (−456 hectare). Based on long-term ground data, abundance (density and biomass) of eelgrass also declined in San Quintin Bay over the same time period. Specific causes for the eelgrass decline in this bay are unknown, but are likely related to decreased water clarity and increased sediment loading associated with natural and anthropogenic events. There is additional evidence indicating that eelgrass declines may be occurring on a larger regional scale.

Implications of Subterranean Aquifers to Seagrass Habitats Along the Caribbean Coast of Mexico

T. Carruthers, B. Van Tussenbroek, and W. Dennison, (TC, WD) University of Maryland Center for Environmental Science, P.O. Box 775, Cambridge MD 21613; (BoT) Universidad Nacional Autonoma de Mexico, Apdo. Postal 1152, Cancun 77500, Quintana Roo, Mexico.

The Mexican Caribbean coast of the Yucatan peninsula has undergone immense growth over the last four decades. There is increasing concern about nutrient loads from anthropogenic sources and the potential impacts to seagrass, coral reef and macroalgal habitats. Yet, little research has been carried out to assess the loads or impacts of nutrients into coastal habitats of the Mexican Caribbean. The Yucatan peninsula protrudes from the far northeast coast of Mexico, with the Gulf of Mexico to the northeast and the Caribbean Sea to the southwest. The eastern coast of the Yucatan, along with Belize, forms the far western shore of the Caribbean Sea. This coastline has the second longest barrier reef in the world, which forms a shallow coastal lagoon from 0.5 to 1.5 km wide. The dominant seagrass growing in the lagoon is *Thalassia testudinum* with some *Syringodium filiforme* and *Halodule wrightii*. The Yucatan limestone is extremely karstic and rainwater rapidly infiltrates into the aquifer, resulting in the absence of surface drainage or rivers. Rainfall varies between 1,100 and 1,300 mm/yr. The aquifer is visible in numerous sink holes (cenotes), and this water passes through an immense network of underground caves and channels to vent into the marine coastal areas through submarine springs (ojos del aqua) and fissures. Nutrients from intensive farming, sewage or trash could potentially enter the groundwater, flow through to submarine springs and provide a localized source of nutrients to the lagoon; these potential loads and impacts are presently undetermined. Stable isotope analysis to determine natural abundance of N15–N14 ratio as well as tissue %N and %P can be used as effective bioindicators of nutrient loads and impacts in seagrass habitats.

Effects of Floodwaters on the Seagrasses of Hervey Bay and the Great Sandy Strait: Implications for Dugong, Turtle and Fisheries Management

L. J. McKenzie, C. A. Roder, A. J. Roelofs, and S. J. Campbell, Northern Fisheries Centre—Department Of Primary Industries, PO Box 5396, Queensland 4870, Australia.

In Feb. 1999, the Mary River flooded into Hervey Bay and the Great Sandy Strait. The flood was the fifth highest in the last 50 yr and produced a large freshwater plume of suspended sediments which
extended 35 km into Hervey Bay. The flood had the greatest adverse effect on the intertidal and shallow subtidal seagrasses in the Great Sandy Strait and Hervey Bay that were in the path of the flood plume. Approximately 50% of intertidal seagrasses in the Great Sandy Strait disappeared and shallow subtidal seagrass resources of Hervey Bay disappeared within 9 mo. Deepwater seagrass resources in Hervey Bay within the path of the flood plume declined significantly in abundance 6 mo after the impact and remained significantly lower than outside the impact area after 9 mo. Recovery of the intertidal and shallow subtidal seagrasses did not begin until mid-2000. By early 2002, the abundances and distribution of seagrass meadows had recovered to preflood levels. Implications of seagrass loss/recovery to sea turtle, dugong and fisheries management are discussed.

The Use of the *Posidonia oceanica* Meadow as a Biological Indicator of Environmental Quality: Application to the Corsican Coasts (France)

V. PASQUALINI, C. Pergent-Martini, AND G. Pergent, Université de Corse, Equipe Écosystèmes Littoraux, 20250 Corte, France.

In order to effectively manage natural resources, it is necessary to lay out information that allows evaluation of the quality of the environment. The use of biological indicators (species or group of species) often seems a well-adapted means to answer to this kind of problem. For this reason, since a few years, a particular interest has been carried out for seagrass beds. Indeed, their broad distribution in the littoral zone, make them good indicators of general water quality. According to the prevalence of *Posidonia oceanica* in the Mediterranean Sea, we have studied the distribution of these meadows all around Corsica Island, and made specific measurements of different parameters (e.g., density, phenology, and trace-metal contamination). According to bibliographic data, we have proposed grids of interpretation of these descriptors, and we have applied these grids to the Corsican coast. The use of a Geographical System Information (GIS) provides a general vision of the quality of the littoral. It seems that *Posidonia* beds exhibit a normal to good health, and these results are in accordance with the low human pressure in this region.

Status of Seagrasses of India

K. Srinivasanand AND N. Rajendran, (KS) Central Pollution Control Board, East Arjun Nagar, Shahadra, Delhi 110032, India; (NR) CAS in Marine Biology, Parangipettai 608502, Tamil Nadu, India.

Seagrass meadows, mangroves and seaweeds associated with coral reefs are important habitat of the marine environment, which are also highly diverse and productive of the earth’s ecosystems. Seagrasses are the flowering plants, which are restricted to saline habitats and intermingle with both mangroves and coral reef communities at their respective seaward and landward boundaries. Seagrasses reduce the particulate pollutants of the sea by trapping and binding the sediments and also serve as shelter and swim-in-restaurants for marine animals. Along the Indian coast, luxuriant seagrass beds are found. *Enhalus acoroides*, *Halophila species*, *Thalassia species*, *Cymodocea species*, *Halodule species*, *Syringodium isoetifolium*, *Urochondra setulosa* and *Zostera marina* are major seagrasses available along the Indian coast. This study was carried out to review the present status of seagrasses along the Indian coasts, i.e., East coast, West coast, Andaman and Nicobar Islands, and Lakshadweep Islands that is covering an area of 8,100 km. The present paper discusses the environmental factors which are influencing the distribution of seagrasses. Also highlighted are the measures to be framed for conservation and management of seagrasses meadows along these coastal belts.

Long-Term Dynamics of Seagrass Beds in Hokkaido, Japan with Reference to Human Land Use

H. Mukai, Akkeshi Marine Station, Field Science Center for Northern Biosphere, Hokkaido University, Akkeshi-gun, Japan.

Coastal ecosystems are maintained by allochthonous inputs from land ecosystems. The processes and patterns of the subsidy affect coastal food webs, trophic cascades and production processes in coastal ecosystems. Dynamics of seagrass beds were also affected by terrestrial inputs. This study focused on
the dynamics of the eelgrass beds in the Akkeshi-ko Estuary, Hokkaido, Japan, during 50 yr. The expansion of the eelgrass beds was estimated by aerophotographs. By our investigations, nitrogen recycling in the Akkeshi-ko Estuary is estimated as following processes. That is, in regular observations, dissolved inorganic nitrogen (DIN), which is main resource of nitrogen at regular flow ing, in river water flow out from terrestrial to coastal ecosystems is used by phytoplankton and eelgrasses/epiphytes. On the other hand, in irregular events, melting snow, floods, and heavy rains, particulate organic nitrogen (PON), which is main resource of nitrogen at irregular events, is accumulated in bay-head sediments of the Akkeshi-ko Estuary, although most DIN flows out to outside by strong currents due to heavy rain. PON accumulated in the sediments is decomposed by microorganisms and/or benthos, and used by eelgrasses with roots. This sediment nutrification by flood would facilitate eelgrass production with a time lag. This process would be examined by the study of inspection, i.e., estimation of nitrogen inputs, distribution of nitrate + nitrite, ammonia and chlorophyll concentration, PON distribution in sediments, etc. After all, the history of human impacts in land use and dynamics of eelgrass beds are compared and it is examined the effects of land alteration on eelgrass production and expansion.

Zostera noltii Bed Responses to Local Hydrodynamic Changes

G. Peralta, J. L. Perez-Lloréns, I. Hernández, and F. G. Brun, (GP, JLP-L, IH, FGB) Department of Biology, University of Cádiz, 11510 Puerto Real (Cádiz), Spain; (GP) Department of Spatial Ecology, NIOO-CEME, P.O. Box 140, 4400 AC Yerseke, The Netherlands.

The Ria Formosa Natural Park (South Portugal) is a tidal lagoon separated from the Atlantic Ocean by several sandy islands. Perennial beds of Zostera noltii Hornem. extend into the intertidal muddy flats of this lagoon. In 1997, a new inlet was opened in the east of the barrier islands, affecting the hydrodynamics and sedimentation at both sides of the inlet. We studied the effects of the new hydrodynamic conditions on a Z. noltii meadow close to the perturbed area. In the first winter, sand inputs partially buried the meadow. Instead of disappearing, the buried area was totally recovered after a period of 6 mo. During the recovery, important divergences in growth and morphometry were observed in the new plants. Rhizome production increased from 27% to 71% of the total growth rate. The higher production of belowground tissues favored a fast recolonization of the bare areas, but reduced the relative production of photosynthetic tissues. The decrease in leaf production was due to a reduction in the new leaf size (i.e., 65% length and 25% width reduction), but not in the leaf appearance rate. This resulted in an increased shoot density (>100%) without leaf biomass increase. In addition, the new plants exhibited higher photosynthetic capacity compared to the large-leaved morphotype that was presented before the disturbance. The ecophysiological consequences of morphometric changes as a response to hydrodynamic variations and the adaptive strength of Z. noltii as colonizer species are discussed.

Are all Seagrass Meadows Equal—Measuring Change and Values for Tropical North Eastern Australian Seagrass Meadows

R. Coles, L. McKenzie, S. Campbell, A. Roelofs, C. Roder, K. Derbyshire, and M. Rasheed, Marine Plant Ecology Group, Department of Primary Industries, Cairns, Queensland, Australia.

A 15-yr program has mapped coastal and nearshore seagrasses in tropical northeastern Australia. Sixteen species have been identified. There is an estimated 4,500 km² of seagrass in east coast waters less than 20 m deep; 520 km² in Gulf of Carpentaria waters, and 13,425 km² in the shallow Torres Strait between Australia and Papua New Guinea. Surveys in water deeper than 20 m have also indicated that approximately 40,000 km² of seafloor area in the Great Barrier Reef World Heritage Area is likely to have some seagrass cover. If it is accepted that species and area are a valid surrogate for seagrass habitat values, then these maps are an excellent baseline for advice to managers making coastal development decisions and to measure change. But are all seagrasses and all areas of seagrass of equal importance? The evidence is conflicting. East coast measurements suggest that intertidal and shallow subtidal seagrasses form obligate nursery grounds for juvenile commercial shrimps, yet almost no juvenile commercial shrimps were found in seagrasses deeper than 10 m. In the Torres Strait however, losses of subtidal seagrasses have been implicated in reduced catches of the painted crayfish Panulirus ornatus. Protective measures required for intertidal seagrass also bear little similarity to the require-
ments to protect seagrasses found in subtidal waters particularly at 30 to 60 m water depths. We examine the advice and approaches being considered.

Ecological Features of Zostera spp. in Some Temperate Euro-Asian Seas (A Review)

N. A. Milchakova, Institute Biology of the Southern Seas, 2 Nakhimov Ave., Sevastopol 99011, Ukraine.

In temperate Euro-Asian seas (Mediterranean, Black, Azov, Caspian and Aral), two Zostera species occur: Zostera noltii everywhere and Z. marina from the Mediterranean to the Azov Sea. The richest beds are found in shallow bays, coves and coastal salt lakes of the Black and the Azov Seas. In the seas studied, Z. noltii grows from 0.2 to 45 m deep, while Z. marina occurs from 0.2 to 17 m depths with the seawater salinity varying from almost freshwater to oceanic. Zostera noltii is found in high salinity (45–50‰, the Caspian and the Aral seas) and Z. marina no more than 33‰. Maximum biomass of Z. marina is similar in the Black and the Mediterranean Seas (712 and 775 gDw m⁻², respectively), while the number of shoots is twice as great (1,136 shoots m⁻² vs 690 shoots m⁻²) in the Black Sea. In the Azov Sea, the corresponding estimates are several times less. For Z. noltii, the greatest biomass and abundance estimates (446 gDw m⁻² and 5,432 shoots m⁻²) were obtained in the Black Sea. In the Azov Sea, similar abundance, and in the Aral Sea, similar biomass were measured. Compared with the Black Sea, the corresponding estimates are half that in the Caspian Sea and several times less in the Mediterranean. In the Mediterranean lagoons, Z. noltii has biomass and abundance 2–3 times greater than in the open coastal seawater (226 gDw m⁻² vs 76 gDw m⁻² and 2,944 shoots m⁻² vs 1,246 shoots m⁻², respectively). In total annual production, Z. marina inhabiting the seas of the Mediterranean basin exceeds Z. noltii by three times.

Preliminary Study of Ruppia filifolia Meadows in Seno Skyring, Magellan’s Region, Chile: Dynamics and Population Structure

P. Ramírez-García, A. Mansilla, N. Navarro, and M. Palacios, (PR-G) Instituto de Biología, Universidad Nacional Autónoma de México, Cancun, Mexico; (AM, NN, MP) Facultad de Ciencias, Universidad de Magallanes, Punta Arenas, Chile.

Ruppia filifolia (Phil.) Skottsb. is the most common species in fiords and channels in Seno Skyring, Magellan’s Region, where it forms dense subtidal populations. Although this species is not a true seagrass, it’s responsible for the high productivity in these coastal ecosystem. Previous studies on their structure and production are scarce. The aim of this study is the characterization of R. filifolia populations, quantifying through the annual reconstruction of their rhizomes, the growth rate, rhizome production, average weight, density and shoot production. Ten cores of 30 cm in diameters for 40 of depth were haphazardly extracted. The results showed an annual rhizome growth rate of about 14.4 cm yr⁻¹ and internodal production of 13 FL yr⁻¹. Other structural parameters obtained were shoot average weight (0.017 g DW shoot⁻¹), highest shoot density (17,643 shoot m⁻³), and dry biomass (223, 200 and 150 g DW m⁻²) for leaves plus sheaths, rhizomes and roots respectively. Finally, through the reconstruction growth curve of R. filifolia showed a positive relationship between visible and ultraviolet radiation.

Changes in Seagrass Distribution as Evidence of Historical Water Quality Conditions

K. A. Moore, B. A. Anderson, D. J. Wilcox, R. J. Orth, and M. Naylor, (KAM, BAA, DJW, RFO) Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Williamsburg, VA; (MN) Maryland Department of Natural Resources, Annapolis, MD.

Strong, positive relationships between water clarity and maximum depth of growth of seagrass populations suggest that knowledge of their historical growth depths may provide insights into historical water clarity conditions. This information, in turn, can be useful in setting water quality targets for restoration of coastal and estuarine systems. In the Chesapeake Bay system, a comprehensive analysis of historical eelgrass and other submersed macrophyte distributions has been completed using aerial photography dating back to the 1930s. Although a precipitous decline in submersed macrophyte populations was observed throughout the system in the early 1970s, many freshwater and low salinity
tidal areas had declined by the 1940s or earlier, with mesohaline regions declining in the 1950s and 1960s. Both current and historical seagrass maximum growth depths decrease with distance up-estuary, reflecting higher turbidity levels. In one sub-estuary, the York River, determination of historical growth depths from interpolation of bottom bathymetry demonstrates that existing seagrass populations are currently growing approximately 0.5 m shallower than populations 50 yr ago. This would equate to an increase in water column light attenuation of 40%.

A Regional Approach to Monitoring Change in Seagrass Meadows


The status of Queensland’s seagrass meadows is poorly understood with a paucity of data available on their condition and the factors affecting their growth, abundance and distribution. To understand the dynamics of seagrass meadows over broad spatial scales, community volunteers, natural resource managers and scientists have worked in partnership to develop a program called Seagrass-Watch. The program monitors the change in seagrass meadows across 5 regions in Queensland, from the regional to the local scale. Within each region a number of locations are monitored, with 2–4 sites at each locality. About sixty sites have been monitored on a seasonal basis since Aug. 1999. Parameters measured at each site, along fixed transects, include percentage seagrass cover, percentage algal and epiphyte cover, canopy height and seagrass species composition. The techniques allow the status of seagrass meadows to be assessed and provide data on rates of seagrass recovery following impact. Estimates of Halodule uninervis seed densities were also measured at some sites to identify the probability of seagrass recovery from seed reserves. The first 2 yr of the program showed that the abundance of seagrass in some meadows increased 10-fold, other meadows declined and some remained stable. Between site variation in seagrass abundance was generally low, but variability between localities and between regions was high. Such a pattern suggests that environmental processes affecting seagrass abundance are relatively uniform at local spatial scales compared with those operating at regional scales. The ability of trained community members to detect seasonal patterns in seagrass abundance, and identify areas of poor seagrass condition, has enormous benefit for the management of seagrass habitats. The ongoing strength of the program depends on the co-operation between a range of stakeholders, regular and accurate assessments of the condition of seagrass meadows, and the use of data by management agencies.

Global Monitoring Presentation

SeagrassNet: Monitoring a Critical Coastal Resource Worldwide

F. T. Short, R. G. Coles, M. D. Fortes, and E. W. Koch, (FTS) Department of Natural Resources, Jackson Estuarine Laboratory, University of New Hampshire, Durham, NH 03824; (RGC) Department of Primary Industries Queensland, Northern Fisheries Centre, Cairns, Queensland 4870 Australia; (MDF) Marine Science Institute CS University of the Philippines, Diliman Quezon City 1101 Philippines; (EWK) Horn Point Laboratory, University of Maryland Center for Environmental Science, Cambridge, MD 21613.

SeagrassNet is a global monitoring program to investigate and document both the status of seagrass resources worldwide and the threats to this important and imperiled marine ecosystem. The program started with an ongoing pilot study in seven countries of the Western Pacific and is now expanding to other countries; a globally applicable monitoring protocol and web-based data reporting system (SeagrassNet.org) have been established. The goal is continued expansion of SeagrassNet to other areas of the globe and establishment of a network of monitoring sites linked via the World Wide Web by an interactive database. SeagrassNet’s efforts to monitor known seagrass areas and to reconnoiter uncharted seagrasses are important first steps in understanding and sustaining the seagrass resource. Synchronous and repeated global sampling of selected plant and environmental parameters will reveal both human impacts and natural fluctuations in coastal environments throughout the world. The monitoring protocol assesses basic plant parameters, including species identification, percent cover, biomass, density, and canopy height along with photographic records, sediment samples, and long-term temperature and light data. At each site, a permanent transect is established and monitored
quarterly so that changes in depth distribution of seagrass, the extent of the meadow, and species composition can be assessed over time. Scientists and managers at locations across the Western Pacific have now been trained in the protocol and are actively sampling and submitting data electronically; other countries are starting to participate and further training workshops are scheduled.