THE SPATIAL DIMENSIONS OF FISHERIES: PUTTING IT ALL IN PLACE

Kai Lorenzen, Robert S. Steneck, Robert R. Warner, Ana M. Parma, Felicia C. Coleman, and Kenneth M. Leber

ABSTRACT

Explicit consideration of space and place in fisheries science and governance holds great promise for addressing management failures caused by inappropriately defined boundaries, disregard for spatial dynamics in assessments, and incompatible ocean uses. Most importantly, it can foster the emergence of sustainable, rights-based governance regimes and protected areas to aid conservation and restoration of marine ecosystems. The proceedings of the 2008 Mote Symposium in Fisheries Ecology review and synthesize recent progress in spatial fisheries science as a basis for effective space- and place-based governance. Ecological, social, and governance systems operate at multiple, nested scales. Identification of these scales and fostering of multiscale linkages and feedback loops is a key challenge in spatial governance. Spatial management measures provide opportunities for effective regulation and conservation at low transaction costs. They also provide new opportunities as well as challenges for fisheries assessment. Effective implementation of spatial governance benefits from participatory planning involving all legitimate stakeholders and responsive, adaptive, learning approaches.

Until relatively recently, most fisheries were exploited under conditions of open access or government regulation applied homogeneously over large areas. Most marine populations were believed to be under "open" recruitment dynamics (see, e.g., Caley et al., 1996) from a wide-spread larval pool and to receive relatively little contribution from local production (Warner and Cowen, 2002). Fisheries science focused on providing management advice for unitary stocks, and fisheries assessments conveniently assumed that stocks were devoid of spatial heterogeneity or any kind of interactions with either other species or with habitats. Since then, we have seen a rapid rise in alternative, market- and community-based approaches to fisheries governance; appreciation of the importance of spatial heterogeneity and dynamics in marine ecosystems and social systems; scientific recognition of smaller-scale connectivity; and movements to set aside marine areas for conservation.

Perhaps the earliest proponent of a paradigm shift toward self-governed, place-based institutions was Bob Johannes, whose 1981 classic *Words of the Lagoon* documented intricate, enduring, and apparently successful local management systems in Micronesia, giving rise to the notion of customary marine tenure. We dedicate this symposium issue to his memory. Although local management systems exist in many artisanal settings, some, like the "lobster gangs" of Maine, occur in U.S. commercial fisheries (Acheson, 1988).

Self-governance of fisheries is gaining recognition as an alternative to bureaucratic governance or privatization, and Ostrom's (1990) metaanalysis provided key generalizations about when and how such systems could be successful and what conditions are likely to facilitate their emergence.

Meanwhile, fisheries ecologists have embraced spatial heterogeneity and dynamics within population models and stock assessments (MacCall, 1990). This trend started

Bulletin of Marine Science

with the mandate to evaluate essential fish habitat (highlighted in the reauthorized Magnuson-Stevens Fishery Conservation and Management Act of 1996), gained momentum with the movement to establish marine reserves (1998 Mote Symposium on "Essential fish habitat and marine reserves"), and accelerated with the advent of ecosystem-based approaches to management, which emphasized fishing impacts on nontarget species and habitats, both of which tend to be spatially differentiated (2002 Mote Symposium on "Confronting trade-offs in the ecosystem approach to fisheries management"). As this brief history illustrates, emphasis on the spatial dimensions of fisheries has arisen from multiple, different perspectives; fisheries social sciences have emphasized place-based human-environment interactions at local scales and the particular conditions under which self-governance works, while the fisheries natural sciences focused on the dynamics of abundance patterns in continuous space, emphasizing the linkages and continuity across spatial scales within physical and ecological systems. These strands are now coming together in the drive toward spatial ecosystem-based fisheries and ocean management (Worm et al., 2009; Norse, 2010). The aim of the Seventh William R. and Lenore Mote Symposium was to foster integration across scales and among the ecological, social, and governance levels of fisheries systems.

The Case for Space and Place in Fisheries

The spatial differentiation and dynamics of habitats, biological resources, fishing fleets, and social and governance structures has long been recognized but not well accounted for in management. Boundaries around physical structures, fisheries resources, and jurisdictional entities have often been drawn in an ad hoc manner. Not surprisingly, mismatch between the scale of resources and of their assessment and management is common and ranks among the primary causes of management failure in fisheries (Hilborn et al., 2005; Prince, 2010). Institutional analysis also shows that clear and appropriate boundaries around resources and those entitled to use them are among the key ingredients of successful common-pool resource governance (Ostrom, 1990). Such boundaries allow development of management policies based on the allocation of exclusive fishing rights to individuals or groups, recurrent tools for achieving sustainability (Berkes, 2010; Castilla, 2010; Prince, 2010).

Even within the overall boundaries of resources, spatial structure and dynamics are important. Range contraction for example, in which stocks and the fisheries exploiting them contract in range as stock abundance declines, has the dual perverse effects of masking stock decline and increasing effective fishing mortality unless accounted for in spatially explicit assessments (Walters and Martell, 2004). Conversely, spatial fishing restrictions or marine reserves provide effective means for protecting resources and habitats and, often, improving fisheries outcomes (Norse, 2010; Kenchington, 2010; Steneck and Wilson, 2010).

A further, important argument for space- and place-based management arises from the growing extent and diversity of ocean uses and interests outside the fisheries sector: recreation, wind and wave power, minerals extraction, aquaculture, shipping, and, of course, conservation. Many of these uses and interests are incompatible with one another. Ocean zoning provides a means of reducing use and interest conflicts as well as rationing the areas over which uses can occur and creating opportunities for establishment of rights-based incentives for sustainable use (Norse, 2010; Kenchington, 2010; Sanchirico et al., 2010).

Spatial Dimensions in Fisheries Science and Management

Incorporating space and place appropriately into fisheries governance is crucial to sustainability but faces conceptual, technical, and implementation challenges. The symposium contributions assembled in this issue address many of these challenges in an innovative and rigorous manner. Key themes emerging from the contributions include (1) the need for explicit consideration of multiple spatial and temporal scales in resources, social systems, and governance and (2) the need to create links between ecological and social systems at multiple scales.

Governance.—Governance systems must deal effectively with diverse uses and interests on multiple, nested spatial and temporal scales. Governance systems must therefore be comprehensive in the sense that they cover the entire area within a jurisdiction and include all legitimate uses and interests (Norse, 2010). Governance systems must also operate at multiple, nested scales matching those at which resources and their uses are structured and interact (Berkes, 2010; Steneck and Wilson, 2010), but doing so does not necessarily require bureaucratic structures to form a neat and nested array of organizational units. Rather, polycentrism—networks of governing bodies that may have partly overlapping jurisdictions and roles and that may arise or dissolve in response to functional needs—is a more realistic and, quite probably, more effective vision (Brewer, 2010).

Ocean zoning is emerging as a key element of effective governance. Zoning of activities is intended to reduce conflict by separating incompatible uses. In effect, zoning also rations the area over which activities can occur. Separating and rationing will therefore create a set of localized goods and services whose set of users are localized and better defined (Sanchirico et al., 2010). This result could pave the way for nested, place-based institutions: integrated (overall regional oversight), coordinating (across-zone coordination), and specialist zone agencies (e.g., fisheries management in one zone). Trading across zones may be positive: e.g., allowing fishing access to a conservation zone in return for better conservation elsewhere. Finally, zoning can act as a catalyst for wider reforms and lead to establishment of integrating institutions (Kenchington, 2010; Sanchirico et al., 2010). Zoning also limits governance tasks to smaller scales, where social connectivity may be higher and feedback about the impact of human activity less ambiguous, permitting rapid learning (Steneck and Wilson, 2010).

Uses such as fishing within spatially delimited zones can be governed by bureaucratic, communal, or market-based means (Castilla, 2010; Fujita et al., 2010;). Different resource, stakeholder, and market attributes call for different means of governance (Fujita et al., 2010). Allocation of use rights, either communal or individual, is widely seen as a key strategy for countering perverse incentives and fostering sustainability in common-pool resources such as fisheries (Berkes, 2010; Castilla, 2010; Prince, 2010). Use rights should be linked directly with responsibilities, including the responsibility to fish for data as well as profit (Prince, 2010). Allocation of use rights can pose challenges to spatial governance when applied on a species level, because of the very different scales that may be appropriate to different species. An emerging solution to this dilemma is a switch from species-specific to spatially bounded ecosystem rights and privileges (Steneck and Wilson, 2010). Use rights must be big enough in space and time to promote conservation (Sanchirico et al., 2010). Yearly permitting, for example, does not create sufficient incentives for conservation (Fujita et al., 2010).

Resources and Habitats.—Space is important to population and community dynamics at two levels: defining boundaries to units of analysis and analyzing finer-scale distribution and dynamics within them. Recent research suggests that, despite wide geographic distribution, many exploited species function demographically as much smaller local stocks (Steneck and Wilson, 2010). A key challenge is therefore to identify scales of demographic processes that set appropriate boundaries for assessment and management.

Caselle et al. (2010) introduce a new technique for identifying demographically relevant scales by analyzing the spatiotemporal variability of larval settlement in relation to oceanographic processes. Applying the technique in the Southern California Bight, they demonstrate that settlement is in fact associated with a combination of large-scale factors at long time lags and with small-scale factors at short time lags, emphasizing the need to consider multiple nested scales in assessment and management.

Parada et al. (2010) investigate changes in the spatial distribution and abundance of snow crab in the Bering Sea, integrating information on snow-crab distribution with results from modeling of circulation and larval transport in a new conceptual model. Their results indicate the importance of suitable near-bottom temperatures in settlement regions for recruitment and highlight the significance of climate change for future distribution and dynamics of resources, particularly at high latitudes.

Analyzing the spatial dynamics of fish communities, its link to habitat, and the likely impacts of spatial management measures remain key challenges for science in support of spatial ecosystem-based management. In many marine organisms, habitat shifts accompany trophic ontogeny, and these shifts can be critical in evaluating impacts of spatial management. Walters et al. (2010) introduce a new way of accounting for habitat shifts in the modeling of population and community dynamics by dividing populations into multistanza spatial packets that track ontogenic movement patterns over mosaics of trophic opportunities and predation risks.

Fisheries Exploitation.—Many fisheries operate at very local scales, whereas others operate at much larger, sometimes global scales (e.g., roving bandits, Berkes, 2010), but independently of the scale of the fishery, fishing operations and thus fishing mortality rates and possible impacts on habitat are spatially differentiated at small scales. Understanding and predicting the spatial dynamics of fishing fleets is crucial to assessing the economic and social implications of spatial governance and could also yield valuable ecological information. Shester (2010) uses spatial statistics to analyze how trap placement and movement behavior influence the catch performance of Baja California spiny-lobster fishermen. His analysis demonstrates the importance of mobility and the use of exploratory fishing strategies to catch performance. Smith (2010) shows how microeconometric models can be used to identify causal drivers of fishing behavior and to predict responses to policy change. The paper also suggests, and tests by simulation, an approach to deducing biophysical characteristics of an ecosystem from information on fisher decision making.

Spatial Management Measures.—Spatial management measures include temporary and permanent fishing restrictions, as well as "supply side" interventions such as fisheries stock or habitat enhancements. Marine protected areas (MPAs) or no-take reserves are perhaps the most widely implemented spatial management measures. The world-wide drive toward implementing MPAs provides a major impetus for development of broad-based spatial governance. Consensus is broad that MPAs provide conservation benefits beyond those of other fisheries management measures, at least for habitats, for sedentary species, for multispecies fisheries, and where broader ecosystem impacts of fishing are a major concern (Hilborn et al., 2004). Nonetheless, the design of effective MPAs remains challenging in scientific and governance terms (Sale et al., 2006; Kenchington, 2010; Norse, 2010). Spatial management measures need not be permanent—for example, a set of zones may be sequentially opened and closed to fishing as part of a rotational harvesting regime. Indeed, the most advanced spatial governance systems, such as that of the Great Barrier Reef Marine Park, involve a diversity of zoned management regimes from strict nature reserves with no fishing or collecting to multiple, verifiably environmentally sustainable, levels of use and impact (Kenchington, 2010).

Fisheries Assessment.—Spatial governance provides new challenges as well as opportunities for fisheries assessment. In line with multiscale, nested governance, assessment requirements will range from the large-scale comprehensive ecosystem level (Walters et al., 2010) to local, stock-specific assessments (Prince, 2010). Development and use of a broad set of assessment and visualization methods intended for different conditions of scale, data availability, and stakeholder expertise are therefore important. Spatial governance and management measures create new opportunities for assessment and adaptive management. For example, MPAs can be used as reference sites for stock assessment, providing estimates of catch rates and population parameters in unexploited populations (Fujita et al., 2010; Kenchington, 2010). Spatial management measures can also be implemented as adaptive experiments to yield crucial information. At the same time, spatial closures can cause problems for the use of established stock assessment methods because of the changes in spatial distribution of fishing effort and fisheries-dependent data coverage they tend to precipitate (Field et al., 2006). More explicit consideration of assessment opportunities and challenges posed by spatial governance is likely to yield substantial long-term benefits to management.

Allocation of use rights in the context of spatial governance provides excellent opportunities for developing cooperative data collection, assessment, and management schemes. Ernst et al. (2010) describe a collaborative effort between a fishing syndicate and independent scientists involving voluntary data sharing and use of the spatially explicit information to compute and standardize a robust and precise index of resource abundance. Likewise, Moreno-Báez et al. (2010) document a systematic approach to collecting, integrating, and validating local ecological knowledge in small-scale fisheries in the northern Gulf of California, Mexico. Fisheries scientists working closely with fishers, armed with a toolbox of pragmatic approaches such as flexible survey designs, scaleless assessment techniques, dataless or rule-of-thumb management prescriptions, and software tools for mapping, modeling, and visualization are likely to become a common sight in fisheries management (Prince, 2010).

Putting It All in Place: Developing and Implementing Spatial Governance

Use a Participatory Process.—How can spatial planning processes be initiated, sustained, and made effective? Spatial governance can emerge at all levels, be it locally in fishing communities, by government decree, or as a result of conservation initiatives (Johannes, 1981; Castilla, 2010, Fujita et al., 2010; Kenchington, 2010; Norse, 2010). Key ingredients for successful development of such initiatives include the adoption of a participatory process and involvement of all legitimate stakeholders, regardless of the initiating group (Pomeroy and Douvere, 2008; Brewer, 2010; Fujita et al., 2010; Kenchington, 2010; Norse, 2010). Transition to spatial governance is often marred by initial controversy. Consensus is not always achievable and may not be necessary: informed consent is a more appropriate goal. If stakeholders feel they had input, they are more likely to accept the outcome of the process and to comply with regulations (Brewer, 2010). The participatory process is best started through a stakeholder analysis, outreach, and engagement process (Fujita et al., 2010).

Identify Relevant Scales, Interactions, and Governance Models.—An important next step is to identify key scales of physical, biological, and social systems. Multiple, nested scales are likely to be relevant at all levels and should be reflected in the planning process. An integrative resource systems framework can be used to identify key ecological, stakeholder, market, and institutional attributes and interactions that influence outcomes of current governance and responses to policy change (Pido et al., 1996; Lorenzen, 2008; Fujita et al., 2010). This framework can also be used to indentify appropriate spatial scales and approaches for governance (Fujita et al., 2010). In the course of initiating or transforming spatial governance arrangements, wider opportunities for improving governance should be sought and promoted (Sanchirico, 2010).

Implement Adaptively.—Implementation of spatial governance is necessarily a learning process and requires “learning institutions”—institutions that respond, learn, and adapt (Berkes, 2010). Cooperative research can contribute greatly to reducing uncertainties and to promoting confidence in and ownership of results (Fujita et al., 2010). It also is often particularly cost effective. Linking data collection, assessment, and decision making closely to use rights and governance systems promotes buy-in, lowers transaction costs, and leads to better outcomes (Prince, 2010). Adaptive management is a constructive way of dealing with uncertainties in spatial planning. In this context, a balance must be struck in the time frame of planning between one that is too short to provide incentives for resource stewardship and one that is too long and sets suboptimal arrangements in stone.

Symposium Details and Awards

The symposium, sponsored by the William R. and Lenore Mote Endowment at Florida State University, was held at the Mote Marine Laboratory in Sarasota, Florida, 11–13 November 2008. The steering committee responsible for developing the topics and the list of speakers and for choosing young investigator award recipients included (in addition to ourselves) Ray Hilborn (University of Washington) and Lobo Orensanz (National Research Council of Argentina, 2003 Mote Visiting Scholar).

The technical editor for the volume was Anne B. Thistle (Florida State University). The award for the best paper by a young investigator went to Geoffrey Shester, Stanford University Hopkins Marine Laboratory, Pacific Grove, California, for his paper entitled "Empirical analysis of fine-scale spatial behavior and fishing strategies in the Baja California lobster fishery." The award for the best poster from a young investigator went to Ronald J. Maliao, Florida Institute of Technology, Melbourne, Florida, for his poster (coauthored with Ralph G. Turingan) entitled "Impacts of comanagement of marine protected areas in the Philippines."

Acknowledgments

We thank the many referees upon whose judgment we relied for assistance in maintaining the high standards of the proceedings of the Mote Symposia and of the *Bulletin of Marine Science.* We thank S. Sponaugle at the University of Miami, editor of *Bulletin of Marine Science,* for agreeing to publish these proceedings. Publication was supported by the FSU William R. and Lenore Mote Endowment, the Florida Fish and Wildlife Conservation Commission, The Curtis and Edith Munson Foundation, the American Fisheries Society Marine Division, and the Florida State University Department of Biological Science. We thank the Gordon and Betty Moore Foundation for supporting travel for young investigators and the American Fisheries Society Marine Division for supporting the poster session. As always, K. Mahadevan, Director of the Mote Marine Laboratory, proved an exceptional host. Finally, we thank J. Travis, Dean of the College of Arts and Sciences at Florida State University, for his guidance and continued support of every aspect of the Mote Eminent Scholar Chair.

Literature Cited

Acheson, J. M. 1988. The lobster gangs of Maine. Univ. Press New England, Lebanon, New Hampshire. 181 p.

Berkes, F. 2010. Linkages and multilevel systems for matching governance and ecology: lessons from roving bandits. Bull. Mar. Sci. 86: 235–250.

Brewer, J. F. 2010. Polycentrism and flux in spatialized management: evidence from Maine's lobster (*Homarus americanus*) fishery. Bull. Mar. Sci. 86: 287–302.

Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones. and B. Menge. 1996. Recruitment and the local dynamics of open marine populations. Ann. Rev. Ecol. Syst. 27: 477–500.

Caselle J. E., B. P. Kinlan, and R. R. Warner. 2010. Temporal and spatial scales of influence on nearshore fish settlement in the southern California Bight. Bull. Mar. Sci. 86: 355–385.

Castilla, J. C. 2010. Fisheries in Chile: small pelagics, management, rights, and sea zoning. Bull. Mar. Sci. 86: 221–234.

Ernst, B., P. Manríquez, J. M. (L.) Orensanz, R. Roa, J. Chamorro, and C. Parada. 2010. Strengthening of a traditional territorial tenure system through protagonism in monitoring activities by lobster fishermen from the Juan Fernández Islands, Chile. Bull. Mar. Sci. 86: 315–338.

Field, J. C., A. E. Punt, R. D. Method, and C. Thomson. 2006. Does MPA mean "Major Problem for Assessments"? Considering the consequences of place-based management systems. Fish Fish. 7: 284–302.

Fujita, R. M., K. T. Honey, A. Morris, J. R. Wilson, and H. Russell. 2010. Cooperative strategies in fisheries management: integrating across scales. Bull. Mar. Sci. 86: 251–271.

Hilborn, R., J. Orensanz, and A. M. Parma. 2005. Institutions, incentives and the future of fisheries. Phil. Trans. R. Soc. Lond. B 360: 47–57.

_________, K. Stokes, J. J. Maguire, A. D. M. Smith, L. W. Botsford, M. Mangel, J. Orensanz, A. Parma, J. Rice, J. Bell, et al. 2004. When can marine reserves improve fisheries management? Ocean Coastal Manage. 47: 197–205.

Johannes, R. E. 1981. Words of the lagoon: fishing and marine lore in the Palau District of Micronesia. Univ. California Press, Berkeley, California. 245 p.

Kenchington, R. 2010. Strategic roles of marine protected areas in ecosystem scale conservation. Bull. Mar. Sci. 86: 303–313.

Lorenzen, K. 2008. Understanding and managing enhancement fisheries systems. Rev. Fish. Sci. 16: 10–23.

MacCall, A. D. 1990. Dynamic geography of marine fish populations. Univ. Washington Press, Seattle. 153 p.

Moreno-Báez, M., B. J. Orr, R. Cudney-Bueno, and W. W. Shaw. 2010. Using fishers' local knowledge to aid management at regional scales: spatial distribution of small-scale fisheries in the northern Gulf of California, Mexico. Bull. Mar. Sci. 86: 339–353.

Norse, E. A. 2010. Ecosystem-based spatial planning and management of marine fisheries: why and how? Bull. Mar. Sci. 86: 179–195.

Ostrom, E. 1990. Governing the commons: the evolution of institutions for collective action. Cambridge Univ. Press, Cambridge, U.K. 280 p.

Parada C., D. A. Armstrong, B. Ernst, S. Hinckley, and J. M. (L.) Orensanz. 2010. Spatial dynamics of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea—putting together the pieces of the puzzle. Bull. Mar. Sci. 86: 413–437.

Pido, M. D., R. S. Pomeroy, L. R. Garces, and M. B. Carlos. 1996. A handbook for rapid appraisal of fisheries management systems. ICLARM, Manila. 85 p.

Pomeroy, R. S., and F. Douvere. 2008. The engagement of stakeholders in the marine spatial planning process. Mar. Policy 32: 816–822.

Prince, J. 2010. Rescaling fisheries assessment and management: a generic approach, access rights, change agents, and toolboxes. Bull. Mar. Sci. 86: 197–219.

Sale, P. F., R. K. Cowen, B. S. Danilowicz, G. P. Jones, J. P. Kritzer, K. C. Lindeman, S. Planes, N. V. C. Polunin, G. R. Russ, Y. J. Sadovy, et al. 2006. Critical science gaps impede use of no-take fishery reserves. Trends Ecol. Evol. 20: 74–80.

Sanchirico, J. M., J. Eagle, S. Palumbi, and B. H. Thompson, Jr. 2010. Comprehensive planning, dominant-use zones, and user rights: a new era in ocean governance. Bull. Mar. Sci. 86: 273–285.

Shester, G. G. 2010. Explaining catch variation among Baja California lobster fishers through spatial analysis of trap-placement decisions. Bull. Mar. Sci 86: 479–498.

Smith, M. D. 2010. Toward an econometric foundation for marine ecosystem-based management. Bull. Mar. Sci 86: 461–477.

Steneck, R. S. and J. A. Wilson. 2010. A fisheries play in an ecosystem theater: challenges of managing ecological and social drivers of marine fisheries at multiple spatial scales. Bull. Mar. Sci. 86: 387–411.

Walters, C. J. and S. J. D. Martell. 2004. Fisheries ecology and management. Princeton Univ. Press, Princeton. 399 p.

__________, V. Christensen, W. Walters, and K. Rose. 2010. Representation of multistanza life histories in ecospace models for spatial organization of ecosystem trophic interaction patterns. Bull. Mar. Sci 86: 439–459.

Warner, R. R. and R. K. Cowen. 2002. Local retention of production in marine populations: evidence, mechanism, and consequences. Bull. Mar. Sci. 70: 245–249.

Worm, B., R. Hilborn, J. J. Baum, T. A. Branch, J. S. Collie, C. Costello, M. J. Fogarty, E. A. Fulton, J. A. Hutchings, S. Jennings, et al. 2009. Rebuilding global fisheries. Science 325: 578–585.

Available Online: 6 April, 2010.

Addresses: (K.L.) *Division of Biology, Imperial College London, Silwood Park, Ascot SL5 7PY, U.K., and Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, Florida 34236. E-mail: <kai.lorenzen@aquaticresources.org>.* (R.S.S.) *School of Marine Sciences,* *University of Maine, Darling Marine Center, 193 Clarks Cove Road, Walpole, Maine 04573. E-mail: <steneck@maine.edu>.* (R.R.W.) *Department of Ecology, Evolution & Marine Biology, University of California, Santa Barbara, California 93106-9610. E-mail: <warner@lifesci.ucsb.edu>.* (A.M.P) *Centro Nacional Patagónico, CONICET, 9120 Puerto Madryn, Chubut, Argentina. E-mail: <parma@cenpat.edu.ar>.* (F.C.C.) *Florida State University Coastal and Marine Laboratory, 3618 Coastal Highway 98, St. Teresa, Florida 32358-2702. E-mail: <coleman@bio.fsu.edu>.* (K.M.L.) *Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, FL 34236. E-mail: <kleber@mote.org>.*