DIVERSITY AND ECOLOGICAL SIGNIFICANCE OF DEEP-BURROWING MACROCRUSTACEANS IN COASTAL TROPICAL WATERS OF THE AMERICAS (DECAPODA: THALASSINIDEA)

DARRYL L. FELDER

Ecology of thalassinidean shrimp in intertidal and subtidal marine and estuarine habitats has gained growing attention in literature of the last decade. Most recent ecological focus has been accorded to a limited set of genera assignable to several of the eleven families comprising this infraorder (see * in box). In accord with Tudge *et al.* (2000), the preferred nomenclature does not conform to that proposed by Sakai (1999). Also, as used here, the abbreviation *"C."* indicates species that remain treated under the genus *Callianassa sensu lato*, despite recent taxonomic restriction of that genus which excludes these species (see Manning and Felder, 1991).

As here evident, genera treated in modern ecological works are for the most part callianassids, a single family that includes a large number of intertidal and shallow subtidal representatives. Recent treatments of thalassinidean reproductive ecology have focused on recruitment, settlement stimuli, reproductive output and environmental constraints on reproduction of callianassids, while those in physiological and behavioral ecology have centered on ventilatory mechanisms, burrow construction and metabolic constraints imposed by hypoxia and reduced nutrients or contami-

INFRAORDER: THALASSINIDEA Latreille, 1831

Superfamily - Thalassinoidea Dana, 1852
   Family   - Thalassinidae Dana, 1852

Superfamily - Callianassoidea Dana, 1852
* Family   - Callianassidae Dana, 1852
   Callianassa sensu stricto, Biffarius,
   Neotrypaea, Trypaea, Lepidophthalmus,
   Callichirus, Sergio, Nihonotrypaea, Glypturus,
   Corallianassa, Eucalliax, Neocallichirus,
   "C." tyrrhena, "C." candida, "C." filholi,
   "C." truncata, "C." kraussi, "C." laurae
   Family   - Ctenochelidae Manning and Felder, 1991
   Family   - Callianideidae Kossmann, 1880
* Family   - Laomediidae Borradaile, 1903
   Axianassa, Jaxea
   Family   - Thomassiniidae de Saint Laurent, 1979
* Family   - Upogebiidae Borradaile, 1903
   Upogebia

Superfamily - Axioidea Huxley, 1879
* Family   - Axiidae Huxley, 1879
   Axius, Axiopsis
* Family   - Calocarididae Ortmann, 1891
   Calocaris
   Family   - Micheleidae Sakai, 1992
   Family   - Strahlaxiidae Poore, 1994

nants in burrow waters for callianassids and members of several other families (Table I). Scant attention among these has been afforded to tropical populations of the Americas except in studies of bur-

row construction by the laomediid *Axianassa australis* Rodrigues and Shimizu in Brazil (Dworschak and Rodrigues, 1997) and recruitment and growth of the callianassid *Lepidophthalmus sinuensis* Lemaitre and Rodrigues on the Caribbean coast of Colombia (Nates and Felder, 1999). Ecological studies at the community and ecosystems level form a larger body of recent work, which calls attention to varied roles of thalassinidean populations in determining assemblage structure and their involvement in biogeochemically modulated processes (Table II). Major contributions in this arena over the last decade have centered on population dynamics, community composition, bioturbation, related geochemical effects, nutrient cycling, and food webs. Among these, works on populations of (at least in part) the callianassids *Eucalliax jonesi* (Heard) and *Neocallichirus rathbunae* (Schmitt) in the British Virgin Islands (Murphy and Kremer, 1992), the callianassids *Glypturus acanthochirus* Stimpson*, Neocallichirus grandimana* (Gibbes)*, Corallianassa longiventris* (A. Milne Edwards) and axiid *Axiopsis serratifrons* (A. Milne Edwards) in Belize (Dworschak and Ott, 1993) and the callianassid *Lepidophthalmus sinuensis* on the Caribbean coast of Colombia (Nates and Felder, 1998) do demonstrate the potential significance of

Darryl L. Felder. **Ph.D., Louisiana State University. Professor of Biology, University of Louisiana –Lafayette (ULL). Director of ULL–Laboratory for Crustacean Research. Associate Research Scientist, NMNH, Smithsonian Institution, Washington, DC. Address: Department of Biology, University of Louisiana, Lafayette, LA 70504-2451, USA. e-mail: dlf4517@louisiana.edu**

SELECTED STUDIES ON ECOLOGY OF THALASSINIDEAN CRUSTACEANS SINCE 1990

Location	Habitat	Focus	Taxa	Authors
Japan	intertidal sand	settling, recruitment	*Nihonotrypaea*	1
Japan	intertidal sand	brooding, development	*Nihonotrypaea*	2
Japan	intertidal-sh subtidal	larval dispersal	*Nihonotrypaea* 3 spp.	3
Japan	intertidal-sh subtidal	burrow construction	*Nihonotrypaea* 2 spp.	4
Japan	intertidal	patterning, density	*Nihonotrypaea*	5
Japan	intertidal	competition/snails	*Nihonotrypaea*	6
Japan	intertidal	competition/isopods	*Nihonotrypaea*	7
Japan	intertidal	competition/eels	*Nihonotrypaea*	8
Japan	intertidal	abundance, life history	*Nihonotrypaea*	9
Australia	intertidal	ventilation, respiration	*Biffarius, Trypaea*	10
Australia	intertidal	community interactions	*Trypaea*	11
Australia	intertidal	associated bivalves/redox	*Trypaea*	12
Australia	intertidal sand	burrow form, function	*Biffarius*	13
Australia	intertidal sand	food sources, burrows	*Biffarius, Trypaea*	14
Australia	intertidal sand	bioturbation, carbon, microbes	*Biffarius*	15
New Zealand	intertidal sand	population dynamics	"C." *filholi*	16
New Zealand	intertidal sand	bioturbation effects	"C." *filholi*	17
New Zealand	intertidal sand	effects on communities	"C." *filholi*	18
New Zealand	intertidal sand	reproduction	"C." *filholi*	19
South Africa	intertidal mudflat	hydrodynamics	*Upogebia*	20
South Africa	intertidal	growth, production	*Upogebia*	21
South Africa	intertidal	hydrocarbon accumulation	"C." *kraussi*	22
South Africa	intertidal	harvest impacts	"C." *kraussi, Upogebia*	23
South Africa	intertidal-sh subtidal	detrital food webs	"C. *kraussi*	24
South Africa-Australia-N Am/P	intertidal	feeding, gut flora	*Upogebia* 2 spp., *Trypaea Neotrypaea*, "C." *kraussi*	25
Red Sea	sh subtidal	organic cycling	"C." *laurae*	26
Mediterranean	subtidal	sediment oxygen flux	"C." *truncata*	27
Mediterranean	subtidal	biogeochemistry	"C." *truncata*	28
Mediterranean	intertidal-sh subtidal	environ effects on larvae	"C." *tyrrhena*	29
Mediterranean	intertidal-sh subtidal	facultative lecithotrophy	"C." *tyrrhena*	30
Mediterranean	intertidal-sh subtidal	pollution, metabolic	"C." *tyrrhena*	31
Mediterranean	intertidal-sh subtidal	reproductive output	"C." *tyrrhena*	32
Mediterranean	intertidal	reproduction, growth	*Upogebia*	33
Mediterranean	intertidal-sh subtidal	burrow construction	"C." *tyrrhena*, "C." *candida*	34
Mediterranean	intertidal	population dynamics	"C." *tyrrhena*, "C." *candida*	35
UK-N Sea	subtidal	gill morph/function	*Upogebia* 3 spp., *Calocaris Callianassa, Jaxea, Axius*	36
UK-N Sea	subtidal	ventilation, respiration	*Calocaris*	37
UK-N Sea	subtidal	sulfide adapt, metabolic	*Calocaris, Jaxea, Callianassa*	38
UK-N Sea	subtidal	burrowing	*Callianassa*	39
UK-N Sea	subtidal	burrowing, feeding adapt	*Callianassa, Jaxea, Upogebia*	40
UK-N Sea	subtidal	activity, bioturbation	*Callianassa*	41
UK-N Sea	subtidal	feeding, mechanics	*Callianassa*	42
UK-N Sea	subtidal	feeding, sorting, gut flora	*Upogebia* 3 spp., *Calocaris Callianassa, Jaxea, Axius*	43
UK-N Sea	subtidal	hydrodynamics, redox	*Callianassa*	44
UK-N Sea	subtidal	bioturbation	*Callianassa, Jaxea, Calocaris, Upogebia*	45
UK-N Sea	subtidal	bioturbation	*Callianassa*	46

such populations in community and ecosystems level dynamics of the American tropics.

One implication of these studies, be they focused on American tropical or other environments, is that deep burrowing thalassinidean shrimp are repeatedly observed to dominate processes in a number of intertidal and subtidal habitats, where they often form dense aggregations. Aggregation may be favored by larvae adapted for estuarine retention or abbreviated development; in at least some cases, specific sedimentary cues favor dense and gregarious settlement of larvae. Physiology and behavior may be adapted to facilitate burrowing within and exploiting of hypoxic or even anoxic sediments for nutrients, with controlling consequences on populations of associated microbes, macrobenthos, rooted autotrophs, or planktonic autotrophs and heterotrophs of the overlying water column. Through their modulation of physiochemical parameters within porewaters and the overlying water column, the activities of thalassinidean populations may touch upon virtually all aspects of productivity in shallow marine systems. Regardless, the scope of this impact remains largely unmentioned in traditional treatments of coastal marine ecology, and the diversity of thalassinideans and their commensal associates responsible for these impacts remains markedly underestimated.

Aside from compiling major ecological works on thalassinideans from the last decade, the present paper briefly treats in further detail three genera among these animals, all now known to occur widely and often in dense accumulations throughout the American tropics, though species-level systematics in this region remain in part unresolved. Recent and ongoing studies of selected species among these genera, some not previously published, are herein used to further exemplify ecological roles of thalassinideans, especially in the context of environmental issues bearing on populations of the American tropics.

Populations of *Lepidophthalmus* along Warm-Temperate to Tropical Coastlines

Emphasis on this genus is warranted because of 1) its potentially dominant role in ecosystem processes of tropical estuaries, 2) its previously underestimated diversity and regional endemism in these habitats, and 3) perception of it as potential threat to penaeid shrimp aquaculture operations in the American tropics. *Lepidophthalmus* populates river mouths and oligohaline estuaries of the Atlantic

TABLE I (continued)
SELECTED STUDIES ON ECOLOGY OF THALASSINIDEAN CRUSTACEANS SINCE 1990

Location	Habitat	Focus	Taxa	Authors
N Am/Atl	intertidal	settling stimuli	*Callichirus* 2 spp.	47
N Am/Atl	intertidal	sediment modification	*Callichirus*	48
N Am/Atl	sh subtidal, sand and rubble	burrows and impact	*Glypturus, Axiopsis, Neocallichirus, Corallianassa*	49
N Am/Atl	intertidal-sh subtidal	community structure	*Lepidophthalmus, Callichirus* 2 spp.	50
N Am/Atl	intertidal-sh subtidal	sulfide adapt, metabol	*Callichirus, Lepidophthalmus*	51
N Am/Atl	intertidal-sh subtidal	metabolic ontogeny	*Lepidophthalmus*	52
S Am/Atl	intertidal-sh subtidal	recruitment, growth	*Lepidophthalmus*	53
S Am/Atl	intertidal	burrow construction	*Axianassa*	54
S Am/Atl	intertidal	feeding mechanics	*Axianassa*	55
S Am/Atl	intertidal-sh subtidal	feeding mechanics	*Upogebia, Pomatogebia*	56
S Am/Atl	intertidal	population dynamics	*Sergio*	57
S Am/Atl	intertidal	population biol/reprod	*Callichirus*	58
S Am/Atl	intertidal	pop dynamics/reprod	*Callichirus*	59
S Am/Atl	sh subtidal	cycling, productivity	*Eucalliax, Neocallichirus*	60
S Am/Atl	intertidal-sh subtidal	cycling, redox in systems	*Lepidophthalmus*	61
N Am/Pac	intertidal	settling, recruitment	*Neotrypaea*	62
N Am/Pac	intertidal	foraging by whales	*Neotrypaea*	63
Am/Pac	intertidal	recruitment, growth	*Neotrypaea, Upogebia*	64
N Am/Pac	intertidal	population control	*Neotrypaea, Upogebia*	65
N Am/Pac	intertidal	pop structure/growth	*Neotrypaea*	66
N Am/Pac	intertidal	community structure	*Upogebia*	67
N Am/Pac	intertidal	bioturbation	*Neotrypaea*	68
S Am/Pac	intertidal	reprod/parasite effects	*Callichirus, Neotrypaea*	69
S Am/Pac	intertidal	effects on ectoparasites	*Callichirus*	70
S Am/Pac	intertidal	physiol effects of parasites	*Neotrypaea*	71

Where used, *"C."*: indicates species that remain treated under genus *Callianassa sensu lato*, despite recent restriction of that genus which excludes these species. "sh": is used to indicate shallow subtidal waters near in embayments or estuaries, or near beaches. Sources: 1: Tamaki *et al.,* 1992a; 2: Tamaki *et al.,* 1996; 3: Tamaki and Miyabe, 2000; 4: Tamaki and Ueno, 1998; 5: Tamaki and Ingole, 1993; 6: Tamaki, 1994; 7: Tamaki and Suzukawa, 1991; 8: Tamaki *et al.,* 1992b; 9: Tamaki *et al.,* 1997; 10: Paterson and Thorne, 1993, 1995; 11: Dittman, 1996; 12: Kerr and Corfield, 1998; 13: Bird and Poore, 1999; 14: Boon *et al.,* 1997; 15: Bird *et al.,* 2000; 16: Berkenbusch and Rowden, 1998; 17: Berkenbusch and Rowden, 1999; 18: Berkenbusch and Rowden, 2000a; 19: Berkenbusch and Rowden 2000b; 20: Allanson *et al.,* 1992; 21: Hanekom and Baird, 1992; 22: Jackson and Bidleman, 1990; 23: Wynberg and Branch, 1994; 24: Schlacher and Wooldridge, 1996; 25: Harris *et al.,* 1991 and Harris, 1993; 26: Vaugelas and Buscail, 1990; 27: Ziebis *et al.,* 1996a; 28: Ziebis *et al.,* 1996b; 29: Thessalou-Legaki, 1990; 30: Thessalou-Legaki *et al.,* 1999; 31: Thessalou-Legaki *et al.,* 1997; 32: T.-Legaki and Kirotsis, 1997; 33: Kevrekidis *et al.,* 1997; 34: Dworschak, 1998a; 35: Dworschak, 1998b; 36: Astall *et al.,* 1997a,b; 37: Anderson *et al.,* 1991, 1994; 38: Johns *et al.,* 1997; 39: Atkinson and Nash, 1990; 40: Nickell and Atkinson, 1995; 41: Stamhuis *et al.,* 1996, 1997; 42: Stamhuis *et al.,* 1998a,b; 43: Pinn *et al.,* 1997, 1998a,b, 1999a,b and Nickell *et al.,* 1998; 44: Forester and Graf, 1992, 1995; 45: Hughes and Atkinson, 1997; 46: Rowden and Jones, 1993; 1994; 1995; Rowden *et al.,* 1997, 1998 and Nickell *et al.,* 1995; 47: Strasser and Felder, 1998, 1999b, 2001; 48: Over 1990; 49: Dworschak and Ott, 1993; 50: Felder and Griffis, 1994; 51: Bourgeois and Felder, 2001; 52: Nates and McKenney, 2000; 53: Nates and Felder, 1999; 54: Dworschak and Rodrigues, 1997; 55: Coelho and Rodrigues, 2001; 56: Coelho *et al.,* 2000; 57: Pezzuto 1998; 58: Rodrigues and Shimizu, 1997; 59: Souza *et al.,* 1998; 60: Murphy and Kremer, 1992; 61: Nates and Felder, 1998; 62: Feldman *et al.,* 1997; 63: Weitkamp *et al.,* 1992; 64: Dumbauld *et al.,* 1996; 65: Dumbauld *et al.,* 1997; 66: Labadie and Palmer, 1996; 67: Posey *et al.,* 1991; 68: Myrick and Flessa, 1996; 69: Muñoz and George-Nascimento, 1999; 70: Marin and George-Nascimento, 1993; 71: Astete-Espinoza and Caceres, 2000.

and Pacific coasts, a distribution facilitated by its osmoregulatory ability in both adult and larval stages (Felder, 1978; Felder *et al.,* 1986; Nates *et al.,* 1997) and its remarkable adaptation to hypoxia in highly organic, sometimes sulfidic, coastal sediments (Felder, 1979; Nates and Felder, 1998; Bourgeois and Felder, 2001). Some species are widely distributed in shallow embayments, provided sediments are clayey or that clay-rich lamina are accessible to the animals for incorporation into burrow walls (Felder and Rodrigues, 1993; Felder and Griffis, 1994). Development appears to be abbreviated in members of this genus, often strongly so, favoring estuarine retention and thus limited dispersal (Nates *et al.,* 1997).

This limited dispersal likely serves in part to maintain remarkable levels of endemism in this genus, most species of which were discovered only within the last decade (Figure 1A, B). Diversity appears to center in the American tropics, with distributions there often restricted to disjunct estuaries. Antitropically distributed warm-temperate forms (Felder and Rodrigues, 1993; Staton *et al.,* 2000), to the north and south of a diverse core of tropical species, suggest a historical model in which members of this genus have been (perhaps repeatedly) compressed into tropical refugia by glaciation (Figure 1C). Given the restriction of this genus to shallow subtidal and intertidal habitats, direct effects of even small temperature changes, including contemporary global warming, could impact distributions.

Dense accumulations of burrows, often exceeding several hundred per m², may occur in natural, perturbated or aquaculture pond settings (Felder and Griffis, 1994; Nates and Felder, 1999), sometimes adjacent to intertidal stands of grasses or fringing mangroves. A short maturation cycle, ready access to mates, high fecundity and limited dispersal of larvae all contribute to rapid, sometimes explosive population increases (Felder and Lovett, 1989; Nates and Felder, 1999). Intense bioturbation in these circumstances can rapidly bury associated epibenthic biota, leading to dominance of *Lepidophthalmus* among the benthic macroinfauna. Burrow depths can exceed 2m, and the cumulative surface areas provided by burrow walls markedly augment zones of redox transition in sedimentary environments.

Ecological studies to date have centered on the warm-temperate species *L. louisianensis* (Schmitt) from the Gulf of Mexico and the narrowly endemized tropical species *L. sinuensis* from the Caribbean coast of Colombia. In both species effluent waters can be richly charged with reduced nutrients (Felder and Griffis, 1994; Nates and Felder, 1998), and thus play a major role in nutrient cycling. It is, however, noteworthy that comparable recent samples of effluent waters from burrows of *L. bocourti* (A. Milne Edwards), *L. eiseni* Holmes and *L.* "sp. D" (DLF, in description) in sandy river mouths along the tropical Pacific coast of Nicaragua to date do not exhibit such marked elevations of reduced nutrients, even though redox lev-

TABLE II
SPECIMENS OF LUCINID BIVALVE *Phacoides pectinatus*
ASSOCIATED WITH BURROWS OF SEVEN *Axianassa australis*

Depth (cm)	Number of live lucinid clams
35	2 attached; 1 adjacent
42	2 attached; 2 adjacent
[sedimentary transition, more sandy with shell debris, at and exceeding 40 - 45cm depth]	
51	7 attached; 16 adjacent
57	9 attached; 31 adjacent
63	8 attached; 23 adjacent
78	7 attached; 34 adjacent
81	11 attached; 26 adjacent

Determined from burrow casts of varied depth, July 1997, beneath fringing red mangroves of Indian River Lagoon, Ft. Pierce, Florida, USA. (attached: fused to resin; adjacent: found against resin during excavation of cast).
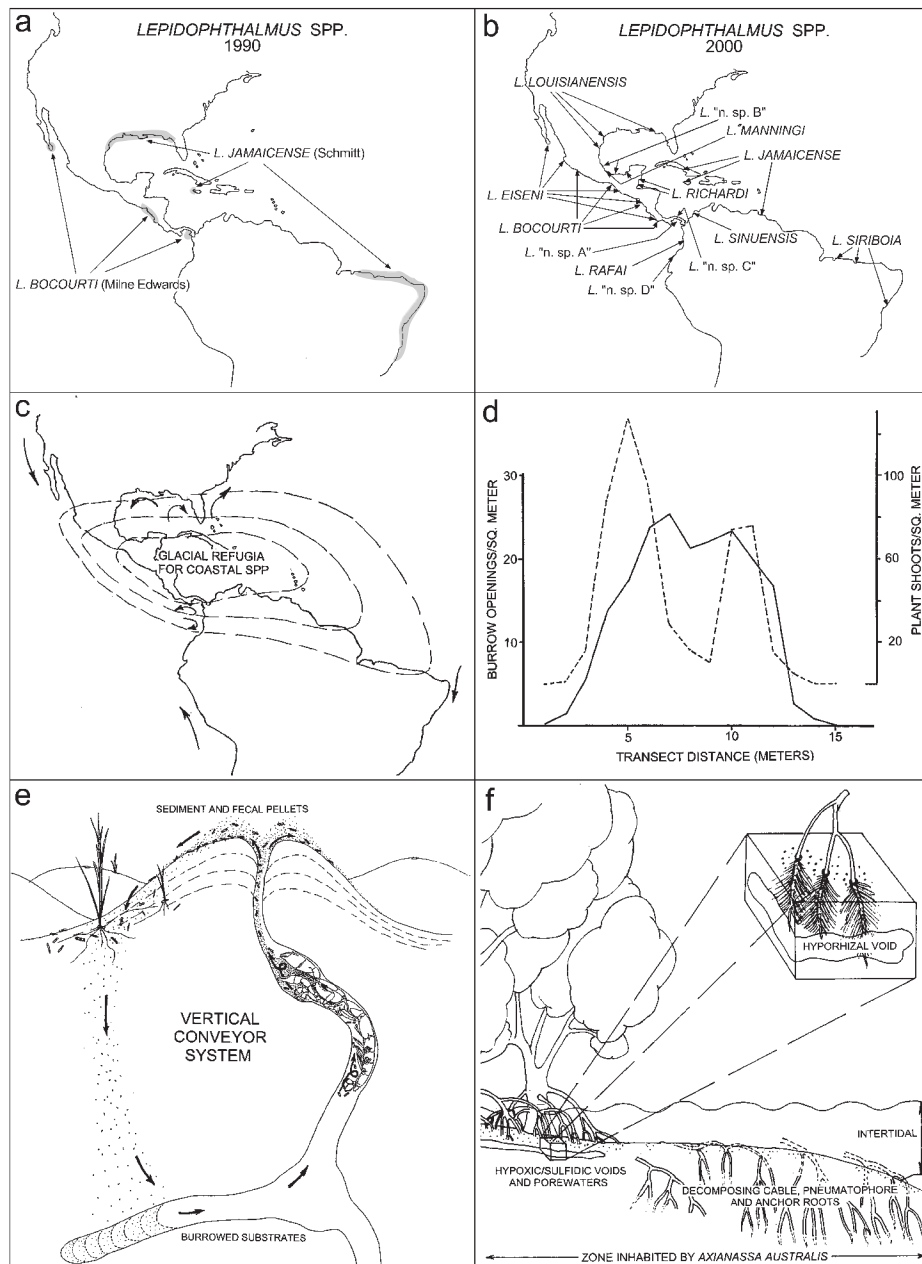
els are comparable; this may reflect the generally nutrient-poor state of some tropical estuaries.

Several *Lepidophthalmus* spp. opportunistically invade hypoxic bottom sediments of coastal shrimp mariculture farms. *L. sinuensis*, an undescribed species at the time it invaded mariculture ponds near the mouth of the Rio Sinú, Colombia (Lemaitre and Rodrigues, 1991), affords the best-documented case of such an invasion. Highly organic pond sediments, enriched by feeding of the penaeid shrimp under culture, appeared to there provide near optimal habitats for rapid colonization and explosive population increases, with burrow densities at times exceeding 1000/m². Detrimental impacts on penaeid shrimp likely stemmed from combined effects of callianassid bioturbation and burrow ventilation, both of which re-suspended highly reduced nutrients (including ammonia and sulfides). Toxicity and BOD of these materials both potentially contributed to negative effects on growth and survival of cultured penaeids. Diel oxygen lows, depressed by BOD and respiratory demands of the thalassinideans themselves (which often exceeded areal biomass of the penaeid shrimp under culture), reached stressful levels. In addition, extreme bioturbation rates may have contributed to burial of penaeid shrimp artificial feeds distributed onto the pond bottoms (Nates and Felder, 1998; 1999).

L. louisianensis is also now known to have invaded shrimp farms in the western Gulf of Mexico (Tamaulipas, Mexico), and an undescribed species, "*L.* sp. D", along with other taxonomically questionable members of what is sometimes called the "*L. bocourti* complex", have invaded shrimp farms on the Pacific coast of Colombia, Panamá and

Figure 1. a: Diversity and distribution of *Lepidophthalmus* as accepted in 1990. b: Diversity and distribution of *Lepidophthalmus* as known by late 2000, including four new species (n. sp.) currently in description. c: Proposed model for impact of glacial advance and retreat, as determinant of diversity and modern coastal species in American warm-temperate to tropical waters and as supported by distributions of *Lepidophthalmus* spp. d: Mean density for burrows of *Callichirus islagrande* and shoots of the cordgrass *Spartina alterniflora*, for three 15m transects across newly established cordgrass patches on bay side of Isles Dernieres, Louisiana, May 94. e: Schematic of the cycle of bioturbation or vertical conveyor in callianassids, which potentially entrains vegetation propagules. f: Schematic of typical habitats for *Axianassa australis* and its symbionts, where associated with mangrove-lined shorelines.
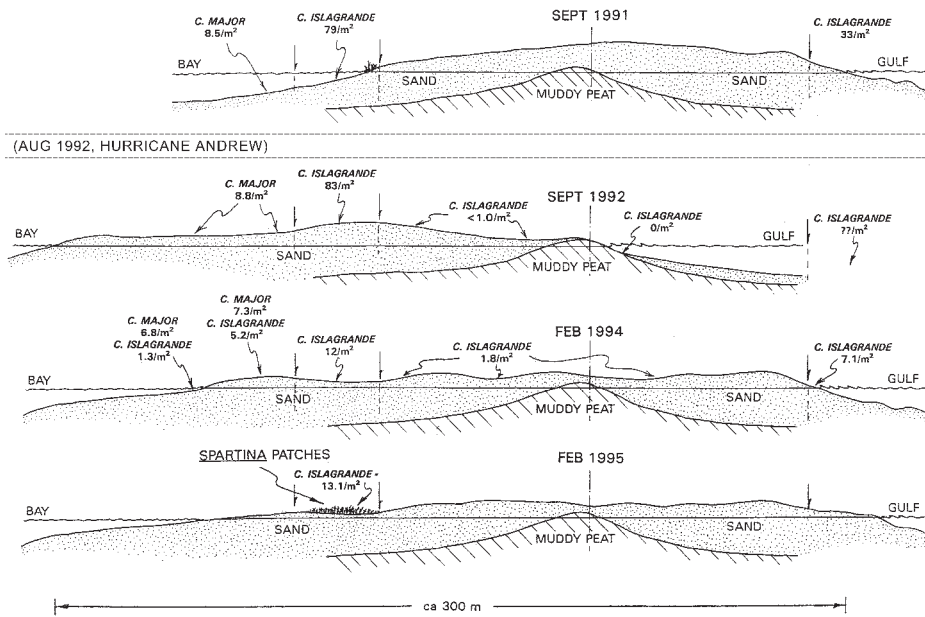
Figure 2. Mean sand elevations and population densities for two species of *Callichirus* (as estimated from burrow counts) for three transects across Isles Dernieres, Louisiana, from September 91 (prior to Hurricane Andrew in August 92) and three occasions following the storm. In September 91 no burrows were present across center (higher elevations) of the island. For February 95, counts are shown only for the zone that was heterogeneously populated by patches of the cordgrass *Spartina alterniflora*.

Costa Rica. Observed densities and effects to date are not apparently of the scale observed with *L. sinuensis*, but early control programs may have avoided such impacts. Even in the case of *L. sinuensis*, moderate densities of this species in shrimp farms, comparable to densities observed in natural rather than aquaculture settings, can be of potential benefit rather than harm to penaeid shrimp production (Nates and Felder, 1998). This perhaps demonstrates direct potential benefits these thalassinidean populations to secondary production, albeit in the somewhat atypical mesocosm of a shrimp farm. Such might be expected with moderate and continuous rates of nutrient re-suspension, bioturbation and oxidation of sediments, as may occur in stable natural populations of these thalassinideans. Such optimal population densities have been achieved in these aquaculture settings, with benefits to penaeid production, but to date only by use of pesticides for population control.

Control has focused primarily on applications of either carbaryl (Sevin®) or the organophosphate trichlorfon (Neguvon®). These are used either to limit the above-discussed direct impacts of thalassinidean invasions or for more general extermination of broader groups of local aquatic species from pond waters, the latter strategy targeted to eradi-

cation of putative penaeid shrimp disease vectors. While the use of carbaryl for control of thalassinideans has been studied in open estuarine habitats of the US northwestern Pacific coast (Dumbauld *et al*., 1997), the efficacy of such practices in distinctly warmer tropical aquaculture settings is largely undocumented, and regulation throughout tropical America appears very limited and poorly enforced. Acute toxic effects of trichlorfon, while believed to be not as persistent as organochlorines, remain poorly known and are reported to become elevated in some marine crustaceans at higher temperatures such as those occurring in tropical estuaries (Brecken-Folse *et al*., 1994; see also, Extension Toxicology Network, http://pmep.cce.cornell.edu).

As *Lepidophthalmus* spp. appear to be highly endemized within the tropics, where they may contribute in substantive or even dominant ways to essential benthic processes of the natural estuaries they inhabit, it is urgently important that potential impacts of pesticides and other potential perturbations to their habitats be included in regional conservation and management planning for the coming millineum. This group of thalassinideans may represent but one of many burrowing invertebrate taxocenes in which both diversity and ecological roles have been long undervalued.

Populations of *Callichirus* in Coastal Louisiana

By contrast to the above taxocene, *Callichirus* is commonly encountered in intertidal to shallow subtidal beach environments of open shores or embayments, usually where sediments are comprised heavily of siliceous sands in "swash" and subtidal bar zones, and often along quartzite beaches of relatively high wave energy (Felder and Griffis, 1994; Rodrigues and Shimizu, 1997). Larval history is more protracted than in *Lepidophthalmus* spp. (Strasser and Felder, 1999a; 2000). The genus ranges widely from temperate to tropical shores, but is of special interest along tropical American coastlines because of 1) its frequent dominance of sandy shoreline infaunal assemblages and processes, 2) its vulnerability to tropical storm perturbations of the readily transported substrates it occupies, and 3) its occupation of sites that are commonly coated by oil and other pollutant spills as they wash ashore. Taxonomy of the group is problematic, with newly defined relationships in even well-studied temperate to warm-temperate habitats yet to be reflected in nomenclature, and relationships in tropical waters currently under study by molecular methods (Staton and Felder, 1995; Felder, unpublished). While even recent references (and herein Figure 2) may refer to populations of "*Callichirus major*" from the American tropics and Gulf of Mexico, that species *C. major* (Say) *sensu stricto* is most likely restricted to the Atlantic US coast, Florida and northward along the US Atlantic coast. Others so labelled from the Gulf of Mexico, Caribbean and Brazil must eventually be assigned to separate taxa. Other species that range into the American tropics include populations of *C. islagrande* (Schmitt) (Figure 3A) in the Gulf of Mexico and varied tropical Pacific populations currently assigned to *C. garthi* (Retamal) or *C. seilacheri* (Bott); however, broad applications of these taxonomic assignments are best considered provisional until ongoing molecular studies are completed.

While studies in the northern Gulf of Mexico are focused on warm-temperate populations of *Callichirus*, they exemplify ecological dynamics and environmental threats as also applicable to many tropical American populations. The potential for mass mortality and population redistribution was demonstrated strikingly along barrier islands of coastal Louisiana following landfall of Hurricane Andrew in August 92 (Figure 2). Long-established populations of *C. islagrande* along beaches facing the Gulf of Mexico were eradicated
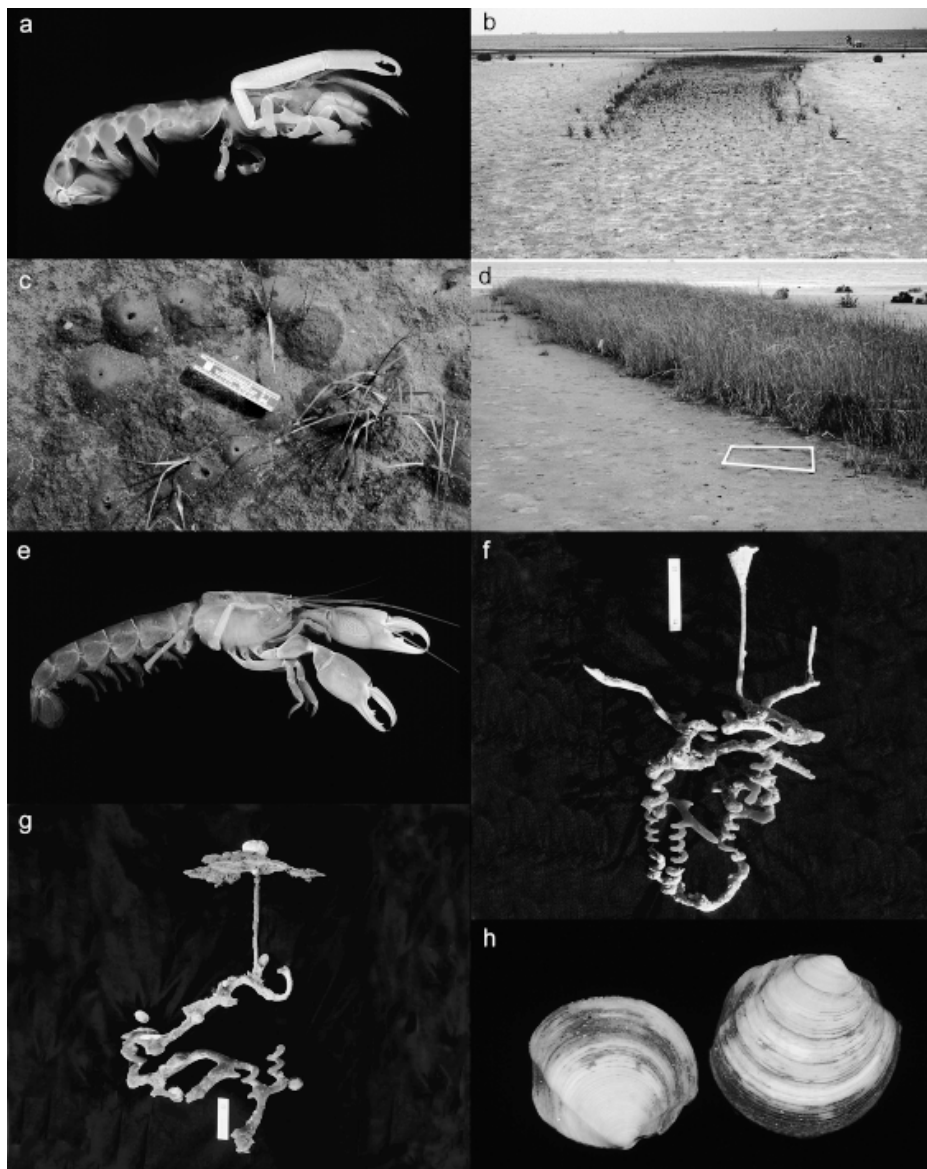
Figure 3. a: Mature male of *Callichirus islagrande* from northern Gulf of Mexico. b: One of several newly established patches of the cordgrass *Spartina alterniflora*, sculptured by dense burrows of *C. islagrande*, along the bayward side of Isles Dernieres, Louisiana, in May 94. c: Close-up of flooded burrows of *C. islagrande*, adjacent to shoots of *S. alterniflora*, near middle of area featured in b, in May 94. d: Mature, seed-bearing patch of cordgrass *S alterniflora*, side view of area featured in b, in October 94. e: Mature male of *Axianassa australis* from mud flats near red mangroves in Indian River Lagoon, southeastern Florida, USA. f: Polyester resin casting of burrow from *A. australis*, with associated *Phacoides pectinatus*, same locality as in e. g: Partially recovered casting of burrow from *A. australis*, including some of the lucinid bivalves (*P. pectinatus*) that adhered to the casting at varied positions, same locality as in e. h: Close-up of live lucinid bivalves *P. pectinatus* recovered in contact with burrows of *A. australis*, same locality as in e.

by wave-erosion and transport of the sands they formerly occupied. However, in storm wash-over fans, a fraction of this population apparently survived the initial relocation and re-burrowed, as evidenced by the rapid appearance of a few mature adults in highest elevations of the newly deposited fan where no populations of *Callichirus* spp. were observed before, and the temporary augmentation of bayward populations of both *C. islagrande* and "*C. major*" that were covered by the new wash-over fan (Figure 2).

It is noteworthy that the dynamics described above occurred while populations were being monitored in coastal Louisiana to establish baseline population censuses (through 1994), in the event that future oil spills should impact population densities. While oil spills clearly impact this species (Thebeau *et al*., 1981; Amos *et al*., 1983), it is clear that catastrophic changes in population structure also occur in response to natural perturbations like storms. The confounding of natural storm and spill effects has previously clouded interpretations in studies along beaches of Texas (Thebeau *et al*., 1981). However, where these impacts occur independently, the means and timecourse of population recovery could differ markedly. Recovery of the Gulf beach population at Isles Dernieres was well underway as beach sands naturally accumulated during 18 months following the storm (Figure 2), and (while not monitored in February 95) populations there had reached a mean density of 31/ m² by May 95 (of no significant difference from pre-storm densities). From size classes in samples, it was evident that repopulation of the Gulf beach between September 92 and February 94 occurred almost exclusively by way of newly settled recruits (decapodids), most of which accumulated between May and September 93. Cues to settlement of this species have recently been the subject of several studies (Strasser and Felder, 1998; 1999b; 2001), and contact with the sand was found to play a highly significant role in stimulus of metamorphosis and burrowing. It would thus be of great interest for such studies to also be conducted with sands variously contaminated with oil and oil degradation products, to determine the magnitude and duration of possible impacts on recruitment.

The Isles Dernieres study produced some provocative observations of proximal events as the bayward beaches of the storm wash-over fan were slowly reworked through 1994 and early 1995 (Figure 2). Where dense populations of *C. islagrande* (79/m²) had existed in a sloped beach prior to the storm, overlayment by sand and isolation from routine tidal inundation contributed to a marked decline by February 1994. Transect means in this region ranged from 12-13/ m² throughout most of 1994, but were very heterogeneous with most of this mean number accounted for by denser populations (up to 63/m²) in depressions that were more frequently flooded by at least by the more extreme high tides. By early summer of 1994, new growth of cordgrass shoots (*Spartina alterniflora* Loisel.) began to appear throughout these depressions, and transects were established to monitor densities of both the plant shoots and burrow numbers, which were highly correlated (p <0.001) (Figures 1d, 3b-c). Examination of small shoots suggested that all were sprouted from sand-entrained propagule fragments

rather than seed, and it is hypothesized that entrainment was facilitated by the bioturbating activity of *C. islagrande* (Figure 1e), which may also have contributed to plant nutrition. Viable seed was uncommon in the immediate area, and had not been observed previously in sparse stands of *S. alterniflora* that had occupied limited areas of this shoreline prior to the storm. However, by October 94, these stands of *S. alterniflora* were densely vegetated and heavily endowed with maturing seed (Figure 3d), remarkably more so than in conspecific stands of cordgrass on the opposite (landward) side of the bay.

While cordgrass reproduction in coastal Louisiana is generally reported to occur by way of propagules, and the limited local seed production is usually of low viability, a small sample of this seed exceeded 70% germination in the laboratory. It thus compels further study of the possible role that an associated thalassinid like *C. islagrande* might play both in the entrainment of propagules and in plant nourishment. The latter could be facilitated by nutrient-loaded burrow effluent waters and fecal pellet production, both of which are well documented (Felder and Griffis, 1994). However, controlled experimentation must be undertaken to confirm this possible relationship.

Populations of *Axianassa australis* Associated with Tropical Red Mangroves

Axianassa, at least as presently constituted, is a broadly distributed genus ranging onto continental shelves of primarily tropical waters, though present focus is restricted to shallow subtidal and intertidal forms. Formerly thought to be rare, only nine specimens from American waters were known when the genus was last revised taxonomically (Kensley and Heard, 1990). However, the animals appear to be not so rare as they are difficult to collect. Discussion of one species, *A. australis* (Figure 3e), is included here primarily because this species is now known to be 1) a common and widespread burrower among coastal mangroves and adjacent mud flats, 2) the architect of remarkable burrows sheltering a newly discovered assemblage of poorly known symbionts, and 3) yet another thalassinidean group apparently adapted to strongly reduced, sulfidic environments.

The distribution of laomediid *A. australis* in the western Atlantic is, in contrast to those of the callianassids discussed above, very broad. It herewith can be confirmed to range from Brazil (the type locality) to Florida, with

the distribution including extreme south Texas and the southwestern Gulf of Mexico. Its range in the western Atlantic very nearly matches that of the red mangrove (*Rhizpora mangle* L.) with which it is commonly, though not exclusively, associated (Figure 1f). Duration of larval development, also currently under study, is protracted, involving a comparatively large number of planktonic stages which would favor wide dispersal.

Among the several remarkable attributes of these animals are their burrows, which appear to occur from near the low tide mark throughout intertidal mudflats that include decomposing roots or other interred vegetation, and well into dense stands of living red mangroves (Figure 1f). Among living prop roots, the animals appear to reside well below the densest concentration of living rootlets in strongly hypoxic and sulfidic muds, sometimes in or near "voids" of hypoxic waters which can sometimes be detected as coring tools break through the dense rootlet mat. Extractions from such areas on the Caribbean coast of Colombia, lower Atlantic coast of Florida, and extreme south Texas have produced a previously undescribed assemblage of associated macrocrustaceans including yet other laomediids, alpheoid shrimp, and brachyuran crabs that are apparently new to science. Males and females of *A. australis* are usually captured together as one pair per burrow, and are almost invariably accompanied by at least one male and female pair of symbiotic alpheoid shrimp (see also Dworschak and Coelho, 1999).

While aggregated in preferred habitats, burrow densities of *A. australis* do not appear to be high, seldom exceeding 4-5/m². but large amounts of detritus-laden sediment and water issue from them during tidal exposure. Where possible to retrieve burrow castings, it is clear that the burrows are often >1m in depth, expansive, and among the most uniquely sculptured of those known for thalassinideans (Figure 3f). First cast in Brazil (Dworschak and Rodrigues, 1997), the spiral elements appear to be unique to the group and remain of questionable function; among possibilities would seem optimization of the burrow wall surface area for microbial linings or porewater exchange, concentrated mining of selected sediments in the course of deposit feeding, deterring movement through burrows by predatory fishes, and ramping of the burrow to facilitate locomotion. A previous explanation invoked entrainment of thalassinideans in turbulent sediment flows as "doomed pioneers" to account for such spiral castings in the fossil record (Grimm and Föllmi, 1994); while

castings of living forms would now cast doubt on that interpretation, is noteworthy that the paleoecological settings for these fossil finds were interpreted as oxygen-depleted and richly organic, much is observed in the modern setting.

Newly noted is the association of these burrows with large numbers of lucinid bivalves, particularly along mangrove-dominated mud banks of the Indian River Lagoon system in eastern Florida and on some degrading seagrass flats of extreme south Texas. In Florida, specimens of what appears to be the bivalve *Phacoides pectinatus* Gmelin commonly adhere to the burrow cast or partially occlude penetration of the resin fully into the burrow lumen (Figures 3g, h). As burrow casts are excavated, it is also evident that yet other individuals of this clam are closely associated with the burrow lumen, touching it or accessing it across a small gap (Table II). Up to 37 living specimens of these bivalves have been to date retrieved from a single burrow. Living examples have been taken from sediment depths near 1m, even though they lack typical incurrent siphons. However, *Phacoides* and related lucinids have gills richly invested with symbiotic, sulfide-metabolizing, chemoautotrophic bacteria, and appear to be highly adapted in exploiting sulfidic substrates as an energy source. Thus, the burrow they share may serve to provide them access to rich stores of sulfide, including resources at otherwise inaccessible depths. As to what benefits this relationship might bring to *Axianassa*, to its alpheoid shrimp symbionts (Dworschak and Coelho, 1999), or to other yet-to-be-described burrow associates, little can be offered at present. Other symbioses between thalassinids and bivalves have been reported (see for example, Kato and Itani, 2000), but these do not appear related to exploitation of sulfides.

Even in tropical marine settings as common as coastal marine mangroves, we have only begun to appreciate the diversity of infaunal assemblages such as here described. It is an even larger and perhaps more urgent task to understand their function and significance. Doing so before we lose this opportunity to environmental degradation and global change is an urgent challenge for the 21st Century.

REFERENCES

Allanson BR, Skinner D, Imberger J (1992) Flow in prawn burrows. *Estuarine, Coastal and Shelf Science 35*: 253-266.

Amos AF, Rabalais SC, Scalan RS (1983) Oil-filled *Callianassa* burrows on a Texas barrier-island beach. *J. Sedimentary Petrol. 53:* 411-416.

Anderson SJ, Atkinson RJA, Taylor AC (1991) Behavioural and respiratory adaptations of the mud-burrowing shrimp *Calocaris macandreae* Bell (Thalassinidea: Crustacea) to the burrow environment. *Ophelia 34*: 143-156.

Anderson SJ, Taylor AC, Atkinson RJA (1994) Anaerobic metabolism during anoxia in the burrowing shrimp *Calocaris macandreae* Bell (Crustacea: Thalassinidea). *Comp. Biochem. Physiol. 108A:* 515-522.

Astall CA, Anderson SJ, Taylor AC (1997a) Comparative studies of the branchial morphology, gill area and gill ultrastructure of some thalassinidean mud-shrimps (Crustacea: Decapoda: Thalassinidea). *J. Zool., London 241:* 665-688.

Astall CM, Taylor AC, Atkinson RJA (1997b) Behavioural and physiological implications of a burrow-dwelling lifestyle for two species of upogebiid mud-shrimp (Crustacea: Thalassinidea). *Estuarine, Coastal and Shelf Sci. 44*: 155-168.

Astete-Espinoza LP, Caceres CW (2000) Effects of parasitism in nutritional physiology of the ghost shrimp *Neotrypaea uncinata* parasitized by the isopod *Ionella agassizi*. *Revista Chilena de Historia Natural 73:* 243-252.

Atkinson RJA, Nash RDM (1990) Some preliminary observations on the burrows of *Callianassa subterranea* (Montagu) (Decapoda, Thalassinidea) from the west coast of Scotland. *J. Natural History 24*: 403-413.

Berkenbusch K, Rowden AA (1998) Population dynamics of the burrowing ghost shrimp *Callianassa filholi* on an intertidal sandflat in New Zealand (Decapoda: Thalassinidea). *Ophelia 49:* 55-69.

Berkenbusch K, Rowden AA (1999) Factors influencing sediment turnover by the burrowing ghost shrimp *Callianassa filholi* (Decapoda: Thalassinidea). *J. Exp. Marine Biol. Ecol. 238:* 283-292.

Berkenbusch K, Rowden AA (2000a) Temporal and spatial variation in macrofauna community composition imposed by ghost shrimp *Callianassa filholi* bioturbation. *Marine Ecology Progress Series 192:* 249-257.

Berkenbusch K, Rowden AA (2000b) Latitudinal variation in the reproductive biology of the burrowing ghost shrimp *Callianassa filholi* (Decapoda: Thalassinidea). *Marine Biol. 136:* 497-504.

Bird FL, Poore GCB (1999) Functional burrow morphology of *Biffarius arenosus* (Decapoda: Callianassidae) from southern Australia. *Marine Biol. 134:*77-88.

Bird FL, Boon PI, Nichols PD (2000) Physico-chemical and microbial properties of burrows of the deposit-feeding thalassinidean ghost shrimp *Biffarius arenosus* (Decapoda: Callianassidae). *Estuarine, Coastal and Shelf Sci. 51:*279-291

Boon PI, Bird FL, Bunn SE (1997) Diet of the intertidal callianassid shrimps *Biffarius arenosus* and *Trypaea australis* (Decapoda: Thalassinidea) in Western Port (southern Australia), determined with multiple stable-isotope analyses. *Marine and Freshwater Res. 48:* 503-511.

Bourgeois RP, Felder DL (2001) Postexposure metabolic effects of sulfide exposure and evidence of sulfide-based ATP production in callianassid ghost shrimp (Crustacea: Decapoda: Thalassinidea). *J. Exp. Marine Biol. Ecol. 263*: 105-121.

Brecken-Folse, JA, Mayer FL, Pedigo LE, Marking LL (1994) Acute toxicity of 4-nitrophenol, 2,4-dinitrophenol, terbufos and trichlorofon to grass shrimp (*Palaemonetes* spp.) and sheepshead minnows (*Cyprinodon variegatus*) as affected by salinity and temperature. *Environmental Toxicol. and Chemistry 13:* 67-77.

Coelho VR, Rodrigues S de A (2001) Trophic behaviour and functional morphology of the feeding appendages of the laomediid shrimp *Axianassa australis* (Crustacea: Decapoda: Thalassinidea). *J. Marine Biological Assoc. United Kingdom 81*: 441-454.

Coelho VR, Wiiliams AB, Rodrigues S de A (2000) Trophic strategies and functional morphology of feeding appendages, with emphasis on setae, of *Upogebia omissa* and *Pomatogebia operculata* (Decapoda: Thalassinidea: Upogebiidae). *Zool. J. Linnean Soc. 30*: 567-602.

Dittmann, S (1996) Effects of macrobenthic burrows on infaunal communities in tropical tidal flats. *Marine Ecology Progress Series 134:* 119-130.

Dumbauld BR, Armstrong DA, Feldman KL (1996) Life-history characteristics of two sympatric thalassinidean shrimps, *Neotrypaea californiensis* and *Upogebia pugettensis*, with implications for oyster culture. *J. Crustacean Biol. 16*: 689-708.

Dumbauld BR, Armstrong DA, Skalski J (1997) Efficacy of the pesticide carbaryl for thalassinid shrimp control in Washington state oyster (*Crassostrea gigas*, Thunberg, 1793) aquaculture. *J Shellfish Res. 16*: 503-518.

Dworschak PC (1998a) The role of tegumental glands in burrow construction by two Mediterranean callianassid shrimp. *Senckenbergiana Maritima 28 (4/6): 143-149*.

Dworschak PC (1998b) Observations on the biology of the burrowing mud shrimps *Callianassa tyrrhena* and *C. candida* (Decapoda: Thalassinidea). *J. Natural History 32*: 535-1548.

Dworschak PC, Coelho VR (1999) On two alpheids from Araçá (São Paulo, Brazil) with a description of a new species of *Leptalpheus* (Decapoda: Caridea: Alpheidae). *Annalen des Naturhistorischen Museums in Wien 101B:* 475-488.

Dworschak PC, Ott JA (1993) Decapod burrows in mangrove-channel and back-reef environments at the Atlantic Barrier Reef, Belize. *Ichnos 2:* 277-290.

Dworschak PC, Rodrigues S de A (1997) A modern analogue for the trace fossil *Gyrolithes*: burrows of the thalassinidean shrimp *Axianassa australis. Lethaia 30:* 41-52.

Felder DL (1978) Osmotic and ionic regulation in several western Atlantic Callianassidae (Crustacea, Decapoda, Thalassinidea). *Biological Bull. 154:* 409-429.

Felder DL (1979) Respiratory adaptations of the estuarine mud shrimp, *Callianassa jamaicense* (Schmitt, 1935) (Crustacea, Decapoda, Thalassinidea). *Biological Bull. 157:* 125-137.

Felder DL, Griffis RB (1994) Dominant infaunal communities at risk in shoreline habitats: Burrowing thalassinid Crustacea. *OCS Study # MMS 94-0007*. U.S. Dept. of the Interior, Minerals Mgmt. Service, Gulf of Mexico OCS Regional Office. New Orleans. 87 pp.

Felder DL, Lovett DL (1989) Relative growth and sexual maturation in the estuarine ghost shrimp *Callianassa louisianensis* Schmitt, 1935. *J. Crustacean Biol. 9:* 540-553.

Felder DL, Rodrigues S de A (1993) Reexamination of the ghost shrimp *Lepidophthalmus louisianensis* (Schmitt, 1935) from the northern Gulf of Mexico and comparison to *L. siriboia*, new species, from Brazil (Decapoda: Thalassinidea: Callianassidae). *J. Crustacean Biol. 13:* 357-376.

Felder JM, Felder DL, Hand SC (1986) Ontogeny of osmoregulation in the estuarine ghost shrimp *Callianassa jamaicense* var. *louisianensis* Schmitt (Decapoda, Thalassinidea). *J. Exp. Marine Biol. Ecol. 99:* 91-105.

Feldmann KL, Armstrong DA, Eggleston DB, Dumbauld BR (1997) Effects of substrate selection and post-settlement survival on recruitment success of the thalassinidean shrimp *Neotrypaea californiensis* to intertidal shell and mud flats. *Marine Ecology Progress Series 150:* 121-136.

Forester S, Graf G (1992) Continuously measured changes in redox potential influenced by oxygen penetrating from burrows of *Callianassa subterranea. Hydrobiologia 235/236*: 527-532.

Forester S, Graf G (1995) Impact of irrigation on oxygen flux into sediment: intermittent pumping by *Callianassa subterranea* and 'piston pumping' by *Lanice conchilega*. *Marine Biol. 123:* 335-346.

Grimm KA, Föllmi KB (1994) Doomed pioneers: Allochthonous crustacean tracemakers in anaerobic basinal strata, Oligo-Miocene San Gregorio formation, Baja California Sur, Mexico. *Palaios 9:* 313-334.

Hanekom N, Baird D (1992) Growth, production and consumption of the thalassinid prawn *Upogebia africana* (Ortmann) in the Swartkops Estuary. *South African J. Zool. 27:* 130-139.

Harris JM (1993) Widespread occurrence of extensive epimural rod bacteria in the hindguts of marine Thalassinidea and Brachyura (Crustacea: Decapoda). *Marine Biol. 116:* 615-629.

Harris JM, Seiderer LJ, Lucas MI (1991) Gut microflora of two saltmarsh detritivore thalassinid prawns, *Upogebia africana* and *Callianassa kraussi. Microbial Ecol. 21:* 277-296.

Hughes DJ, Atkinson RJA (1997) A towed video survey of megafaunal bioturbation in the north-eastern Irish Sea. *J. Marine Biological Assoc. United Kingdom 77:* 635-653.

Jackson LF, Bidleman TF (1990) Fluorescence spectroscopic studies of differential accumulation of aromatic hydrocarbons by *Callianassa kraussi. Oil and Chemical Pollution 6:* 1-19.

Johns AR, Taylor AC, Atkinson RJA, Grieshaber MK (1997) Sulphide metabolism in thalassinidean Crustacea. *J. Marine Biological Assoc. United Kingdom 77:* 127-144.

Kato M, Itani G (2000) *Peregrinamor gastrochaenans* (Bivalvia: Mollusca), a new species symbiotic with the thalassinidean shrimp *Upogebia carinicauda* (Decapoda: Crustacea). *Species Diversity 5:* 309-316.

Kensley B, Heard R (1990) The genus *Axianassa* (Crustacea: Decapoda: Thalassinidea) in the Americas. *Proc. Biological Soc. Washington 103:* 558-572.

Kerr B, Corfield J (1998) Association between the ghost shrimp *Trypaea australiensis* Dana 1852 (Crustacea: Decapoda) and a small deposit-feeding bivalve *Mysella vitrea* Laserson 1956 (Mollusca: Leptonidae). *Marine and Freshwater Res. 49:* 801-806.

Kevrekidis T, Gouvis N, Koukouras A (1997) Population dynamics, reproduction and growth of *Upogebia pusilla* (Decapoda, Thalassinidea) in the Evros Delta (North Aegean Sea). *Crustaceana 70:* 799-812.

Labadie LV, Palmer AR (1996) Pronounced heterochely in the ghost shrimp, *Neotrypaea californiensis* (Decapoda: Thalassinidea: Callianassidae): Allometry, inferred function and development. *J. Zool. London 240:* 659-675.

Lemaitre R, Rodrigues S de A (1991) *Lepidophthalmus sinuensis:* A new species of ghost shrimp (Decapoda: Thalassinidea: Callianassidae) of importance to the commercial culture of penaeid shrimps on the Caribbean coast of Colombia, with observations on its ecology. *Fishery Bull. 89:* 623-630.

Manning RB, Felder DL (1991) Revision of the American Callianassidae (Crustacea: Decapoda: Thalassinidea). *Proc. Biological Soc. Washington 104:* 764-792.

Marin SL, George-Nascimento M (1993) Host body size and habitat as factors affecting the distribution and abundance of the copepod *Clausidium* sp. (Cyclopoida), ectosymbiont of the ghost shrimp *Callianassa garthi* Retamal, 1975 (Crustacea, Thalassinidea). *Revista Chilena de Historia Natural 66:* 427-437.

Muñoz G, George-Nascimento M (1999) Reciprocal reproductive effects in the symbiosis between ghost shrimps (Decapoda: Thalassinidea) and bopyrid isopods (Isopoda: Epicaridea) at Lenga, Chile. *Revista Chilena de Historia Natural 72:* 49-56.

Murphy RC, Kremer JN (1992) Benthic community metabolism and the role of deposit-feeding callianassid shrimp. *J. Marine Res. 50:* 321-340.

Myrick JL, Flessa KW (1996) Bioturbation rates in Bahía La Choya, Sonora, Mexico. *Ciencias Marinas 22:* 23-46.

Nates SF, Felder DL (1998) Impacts of burrowing ghost shrimp, genus *Lepidophthalmus* (Crustacea: Decapoda: Thalassinidea), on penaeid shrimp culture. *J. World Aquaculture Soc. 29*: 188-210.

Nates SF, Felder DL (1999) Growth and maturation in the burrowing mud-shrimp *Lepidophthalmus sinuensis* Lemaitre and Rodrigues 1991 (Crustacea, Decapoda, Callianassidae), a burrowing pest in shrimp mariculture ponds. *Fishery Bull., U.S. 97:* 526-541.

Nates SF, McKenney CL Jr (2000) Ontogenetic changes in biochemical composition during larval and early postlarval development of *Lepidophthalmus louisianensis*, a ghost shrimp with abbreviated development. *Comp. Biochem. Physiol. 127B:* 459-468.

Nates SF, Lemaitre R, Felder DL (1997) Comparative larval development among two species of burrowing mud-shrimp, genus *Lepidophthalmus* (Crustacea, Decapoda, Callianassidae). *J. Crustacean Biol. 17:* 497-519.

Nickell LA, Atkinson RJA (1995) Functional morphology of burrows and trophic modes of three thalassinidean shrimp species, and a new approach to the classification of thalassinidean burrow morphology. *Marine Ecology Progress Series 128:* 181-197.

Nickell LA, Hughes DJ, Atkinson, RJA (1995) Megafaunal bioturbation in organically enriched Scottish sea lochs. In Eleftheriou A, Ansell AD, Smith CJ (Eds) *Biology and Ecology of Shallow Coastal Waters, Proceedings of the 28th European Marine Biology Symposium, Crete.* Olsen and Olsen. Fredensborg. pp. 315-322.

Nickell LA, Atkinson RJA, Pinn EH (1998) Morphology of thalassinidean (Crustacea: Decapoda) mouthparts and pereiopods in relation to feeding, ecology and grooming. *J. Natural History 32:* 733-761.

Over DJ (1990) Trace metals in burrow walls and sediments, Georgia Bight, USA. *Ichnos 1:* 31-41.

Paterson BD, Thorne MJ (1993) The effect of oxygen tension on the swimmeret rate of *Callianassa australiensis* and *C. arenosa* (Crustacea, Decapoda, Thalassinidea). *Marine Behav. Physiol. 24:* 15-24.

Paterson BD, Thorne MJ (1995) Measurements of oxygen uptake, heart and bill bailer rates of callianassid burrowing shrimp *Trypaea australiensis* Dana and its responses to low oxygen tensions. *J. Exp. Marine Biol. Ecol. 194:* 39-52.

Pezzuto PR (1998) Population dynamics of *Sergio mirim* (Rodrigues 1971) (Decapoda: Thalassinidea: Callianassidae) in Cassino Beach, southern Brazil. *Marine Ecology. Pubblicazioni della Stazione Zoologica di Napoli 19:* 89-109.

Pinn EH, Rogerson A, Atkinson RJA (1997) Microbial flora associated with the digestive system of *Upogebia stellata* (Crustacea: Decapoda: Thalassinidea). *J. Marine Biological Assoc. United Kingdom 77:* 1083-1096.

Pinn EH, Atkinson RJA, Rogerson A (1998a) Particle size selectivity and resource partitioning in five species of Thalassinidea (Crustacea: Decapoda). *Marine Ecology Progress Series 169:* 243-250.

Pinn EH, Atkinson RJA, Rogerson A (1998b) The diet of two mud-shrimps, *Calocaris macandreae* and *Upogebia stellata* (Crustacea: Decapoda: Thalassinidea). *Ophelia 48:* 211-223.

Pinn EH, Nickell LA, Rogerson A, Atkinson RJA (1999a) Comparison of gut morphology and gut microflora of seven species of mud-shrimp (Crustacea: Decapoda: Thalassinidea). *Marine Biol. 133:* 103-114.

Pinn EH, Nickell LA, Rogerson A, Atkinson RJA (1999b) Comparison of the mouthpart setal fringes of seven species of mud-shrimp (Crustacea: Decapoda: Thalassinidea). *J. Natural History 33:* 1461-1485.

Posey MH, Dumbauld BR, Armstrong DA (1991) Effects of a burrowing mud-shrimp, *Upogebia pugettensis* (Dana), on abundances of macroinfauna. *J. Exp. Marine Biol. Ecol. 148:* 283-294.

Rodrigues S de A, Shimizu RM (1997) Autoecologia de *Callichirus major* (Say, 1818). *Oecologia Brasiliensis 3:* 155-170.

Rowden AA, Jones MB (1993) Critical evaluation of sediment turnover estimates for Callianassidae (Decapoda: Thalassinidea). *J. Exp. Marine Biol. Ecol. 173:* 265-272.

Rowden AA, Jones MB (1994) A contribution to the biology of the burrowing mud-shrimp, *Callianassa subterranea* (Decapoda: Thalassinidea). *J. Marine Biological Assoc. United Kingdom 74:* 623-635

Rowden AA, Jones MB (1995) The burrow structure of the mud-shrimp *Callianassa subterranea* (Decapoda, Thalassinidea) from the North Sea. *J. Natural History 29:* 1155-1165.

Rowden AA, Jones MB, Morris AW (1997) The role of *Callianassa subterranea* (Montagu) (Thalassinidea) in sediment resuspension in the North Sea. *Continental Shelf Res. 18:* 1365-1380.

Rowden AA, Jago CF, Jones SE (1998) Influence of benthic macrofauna on the geotechnical and geophysical properties of surficial sediment, North Sea. *Continental Shelf Res. 18:* 1347-1363.

Sakai K (1999) Synopsis of the family Callianassidae, with keys to subfamilies, genera and species and the description of new taxa (Crustacea: Decapoda: Thalassinidea). *Zoologische Verhandelingen, Leiden 326:* 1-152.

Schlacher TA, Wooldridge TH (1996) Origin and trophic importance of detritus – Evidence from stable isotopes in the benthos of a small, temperate estuary. *Oecologia 106:* 382-388.

Souza JRB de, Borzone CA, Brey T (1998) Population dynamics and secondary production of *Callichirus major* (Crustacea: Thalassinidea) on a southern Brazilian sandy beach. *Arch. Fishery Marine Res. 46:* 151-164.

Stamhuis EJ, Reede-Dekker T, Etten Y van, Wiljes JJ de, Videler JJ (1996) Behaviour and time allocation of the burrowing shrimp *Callianassa subterranea* (Decapoda, Thalassinidea). *J. Exp. Marine Biol. Ecol. 204:* 225-239.

Stamhuis EJ, Schreurs CE, Videler JJ (1997) Burrow architecture and turbative activity of the thalassinid shrimp *Callianassa subterranea* from the central North Sea. *Marine Ecology Progress Series 151:* 155-163.

Stamhuis EJ, Dauwe B, Videler JJ (1998a) How to bite the dust: morphology, motion pattern and function of the feeding appendages of the deposit-feeding thalassinid shrimp *Callianassa subterranea. Marine Biol. 132:* 43-58.

Stamhuis EJ, Videler JJ, Wilde PAWJ de (1998b) Optimal foraging in the benthic shrimp *Cal-*

lianassa subterranea: improving food quality by mechanical selection on grain size. *J. Exp. Marine Biol. Ecol. 228:* 197-308.

Staton JL, DL Felder (1995) Genetic variation in populations of the ghost shrimp genus *Callichirus* (Crustacea: Decapoda: Thalassinoidea) in the western Atlantic and Gulf of Mexico. *Bull. Marine Sci. 56:* 523-536.

Staton JL, Foltz DW, Felder DL (2000) Genetic variation and systematic diversity in the ghost shrimp genus *Lepidophthalmus* (Decapoda: Thalassinidea: Callianassidae). *J. Crustacean Biol. 20,* Special Number *2:* 157-169.

Strasser KM, Felder DL (1998) Settlement cues in successive development stages of the ghost shrimp *Callichirus major* and *C. islagrande* (Crustacea: Decapoda: Thalassinidea). *Marine Biol. 132:* 599-610.

Strasser KM, Felder DL (1999a) Larval development in two populations of the ghost shrimp *Callichirus major* (Crustacea: Decapoda: Thalassinidea) under laboratory conditions. *J. Crustacean Biol. 19:* 844-878.

Strasser KM, Felder DL (1999b) Settlement cues in an Atlantic coast population of the ghost shrimp *Callichirus major* (Crustacea: Decapoda: Thalassinidea). *Marine Ecology Progress Series 183:* 217-225.

Strasser KM, Felder DL (2000) Larval development of the ghost shrimp *Callichirus islagrande* (Schmitt) (Decapoda: Thalassinidea: Callianassidae) under laboratory conditions. *J. Crustacean Biol. 20:* 100-117.

Strasser KM, Felder DL (2001) Effects of salinity on development in the ghost shrimp *Callichirus islagrande* and two populations of *C. major* (Crustacea: Decapoda: Thalassinidea). *Gulf and Caribbean Res. 13:* 9-18.

Tamaki A (1994) Extinction of the trochid gastropod, *Umbonium (Suchium) moniliferum* (Lamark), and associated species on an intertidal mudflat. *Researches on Population Ecol. 36:* 225-236.

Tamaki A, Ingole B (1993) Distribution of juvenile and adult ghost shrimps, *Callianassa japonica* Ortmann (Thalassinidea), on an intertidal sand flat: intraspecific facilitation as a possible pattern-generating factor. *J. Crustacean Biol. 13:* 175-183.

Tamaki A, Miyabe S (2000) Larval abundance patterns for three species of *Nihonotrypaea* (Decapoda: Thalassinidea: Callianassidae) along an estuary-to-open-sea gradient in western Kyushu, Japan. *J. Crustacean Biol. 20,* Special No. 2*:* 182-191.

Tamaki A, Suzukawa K (1991) Co-occurrence of the cirolanid isopod *Eurydice nipponica* Bruce and Jones and the ghost shrimp *Callianassa japonica* Ortmann on an intertidal sand flat. *Ecological Res. 6:* 87-100.

Tamaki A, Ueno H (1998) Burrow morphology of two callianassid shrimps, *Callianassa japonica* Ortmann, 1891 and *Callianassa* sp. (= *C. japonica*: de Man, 1928) (Decapoda: Thalassinidea). *Crustacean Res. 27:* 28-38.

Tamaki A, Ikebe K, Muramatsu K, Ingole B (1992a) Utilization of adult burrows by juveniles of the ghost shrimp, *Callianassa japonica* Ortmann: evidence from resin casts of burrows. *Researches on Crustacea 21:* 113-120.

Tamaki A, Miyamoto, Yamazaki T, Nojima S (1992b) Abundance pattern of the ghost shrimp *Callianassa japonica* Ortmann (Thalassinidea) and the snake eel *Pisodonophis cancrivorus* (Richardson) (Pisces, Ophichthidae) and their possible interaction on an intertidal sand flat. *Benthos Res. 43:* 11-22.

Tamaki A, Tanoue H, Itoh J, Fukuda Y (1996) Brooding and larval developmental periods of the callianassid ghost shrimp, *Callianassa japonica* (Decapoda: Thalassinidea). *J. Marine Biological Assoc. United Kingdom 76:* 675-689.

Tamaki A, Ingole B, Ikebe K, Muramatsu K, Taka M, Tanaka M (1997) Life history of the ghost shrimp, *Callianassa japonica* Ortmann (Decapoda: Thalassinidea), on an intertidal sandflat in western Kyushu, Japan. *J. Exp. Marine Biol. Ecol. 210:* 223-250.

Thebeau LC, Tunnell JW Jr., Dokken QR, Kindinger ME (1981) Effects of the Ixtoc I oil spill on the intertidal and subtidal infaunal populations along lower Texas coast barrier island beaches. *Proceedings of the Oil Spill Conference, 1981.* American Petroleum Institute, Washington, D.C. pp. 467-475.

Thessalou-Legaki M (1990) Advanced larval development of *Callianassa tyrrhena* (Decapoda: Thalassinidea) and the effect of environmental factors. *J. Crustacean Biol. 10:* 659-666.

Thessalou-Legaki M, Kiortsis V (1997) Estimation of the reproductive output of the burrowing shrimp *Callianassa tyrrhena*: a comparison of three different biometrical approaches. *Marine Biol. 127:* 435-442.

Thessalou-Legaki M, Peppa A, Zacharaki M (1999) Facultative lecithotrophy during larval development of the burrowing shrimp *Callianassa tyrrhena* (Decapoda: Callianassidae). *Marine Biol. 133:* 635-642.

Tudge CC, Poore GCB, Lemaitre R (2000) Preliminary phylogenetic analysis of generic relationships within the Callianassidae and Ctenochelidae (Decapoda: Thalassinidea: Callianassoidea). *J. Crustacean Biol. 20,* Special No. 2: 129-149.

Vaugelas J de, Buscail R (1990) Organic matter distribution in burrows of the thalassinid crustacean *Callichirus laurae*, Gulf of Aqaba (Red Sea). *Hydrobiologia 207:* 269-277.

Weitkamp LA, Wissmar RC, Simenstad CA, Fresh KL, Odell JG (1992) Gray whale foraging on ghost shrimp (*Callianassa californiensis*) in littoral sand flats of Puget Sound, USA. *Canadian J. Zool. 70:* 2275-2280.

Wynberg RP, Branch GM (1994) Disturbance associated with bait-collection for sandprawns (*Callianassa kraussi*) and mudprawns (*Upogebia africana*) – long-term effects on the biota of intertidal sandflats. *J. Marine Res. 52:* 523-558.

Ziebis W, Forster S, Huettel J, Jorgensen BB (1996a) Complex burrows of the mud shrimp *Callianassa truncata* and their geochemical impact in the sea bed. *Nature 382:* 619-622.

Ziebis W, Huettel J, Forster S (1996b) Impact of biogenic sediment topography on oxygen fluxes in permeable seabeds. *Marine Ecology Progress Series 140*: 227-237.