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FEATURE ARTICLE: REVIEW

Mangroves as fish habitat: 50 years of field studies

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ABSTRACT: Mangroves dominate undisturbed natural shorelines of many sub-tropical and tropical regions, yet their utilization by fishes is poorly understood. To provide the first comprehensive list of empirical field studies for comparative and reference purposes, we assembled and quantified aspects of 111 mangrove-fish surveys published between 1955 and 2005. Differences in the location, purpose, methodology, data gathered, and analyses performed among studies have resulted in a fragmented literature making cross-study comparisons difficult, at best. Although the number of published studies has increased over time, a geographical bias in the literature has persisted towards studies performed in the USA and Australia, and against studies performed in Southeast Asia and West Africa. The typical survey design has examined <10 fixed locations on a monthly or bimonthly basis for a period of less than 2 yr. Water temperature and salinity measurements have been the most reported habitat variables; others, such as structural and landscape measures, continue to be rare. Moreover, the focus to date has been on identifying assemblage-level patterns of fish use, with very few studies providing species-specific estimates of abundance, growth, mortality, and secondary production. Unless future studies strive towards obtaining such estimates, gauging the importance of mangroves as fish habitat and their broader contribution to ecosystem diversity and production will remain elusive.

KEY WORDS: Fishes · Essential fish habitat · Mangroves · Nursery · Review

Faunce & Serafy review mangrove fish studies, focusing on sampling methodology, and on the types of fish and habitat data reported. While most studies have addressed spatio-temporal patterns in fish assemblage structure, species-specific estimates of fish mortality, growth and secondary production are still required for appraisal of the importance of mangroves as fish habitat.

Photo: Jiangang Luo

INTRODUCTION

Mangrove wetlands are a dominant feature of undisturbed tropical and subtropical shorelines around the globe. Throughout their range, however, these habi-

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tats are in a state of decline. Approximately one-third of the world's mangrove forests has been lost to coastal development over the past 50 yr (Alongi 2002). While there is general agreement that mangroves provide a buffer against storm surges, reduce shoreline erosion and turbidity, absorb and transform nutrients, and are inhabited by a variety of organisms, opinions vary as to the importance of mangrove habitats to fishes and, by extension, to offshore fisheries (Thollot & Kulbicki 1988, Blaber et al. 1989, Thollot 1992, Nagelkerken et al. 2001). For example, the sub-tidal prop-root habitats of mangroves are often cited as nurseries for fishes of economic importance. Today, the protection of mangroves worldwide is based almost entirely on their purported importance to fisheries and/or a number of rare and endangered species (Snedaker 1989, Baran & Hambrey 1998). However, because the same mangrove species can often occur under marine, estuarine, and freshwater conditions, a wide variety of fish assemblages can be found among their inundated prop-roots (hereafter termed 'mangrove habitats'). As such, mangrove habitats likely play a variety of roles in the lives of associated fishes; feeding areas for some species or life stages, daytime refugia for others, nursery and/or nesting areas for yet more. This situation suggests that questions regarding the contribution of a given mangrove habitat to the diversity, productivity and stability of broader fish communities (and their exploited components) must be carefully qualified, or, in some cases, may be premature.

The purpose of this paper is to address some of the most basic questions regarding the body of literature on mangrove fishes that has been published over the past 5 decades. These questions include: How many field studies have been conducted, why and where were they performed, and what techniques were used? What types of measurements have been made of the fish assemblages, their component species and their habitats? Is there sufficient basis for comparing assemblages of mangrove fishes with those associated with other, structurally-complex habitats, such as seagrass beds and coral reefs? The answers to these questions are pertinent to researchers about to embark on new studies, as well as to those making efforts to balance natural resource protection with pressing socio-economic considerations.

METHODS

Publications for this review were selected from 3 databases. First, a search of the Aquatic Sciences and Fisheries Abstracts (ASFA) electronic database was conducted (Cambridge Scientific Abstracts; www.csa.com) using keyword and title searches for the words 'mangrove(s)' and/or 'fish(es)'. Records were selected from the earliest available time period (1971) to January, 2005. The resulting list of over 500 publications was reduced to relevant works according to 2 main criteria: (1) the study must have been published in readily available outlet (i.e. in the 'primary literature'); and (2) each publication must have contained a field-based survey of the ichthyofauna that was conducted within a natural mangrove system. Second, the Science Citation Index (Web of Science; http://isi5.newisiknowledge.com) was used to identify articles that cited works from our reduced ASFA list. Again, any additional publications were vetted according to the selection criteria above. Third, articles from the authors' personal libraries and those introduced through peer review (of this paper) were added. The references cited in each relevant article were examined for new items and this process was continued until no additional publications emerged.

Study locations were grouped into 5 geographic regions following the World Mangrove Atlas (Spalding et al. 1997): (1) South and Southeast Asia (Pakistan to the west, China and Japan to the northeast, including Indonesia), (2) Australasia (Australia, Papua New Guinea, New Zealand, and the South Pacific islands), (3) the Americas (north, central, and south), (4) West Africa, and (5) East Africa and the Middle East (Iran to South Africa eastwards, including the islands in the Indian Ocean). Using the selection (foraging) ratio of Savage (1931), geographical bias in the literature was expressed as the proportion of total studies realized per region relative to the area of mangrove coverage within each region (Manly et al. 1993).

The study purpose, methodology, data gathered, and analyses performed were extracted and tabulated using vote-counting procedures, where 'present' was given a value of 1 and 'absent' was given a value of 0. Data were expressed as proportions of the total number of votes per attribute. Study purposes included identifying spatial or temporal patterns, generating species lists, identifying explanatory variables, biogeographic comparisons, restoration, water management, and gear evaluations. Methodologies included the sampling design (fixed, random, haphazard, or various), sampling frequency (daily, weekly, fortnightly, monthly, bimonthly, quarterly, seasonally, semi-annually) sampling duration, and gear type. Gear types were classified according to Rozas & Minello (1997) and included entanglement gear (gill or trammel nets), towed nets (trawls, seines), passive samplers (fyke nets, flume nets, rotenone-used with or without nets, fish traps, e.g. breder, plankton), and 'enclosure samplers' (block or drop nets, drop traps, and cast nets). Visual surveys and angling were added as additional gears. The type of mangrove forest sampled was noted using the classification scheme of Lugo & Snedaker (1974), which included fringing, riverine and/or basin forest. The data gathered in each study included biotic and abiotic habitat metrics. Fish metrics included groupings by family, maturation stage, residency status, trophic level, or diel habits as well as the type of fish data gathered and analyzed. We classified the types of fish metric data reported in each study according to the criteria recommended for determining 'essential fish habitat' (EFH) (USDOC 1996) which included: presence/absence, frequency of occurrence, percent composition, size, biomass (g), density (number/area), standing crop (g/area), growth and mortality rates, and rates of secondary production. Finally, the focus of analyses (e.g. defining spatial and/or temporal patterns, examining fish–habitat correlations) was tabulated and the type of statistical test(s) or data treatment(s) performed (similarity measures, analysis of variance, ordination, or regression) were recorded.

RESULTS AND DISCUSSION

Chronology and geography

A total of 111 publications were examined from 104 independent field surveys of mangrove fishes published between 1955 and 2005 (Table 1). The earliest records of mangrove-associated fishes were species lists compiled by Inger (1955) and Boeseman (1963) as part of broad ecological inventories of forests in Borneo (South and Southeast Asia region) and the Niger Delta (West Africa region), respectively. Austin (1971) provided the first inventory of mangrove fishes from Puerto Rico (American region), and Day (1974) from Mozambique (i.e. the East Africa and Middle East region). Blaber (1980), and Blaber & Blaber (1980) published the first of many works on assemblages of mangrove fishes from Australia (Australasian region).

While the cumulative number of publications has grown steadily since the mid 1980s, the sharpest increases occurred for the regions of South and Southeast Asia and the Americas (Fig. 1). Selection indices indicate that the geographic distribution of studies among regions has not been commensurate with the proportion of the world's mangrove acreage that they contain (Table 2). Nearly 70% of studies have been conducted in either the Americas or Australasia, and the South and Southeast Asia and West Africa regions are clearly under-represented in the literature. Because South and Southeast Asia contains the largest proportion of the world's mangrove coverage, it is encouraging that more literature is emerging from this region where coastal fish assemblages are also relatively diverse (Blaber 2002). However, a literature void remains for the West Africa region — an area that is likely to continue to be under-represented unless specifically targeted for study. Interestingly, the first 2 studies of mangrove fishes were conducted in the 2 regions that are least represented today.

Although disproportionate, the spatial distribution of studies we examined covers much of the known global distribution of mangroves (Fig. 2). Specific areas that have received the most thorough study include Florida (USA) and Moreton Bay (Australia). Similar dominance of studies from the USA and Australia in the literature has beset previous reviews of fishes occupying seagrass beds (Heck et al. 2003), mangroves (Sheridan & Hays 2003), and studies of ontogenetic fish movements (Gillanders et al. 2003). Regions outside US and Australian waters where data are particularly lacking include: (1) Pacific Panama; (2) Colombia; (3) Central Brazil; (4) the Red Sea; (5) Mozambique; (6) the Bay of Bengal and the Andaman Sea; and (7) Borneo (Fig. 2). However, there are several important cases where fishes inhabiting tropical estuaries from these areas have been reported. In such cases, data summaries were made from multiple surveys of fishes that rarely mentioned study objectives, methods, gear, or habitat(s) sampled, making their inclusion here difficult, at best. In Florida (USA), species lists of mangrove fishes were compiled from numerous studies by Odum et al. (1982) and presented for tidal streams, estuarine bays, and oceanic bays. Off Columbia, Alvarez León & Blanco Racedo (1985) reviewed aspects of 31 studies conducted in the Cartagena Bay system. They provided an overall species list for the system, and sum-

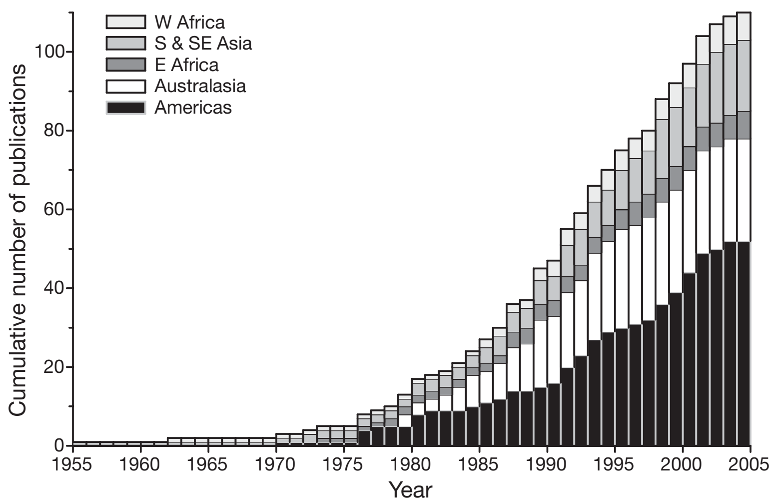

Fig. 1. Cumulative number of publications on mangrove fishes by each geographic region from 1955 to 2005 (n = 111)

Table 1. Chronological list of surveys of mangrove fishes conducted during 1955 to 2005. Design codes: FX: fixed; HZ: haphazard; RM: random; VAR: various. SU: sample unit; Prop. mangrove: proportion of sites that were within mangrove habitats. Frequency codes: BM: bimonthly; D: daily; F: fortnightly; M: monthly; S: seasonal; Q: quarterly; Var: various. Gear codes: A: anglers; B: block net; C: cast net; F: fyke net; G: gill or trammel net; P: plankton net; R: rotenone; S: seine net; T: trap; TP: trap or flume net; TW: trawl; V: visual surveys. Published studies with same letter [in brackets] are from the same fish survey. nr = not reported

Location	Region	Design	SU	No. SU	No. sites	Prop. mangrove	Fre-quency	Duration (yr)	Gear	Basin	Fringe	Riverine	Source
Dewhurst Bay, Borneo	SA	FX	Site	11	11	0.36	1	nr	A,C,R,S			x	Inger (1955)
Niger Delta	WA	nr	Region	4	4	1.00	Var		NR			x	Boseman (1963)
Western Puerto Rico	AM	FX	Estuary	8	8	1.00	Var		G,S		x	x	Austin (1971)
Ponggol Estuary, Singapore	SA	FX	Site	3	3	1.00	M	1.0	S			x	Thia-Eng (1973)
Morrumbene Estuary, Mozambique	EA	FX	Site	6	6	0.50	3		A,S		x	x	Day (1974)
Old Rhodes Key lagoon, USA	AM	FX	Site	6	6		M	0.4	A,T,V				Holm (1977)
Guadeloupe	AM	FX	Site	12	12	0.33	M	0.1	F,TP		x		Lasserre & Toffart [a] (1977)
Marco Island Estuary, USA	AM	FX	Site	11	11	0.00	M	4.1	TW				Weinstein et al. (1977)
Huizache and Caimanero lagoons, Mexico	AM	FX	Site	5	5	0.80	M	1.3	C,S		x		Warburton (1978)
Mngazana Estuary, S Africa	EA	FX	Site	7	7	1.00	3		G,P,S		x	x	Branch & Grindley (1979)
Trinity Inlet System, Australia	AU	FX	Site	18	18	0.39	nr		B,G,P,S		x		Blaber (1980)
Moreton Bay, Australia	AU	FX	Site	4	4	0.50	M	1.0	B,P,S		x		Blaber & Blaber (1980)
Serpentine Creek, Australia	AU	FX	Site	10	10	0.00	F	1.2	TW				Quinn (1980)
Tamil Nadu coast, India	SA	nr	Region	1			nr		P		x		Krishnamurthy & Prince Jeyaseelan (1981)
Jiquilisco Bay, El Salvador	AM	FX	Site	6	6	0.00	M	1.3	TW				Phillips [b] (1981b)
Jiquilisco Bay, El Salvador	AM	FX	Site	6	6	0.00	M	1.3	C,G,TW				Phillips [b] (1981b)
Isle of Youth, Cuba	AM	FX	Site	4	4	1.00	S	1.0	V		x	x	Valdéz-Muñoz (1981)
Bahia de la paz, Mexico	AM	FX	Site	3	7	0.00	M	0.5	TW				Martínez et al. (1982)
Papua New Guinea	AU	FX	Site	14	14	1.00	nr		R	x	x	x	Collette (1983)
Botany Bay, SE Australia	AU	FX	Site	1	1	1.00	BM	1.5	B,R			x	Bell et al. (1984)
Wairiki Creek, Fiji	AU	FX	Site	6	6	1.00	M	1.0	G			x	Lal (1984)
Dampier region, NW Australia	AU	FX	Biotope	2	9	0.67	Q	1.0	G,R,S,V	x	x	x	Blaber et al. (1985)
Guadeloupe	AM	FX	Bay	2	12	0.33	Var	Var	TP		x		Louis et al. [a] (1985)
Papua New Guinea	AU	FX	Estuary	2	5	0.00	F	2.0	TW				Quinn & Kojis (1985)
Phuket Island, Thailand	SA	FX	Site	4	4	0.50	M	1.6	P,TW		x	x	Janekarn & Boonruang (1986)
Laguna Joyuda, Puerto Rico	AM	FX	Site	5	5	0.00	M	1.0	TW				Stoner (1986)
Elichi Creek, Nigeria, W Africa	WA	FX	Site	2	2	1.00	M	1.1	B			x	Wright (1986)
Pagbilao Bay, Phillipines	SA	FX	Site	6	6	1.00	M	1.5	G,TW			x	Pinto (1987)
Alligator Creek, Australia	AU	nr	Biotope	3.5	8	0.50	BM	1.2	S			x	Robertson & Duke [c] (1987)
Western Florida Bay, USA	AM	FX	Site	8	8	1.00	Var	Var	B,R,TW	x	x		Thayer et al. (1987)
Sinnamary river, French Guiana	AM	nr	Region	3			M	Var	C,G,TP,R,TW		x	x	Boujard & Beltran (1988)
Leanyer Swamp, N Australia	AU	FX	Site	2	2	1.00	F	0.5	R,T	x		x	Davis (1988)
Tudor Creek, Kenya, E Africa	EA	FX	Site	4	4	0.75	F	0.6	P,S		x		Little et al. [d] (1988b)
Tudor Creek, Kenya, E Africa	EA	FX	Site	5	5	0.60	nr	nr	P		x		Little et al. [d] (1988a)
Saint-Vincent Bay, New Caledonia	AU	nr	Biotope	3	121	0.01	Var	Var	F,G,TW,R,V		x	x	Thollot & Kulbicki (1988)
Teminos Lagoon, Mexico	AM	FX	Biotope	2	2	0.00	M	1.0	TW				Yáñez-Arancibia et al. [e] (1988)
Embley Estuary, NE Australia	AU	FX	Biotope	5	6	0.83	Q	2.0	B,G,R,S,TW			x	Blaber et al. (1989)

Table 1 (continued)

Location	Region	Design	SU	No. SU	No. sites	Prop. mangrove	Fre-quency	Duration (yr)	Gear	Basin	Fringe	Riverine	Source
Nigerian Coast, W Africa	WA	FX	Estuary	4			nr		P,S	nr	nr	nr	Amadi et al. (1990)
Solomon Islands, W Pacific	AU	FX	Estuary	13	13	1.00	nr		B,G,R,S	x		x	Blaber & Milton (1990)
Selangor, Malaysia	SA	FX	Biotope	4	41	0.22	Var	Var	F,G,TW		x	x	Chong et al. [f] (1990)
Tecapan-Aqua Brava, Mexico	AM	FX	Site	15	15	1.00	M	1.0	S,TW				Flores-Verdugo et al. (1990)
Moreton Bay, E Australia	AU	FX	Site	1	3	1.00	M	1.2	B,G,S	x	x		Morton (1990)
Alligator Creek, Australia	AU	nr	Estuary	1			BM	1.2	G,S,TP	x		x	Robertson & Duke [c] (1990b)
Alligator Creek, Australia	AU	nr	Estuary	4			BM	1.2	G,S,TP	x		x	Robertson & Duke [c] (1990a)
Moreton Bay, Australia	AU	FX	Biotope	5	5	0.60	M	0.8	TW		x		Weng (1990)
Dubreka and Tabunsu estuary, Guinea	WA	FX	Estuary	2			nr		A,C,G,TW	nr	nr	nr	Boltachev (1991)
Cayo Collado, Puerto Rico	AM	FX	Site	8	8	1.00	S	0.2	V		x		Rooker & Dennis (1991)
Northern US Virgin Islands	AM	FX	Site	5	5	1.00	M	1.8	T,V		x		Boulon (1992)
La Parguera, Puerto Rico	AM	FX	Biotope	4	4	0.50	M	1.1	P		x		Dennis (1992)
Fort-de-France, Martinique	AM	FX	Site	8	8	1.00	Q	2.3	TP		x		Louis et al. [g] (1992)
Selangor, Malaysia	SA	FX	Biotope	3	41	0.22	Var	Var	F,G,TW		x	x	Sasekumar et al. [f] (1992)
Alligator Creek, Australia	AU	RM	Region	3	6	0.50	M	0.4	A,S,T		x		Sheaves (1992)
Rookery Bay, USA	AM	VAR	Biotope	3	30	0.33	Q	1.3	TP		x		Sheridan (1992)
Saint-Vincent Bay, New Caledonia	AU	VAR	Biotope	2	577	0.03	M	1.0	G,R,TM,TP,V		x		Thollot (1992)
Tanshui River, Taiwan	SA	FX	Site	3	3	0.00	M	2.8	B			x	Tzeng & Wang (1992)
Bonaire, Netherlands Antilles	AM	nr	Biotope	6			nr		V		x		van der Velde et al. [h] (1992)
Sabana-Camaguey, N Cuba	AM	RM	Region	3	63	1.00	1	nr	V		x		Claro & García-Arteaga (1993)
Phang-Nga Bay, Thailand	SA	FX	Site	1	1	0.00	M	1.2	TW				Janekarn (1993)
Ambergis Cay, Belize	AM	FX	Biotope	3	3	0.33	BM	1.0	TW			x	Sedberry & Carter (1993)
Terminos Lagoon, Mexico	AM	FX	Biotope	2	2	0.00	BM	1.2	TW				Yáñez-Arancibia et al. [e] (1993)
Gulf of Carpentaria, N Australia	AU	FX	Biotope	4			S	Var	B,F,G,R,S,TW	x	x	x	Blabler et al. (1994)
Clarence River, Australia	AU	FX	Site	18	18	0.28	Q	2.5	B,R		x		Pollard & Hannan (1994)
Gulf of Nicoya, Costa Rica	AM	FX	Site	3	3	1.00	M	0.9	G,S		x		Rojas et al. [i] (1994a)
Gulf of Nicoya, Costa Rica	AM	FX	Site	3	3	1.00	M	0.9	G,S		x		Rojas et al. [i] (1994b)
Celestum Lagoon, Mexico	AM	FX	Site	1	1	1.00	S	1.5	B,R	x	x		Vega-Cendejas et al. (1994)
Upper Tampa Bay, USA	AM	RM	Bay	2	24		M	2.9	T	x	x	x	Vose & Bell (1994)
Raby Bay, E Austalia	AU	FX	Biotope	2	7	0.43	M	1.1	S		x		Williamson et al. (1994)
Moreton Bay, E Australia	AU	FX	Biotope	2	6	0.33	M	2.0	S,TP	x	x		Laegdsgaard & Johnson (1995)
Fort-de-France, Martinique	AM	FX	Site	8	8	1.00	Q	2.3	TP		x		Louis et al. [g] (1995)
Placido Bayou, USA	AM	FX	Site	6	6	1.00	Var		B,S	x	x		Mullin (1995)
Lagos Lagoon, Nigeria	WA	FX	Site	2	2	0.50	M		S		x		Nwadukwe (1995)
Sao Luis, Brazil	AM	FX	Site	4	4	1.00	M	0.8	TP			x	Batista & Rego (1996)
Tin Can Bay, NE Austalia	AU	FX	Site	4	4	1.00	BM	2.2	B	x			Halliday & Young (1996)
Gazi Creek, Kenya, E Africa	EA	FX	Site	3	3	0.67	M	0.8	S		x		Kimani et al. (1996)
Negombo Estuary, W Sri Lanka	SA	FX	Site	6	4	1.00	M	2.1	S		x		Pinto & Punchihewa (1996)
Embley River, N Australia	AU	FX	Site	4	4	1.00	D,S	Var	B	x			Vance et al. (1996)
La Parguera, Puerto Rico	AM	RM	Biotope	3	43	0.21	nr		G,V		x		Acosta (1997)
Karachi, Pakistan	SA	FX	Site	2	2	0.50	F	0.9	C	nr	nr	nr	Atiqullah et al. (1997)

Table 1 (continued)

Location	Region	Design	SU	No. SU	No. sites	Prop mangrove	Fre-quency	Duration (yr)	Gear	Basin	Fringe	Riverine	Source
Tulear Lagoon, SW Madagascar	EA	FX	Site	1	1	1.00	M	1.0	G				Laroche et al. (1997)
Guaratuba, Brazil	AM	RM	Region	1	1	1.00	nr		C,S,TW				Chaves & Correa (1998)
Sao Luis, Brazil	AM	FX	Site	4	4	1.00	M	0.8	TP			x	Batista & Rego (1996)
Tin Can Bay, NE Australia	AU	FX	Site	4	4	1.00	BM	2.2	B	x			Halliday & Young (1996)
Gazi Creek, Kenya, E Africa	EA	FX	Site	3	3	0.67	M	0.8	S		x		Kimani et al. (1996)
Negombo Estuary, W Sri Lanka	SA	FX	Site	6	4	1.00	M	2.1	S		x		Pinto & Punchihewa (1996)
Embley River, N Australia	AU	FX	Site	4	4	1.00	D, S	Var	B	x			Vance et al. (1996)
La Parguera, Puerto Rico	AM	RM	Biotope	3	43	0.21	nr		G,V		x		Acosta (1997)
Karachi, Pakistan	SA	FX	Site	2	2	0.50	F	0.9	C	nr	nr	nr	Atiqullah et al. (1997)
Tulear Lagoon, SW Madagascar	EA	FX	Site	1	1	1.00	M	1.0	G				Laroche et al. (1997)
Guaratuba, Brazil	AM	RM	Region	1	1	1.00	nr		C,S,TW				Chaves & Correa (1998)
NE tropical Australia	AU	HZ	Region	4	12	1.00	Q	2.3	T		x		Sheaves (1998)
Yingluo Bay, China	SA	FX	Site	2	2	1.00	Q	1.0	B		x	x	He et al. (2001)
Guaratuba, Brazil	AM	RM	Region	1	1	1.00	M	2.9	TW				Chaves & Bouchereau (1999)
Bay of La Paz, Mexico	AM	FX	Site	1	1	1.00	nr		F			x	Gonzalez-Acosta et al. (1999)
N & S Taiwan	SA	FX	Region	6	6	1.00	BM	1.0	F			x	Kuo et al. (1999)
NE Florida Bay, USA	AM	FX	Bay	6	42	1.00	M	1.1	B,R,V	x	x		Ley et al. [j] (1999)
N Taiwan	SA	FX	Site	1	1	1.00	M	1.0	F			x	Lin & Shao (1999)
NE Florida Bay, USA	AM	FX	Site	4	24	1.00	BM	5.2	R,T	x			Lorenz (1999)
Pagbilao, Philippines	SA	FX	Site	4	4	1.00	D	0.0	B	x			Rönnbäck et al. (1999)
Curacao, Netherlands Antilles	AM	FX	Biotope	6	12	1.00	Var		V		x		Nagelkerken et al. [k] (2000a)
Curacao, Netherlands Antilles	AM	FX	Biotope	6	12	1.00	Var		V		x		Nagelkerken et al. (2000b)
Bonaire, Netherlands Antilles	AM	FX	Biotope	6	27	0.22	M	0.6	V		x		Nagelkerken et al. [h] (2000c)
Sine Saloum, Senegal	WA	FX	Site	3	6	1.00	M	0.2	F				Vidy (2000)
Guaratuba, Brazil	AM	RM	Region	1	1	1.00	nr		F,S,TW				Chaves & Vendel (2001)
NE Florida Bay, USA	AM	FX	Bay	6	17	1.00	M	1.1	V		x		Ley & McIvor [j] (2001)
Curacao, Netherlands Antilles	AM	FX	Bay	3	11	0.00	D, M	Var	S,V				Nagelkerken et al. (2001)
St. Croix, US Virgin Islands	AM	HZ	Site	10	10	1.00	M	2.0	S,T		x		Tobias (2001)
Rio da Fazenda, Brazil	AM	nr	Region	3	3	0.33	BM	1.0	A,T,V		x		Uieda & Uieda (2001)
Sepetiba Bay, Brazil	AM	RM	Region	3	158	0.00	M	3.0	TW				Araujo et al. (2002)
Caete River Estuary, Brazil	AM	FX	Site	3	3	1.00	M	1.0	TP			x	Barletta-Bergan et al. (2002)
Curacao, Netherlands Antilles	AM	FX	Biotope	3	11	3.00	S	nr	V		x		Cocheret de la Morinière et al. [k] (2002)
Lower Volta, Ghana	WA	FX	Site	7	7	0.71	nr	nr	C,G,S		x	x	Dankwa & Gordon (2002)
Curacao, Netherlands Antilles	AM	FX	Biotope	8	17	0.71	S	1.0	V		x		Nagelkerken & van der Velde [k] (2002)
Eastern Caribbean	AM	FX	Biotope	3	23	0.00	Var	Var	V		x		Nagelkerken et al. (2002)
Bimini, Bahamas	AM	FX	Biotope	4	4	0.25	nr		B,S		x		Neuman & Gruber (2002)
Sikao Creek Estuary, Thailand	SA	FX	Site	6	6	0.67	Q	26.7	F,R,S	x	x	x	Tongnunui et al. [l] (2002)
Johor Strait, Malaysia	SA	FX	Site	4	4	0.25	M	1.5	S		x		Hajisamae & Chou (2003)
Sikao Creek, Thailand	SA	FX	Site	3	3	0.67	Q	2.4	S		x	x	Ikejima et al. [l] (2003)
Biscayne Bay, USA	AM	RM	Region	2	129	1.00	S	2.0	V		x		Serafy et al. (2003)
SE Everglades, USA	AM	FX	Site	3	12	1.00	BM	3.2	V			x	Faunce et al. (2004)
Rio Lagartos, Mexico	AM	FX	Site	28	28	0.00	Var	Var	S,TW				Vega-Cendejas & Santillana (2004)
Chwaka Bay, Tanzania	EA	FX	Biotope	5	5	0.40	Var	Var	S,V			x	Lugendo et al. (2005)

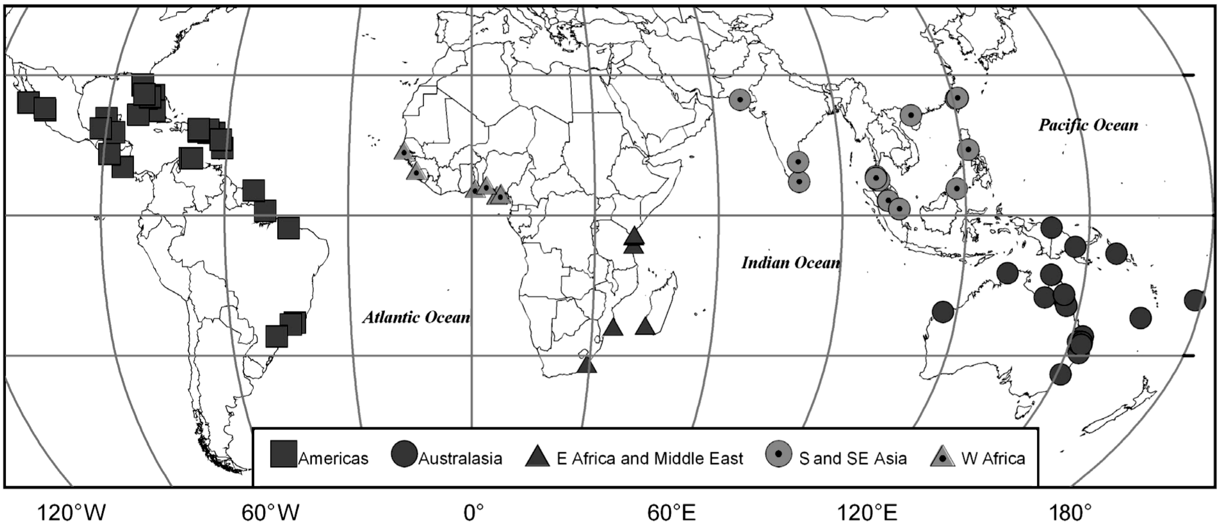

Fig. 2. Location of studies of mangrove fishes used in the present review (coded by geographic region)

marized their data based on the number of species belonging to various salinity regimes and trophic levels for Bahía de Cartagena, Ciénaga de Tesca, and Ciénaga Grande de Santa Marta. Similarly, Cervigón (1985) used data from an earlier study and historical records to generate a list of fish species for the Orinoco estuary (Venezuela) according to salinity regime. Finally, the ecology of the Itamaracá ecosystem (Brazil) was summarized by Paranagua & Eskinazi-Leça (1985), who provided a family and species list of fishes. For more complete summaries of fish studies conducted from large tropical estuarine systems, the reader should consult the comprehensive works of Blaber (2000) and Yáñez-Arancibia (1985).

Study design

Study design incorporates a study's purpose with its methodology. Over half of the examined surveys of mangrove fishes aimed to identify spatial and/or temporal patterns of mangrove utilization, while a lesser proportion were conducted to provide an inventory of fishes (21.7%) or identify explanatory variables for observed utilization patterns (15.6%). Less than 10% of studies were concerned with the remaining topics (Fig. 3a). Most studies aimed to identify temporal patterns, and typically achieved this goal through monthly sampling for a period of 0.5 to 1.5 yr (Fig. 3b,c). Sampling durations of more than 2 yr were uncommon (<5%) with the longest published survey spanning 5 yr (Lorenz 1999). In addition, most studies sampled, or otherwise quantified, fishes at a small number of locations. Only 4 studies sampled mangroves at more than 20 locations: Serafy et al. (2003) sampled 129 locations, Claro & García-Arteaga (1993) sampled 63 locations, Ley et al. (1999) sampled 42 locations, and Lorenz (1999) sampled 24 locations (Table 1). Fixed sampling designs were employed much more often (81%) than random-stratified (8.5%) or haphazard designs (1.8%) or various other sampling designs (1.8%). In fixed- and mixed-design surveys, the rationale for selecting site locations was rarely provided.

These results highlight some limitations with our knowledge of mangrove habitat utilization by fishes. For example, if not selected remotely, or *a priori*, the

Table 2. Comparison of mangrove area and the number of published studies from within each geographic region. The selection ratio (w_i) of Savage (1931) was used to compare the proportion of studies to the proportion of mangrove area within each region

Region	Mangrove area (km^2)	Proportion of total area	Number of total studies	Proportion of total studies	w_i
Americas	49 096	0.271	53	0.477	1.762
Australasia	18 789	0.104	26	0.234	2.252
East Africa and Middle East	10 024	0.055	7	0.063	1.147
South and Southeast Asia	75 173	0.415	18	0.162	0.391
West Africa	27 995	0.155	7	0.063	0.407
Total	181 077		111		

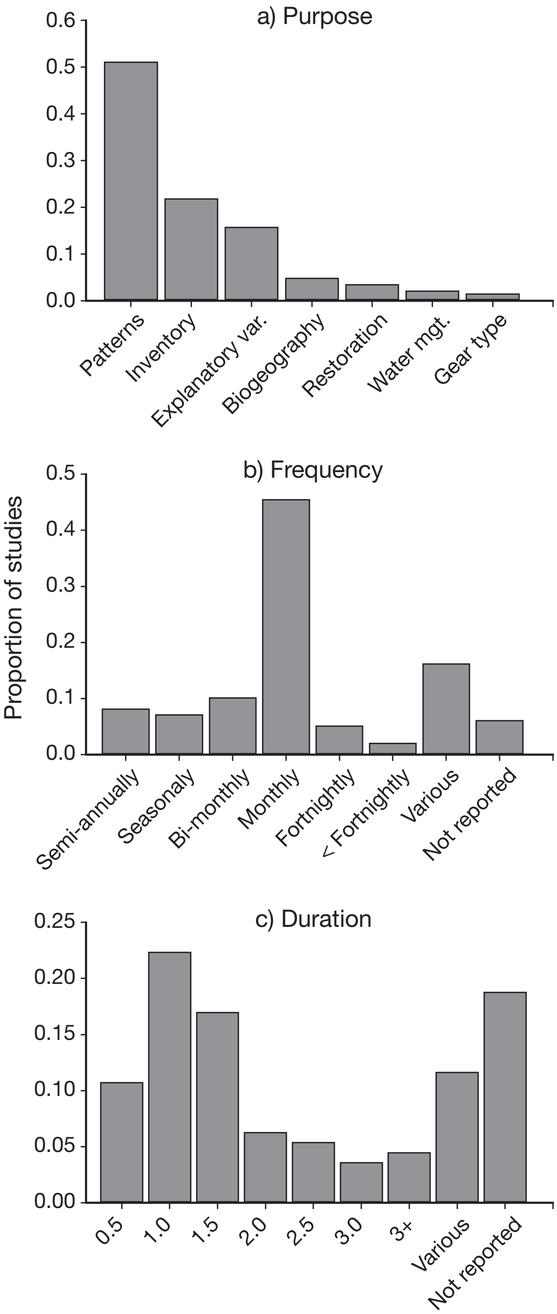

Fig. 3. (a) Purpose, (b) sampling frequency, and (c) sampling duration (in yr) of studies of mangrove fishes. Var: variable; mgt: management. Note difference in *y*-axis scales

choice of sampling locations may be biased, which in turn can be reflected in the data gathered (Rozas & Minello 1997). In addition, the limited spatial extent and/or small number of sites sampled in most studies may not be representative of a given area or region, and thus may be of limited use to coastal resource managers if they must determine the costs and benefits of developing one mangrove area over another. Similarly, the lack of multi-year studies precludes assessment of what constitutes a 'typical' year, or of the extent of inter-annual variability in both the fish assemblages and their environment. While the seasonal dynamics of mangrove use by fishes has received attention, only a few studies have focused on shorter temporal scales. In the future, researchers should better describe how and why sampling locations were selected, and when possible include the rationale behind their sampling intensity/allocation decisions.

How fish samples have been acquired from mangroves is of particular importance due, in part, to issues of species- and size-selectivity. Indeed, one of the major reasons mangroves have received relatively little attention as fish habitats is that it is inherently difficult to quantitatively sample fishes within them. Consequently, our understanding of the role(s) that these habitats play in the lives of fishes has been hindered by the fact that the same sampling methods have rarely been used from one study to the next. Over one-third of all studies we reviewed used towed gears, which is a consistent finding among geographic regions (Fig. 4a,b). While towed nets can be effective in seagrass beds, they are of little or no use within the dense, rigid, entangled roots of mangrove trees. Use of pas-

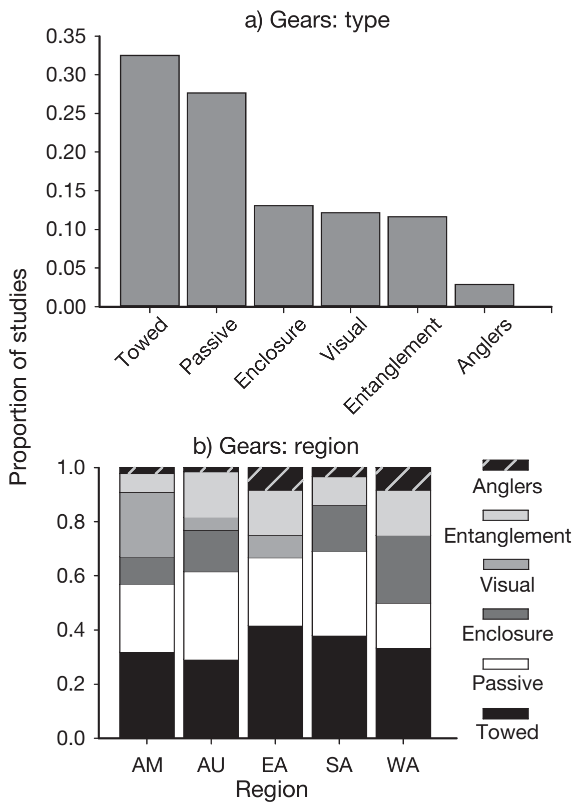

Fig. 4. The gear type used to collect fishes from mangrove habitats (a) among studies, and (b) by geographic region. AM: Americas; AU: Australasia; EA: East Africa and the Middle East; SA: South and Southeast Asia; WA: West Africa. Note difference in *y*-axis scales

sive gears has also been common (27% of studies). Most passive gears are difficult to place in dense mangrove prop-roots without constituting additional structure, and like towed gears are often actually employed at the periphery of the mangrove shoreline. This considered, one out of 5 purported studies of mangrove fishes that we reviewed failed to sample within mangrove habitat. This has undoubtedly produced unrepresentative data in specific cases, and has probably led to unfounded conclusions about the nature and extent of fish utilization of mangroves in general.

There are notable exceptions, however, where more appropriate sampling techniques have been applied to quantitatively sample fish within the mangroves proper. These include enclosure, entanglement, and visual techniques, which have each been employed with similar frequency (i.e. 11 to 13% of studies). A common type of enclosure gear uses a fine mesh net to encompass a mangrove area and fishes are subsequently removed with poison and/or a smaller net (e.g. Bell et al. 1984, Thayer et al. 1987, Blaber & Milton 1990). Such block netting can result in estimates of both abundance and biomass per unit area (standing crop), and is an especially effective method for collecting small, cryptic fishes. However, sampling efficiency is dependent on the clearing method used. Two drawbacks of enclosure samplers are that they often involve both short- and long-term disturbance of the habitat under study (e.g. prop-root and canopy removal), and are relatively labor intensive. In contrast, passive samplers such as fyke, flume, or channel nets do not greatly modify the mangrove habitat, but are limited to situations where tides are sufficient to drain the habitat and effectively force fishes into these capture devices (McIvor & Odum 1986). Most traps, like entanglement gears, can be rapidly deployed and cause minimal habitat disturbance. These gears can also be effective for catching relatively large (ca. 10 cm total length) mobile fishes often missed by other gears; however, there are size- and species-selectivity constraints. Size selectivity problems can be reduced by sampling with traps of different mesh sizes and openings, or by sampling with nets with multiple panels composed of different meshes (Sogard et al. 1989, Sheaves 1995). Unfortunately, like all passive samplers, only relative abundance or biomass, rather than density or biomass per unit area, can be estimated using traps and entanglement nets. Finally, underwater visual fish census can be a rapid and effective technique for gathering data and making quantitative comparisons of fish distribution, abundance, and size-structure within and among habitat types. Visual fish census has been utilized in seagrass beds, mangroves, and hardbottom communities, and has become the most accepted method for estimating fish abundance and diversity in coral reef environments (e.g. Lindeman & Snyder 1999, Nagelkerken et al. 2000b, Russ et al. 2005). An important distinction between visual surveys and other methods is that the former does not capture fishes, and thus is advantageous for studying threatened or endangered species. Limitations of visual surveys stem from variations in visibility, size- and species-specific responses of fish to those performing the survey, observer experience, recording errors, as well as safety concerns (Cheal & Thompson 1997, Thompson & Mapstone 1997, Ley et al. 1999). While precision varies by methodology (e.g. roving, timed, or belt transect, written or audio recording media), accuracy problems can be reduced by performing observer training and using a limited number of personnel (Bell et al. 1985, Greene & Alevizon 1989, St. John et al. 1990). Visual survey techniques were used far more often in studies conducted in the Americas (Caribbean), than in either Australasia or East Africa, and were absent from South and Southeast Asia and West Africa (Fig. 4b).

Given the above, there is clearly no 'best' method for sampling fishes within mangrove habitats. The optimal method will vary according to study constraints and have bias and precision that should be weighed in accordance with the goals of the project. In studies that focus on analyzing the entire assemblage, the application of multiple gear types has been used with success and is preferred (Blaber et al. 1985). With respect to single gear studies, we agree with Rozas & Minello (1997) that enclosure samplers are superior for quantifying fishes in structurally-complex habitats, especially in turbid waters, and add that visual surveys are particularly useful in clearer waters.

Habitat metrics

An historical summary of abiotic and biotic measures collected aids our present ability to assess the value of mangroves as fish habitat. Unlike experimental studies that benefit from being able to isolate and manipulate specific variables for study, in the field it is difficult to choose appropriate abiotic (habitat) factors to measure since they are often autocorrelated with one another. While the appropriate environmental variables measured in a study should differ depending on the goals of the project and on local conditions, over half of the habitat metrics recorded in the literature database consisted of temperature and salinity measurements, and this trend was observed across all geographic regions (Fig. 5a,b). Certainly temperature is linked to broad spatial patterns in the use of mangroves by fishes, as more fish species are noted from tropical estuaries than from sub-tropical estuaries, and a positive correlation between temperature and overall assemblage

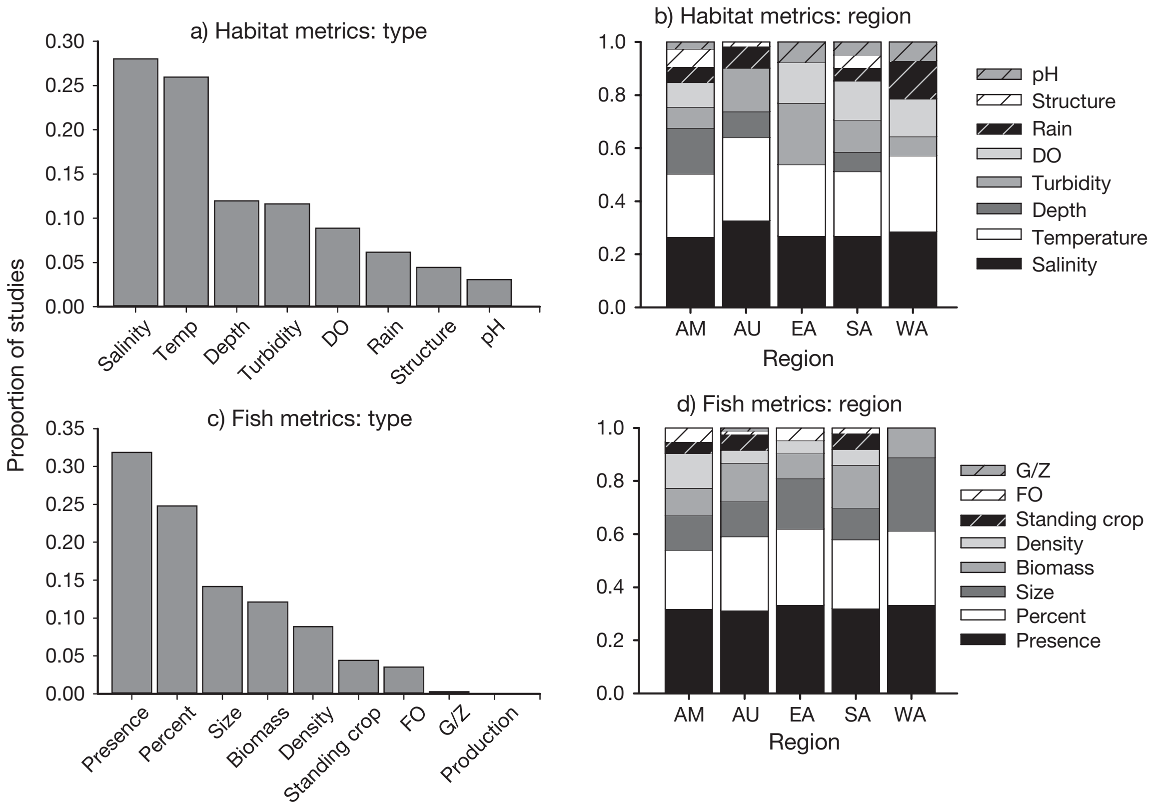

Fig. 5. Summary of (a,b) habitat and (c,d) fish metrics collected from mangroves (a,c) among studies and (b,d) by geographic region. DO: Dissolved oxygen; FO: frequency of occurrence; G/Z: growth and/or mortality estimates; rain: rainfall; temp: temperature. Geographic regions abbreviated as in Fig. 4

richness, diversity, and abundance has been noted by several authors (Robertson & Duke 1987, Williamson et al. 1994, Lin & Shao 1999). While seasonal and diel changes in temperature are typically predictable, changes in salinity within a mangrove habitat can be more dynamic. Salinity can either remain relatively stable throughout the year (e.g. along well-connected oceanic islands), exhibit seasonal changes resulting from fluvial runoff, or change dramatically as a result of anthropogenic freshwater releases (Faunce et al. 2004). In addition, observed fish patterns in mangrove habitats may be correlated with: (1) water depth, where the habitat is temporally inundated (e.g. Robertson & Duke 1990a, Laegdsgaard & Johnson 1995); (2) turbidity, where sediment transport is (a) high (e.g. Blaber 1980) or (b) in areas without large salinity fluxes; and (3) dissolved oxygen in areas with poor water flow or located downstream of large industrial or agricultural areas (e.g. Claro et al. 2001).

Abiotic regime (i.e. mean, range, and stability) may be of more importance in structuring the assemblage of mangrove fishes than 'snapshot' metrics collected at the time of sampling. For example, a negative relationship between environmental stability and species diversity has been well documented outside the literature on mangrove fishes (Connell 1978, Leigh 1990). However, there is scant evidence suggesting such relationships may also hold for fishes inhabiting mangroves (Serafy et al. 2003). Although regime characterization requires that dynamic abiotic variables are measured over longer periods of time than just on the day of fish sampling, few studies in the literature have examined fish-habitat relationships on multiple time scales (Bell et al. 1984, Lorenz 1999, Faunce et al. 2004).

As in the case for temporal scales, examination of multiple spatial scales may be integral to determining which fishes utilize mangrove habitats and why; yet this has also been largely ignored in the literature on mangrove fishes. At the smallest scales, structural complexity may be important, but this was reported in less than 5% of studies. It is likely that few field-based studies measured and reported structural measurements because early attempts failed to find meaningful correlations with fish measures (Sheridan 1992, Mullin 1995). Interestingly, experimental studies have demonstrated that the increased structural complexity of mangroves reduces the efficiency of predators (Primavera 1997, Laegdsgaard & Johnson 2001). At larger scales, many studies have sampled sites located at various distances from features upstream (e.g. fresh water) versus downstream (e.g. coral reefs). However, distance values were reported in less than 10% of studies, and in only 2 instances were they used in analyses with fish metrics (Nagelkerken et al. 2000b, Hajisamae & Chou 2003). Such analyses can be performed readily given the advances in global positioning satellites and geographic information system technology (e.g. Kendall et al. 2003).

Fish metrics

Recently, several fish metrics have been reviewed and ranked according to their usefulness for determining the importance of fish habitats, including mangroves. In 1996, the US government mandated that all stock assessments include EFH provisions and consider 4 levels of information (USDOC 1996). On a habitat-specific basis, these include fish presence-absence (Level 1), densities (Level 2), growth, reproduction, and survival rates (Level 3), and secondary production rates (Level 4). A refined definition of 'nursery habitat' emerged with a paper by Beck et al. (2001). They contend that a nursery habitat contains one or more of the following traits compared to other non-nursery habitats: (1) greater densities of young fishes; (2) lower predation rates; (3) higher growth rates; and (4) more successful migration to subsequent habitats (Beck et al. 2001).

In light of these developments, this literature review can be used to answer the question: What information is available to assess the value of mangroves as fish habitat? Presence/absence information was the most widely reported form of fish data, followed closely by percentage composition (Fig. 5c). These 2 metrics accounted for over half the reported entries (31 and 24%, respectively) and were available from almost all surveys of mangrove fishes that we examined. Size information was less prevalent, and was present most often as part of a description of collected fishes. Only 1 publication presented detailed size information for several species over time (Robertson & Duke 1990b). Biomass information was more prevalent in the literature than either density or standing crop (i.e. numbers and biomass per unit area, respectively), both of which require information about the area sampled (Fig. 5c). Remarkably, frequency of occurrence information (i.e. the proportion of sites or repeated samples that contained at least 1 individual), available from any survey, went unreported in >90% of studies. Density, standing crop, and frequency of occurrence data have not been reported from the West African region (Fig. 5d). Perhaps most limiting to mangrove fish habitat assessment is that only 1 estimate of growth (Robertson & Duke 1990b), and no estimates of habitat-specific mortality or production have appeared in the literature. Because such studies may have been specifically focused on these biological metrics, it is possible that such studies exist outside the realm of this review. Other biotic factors such as larval supply, predation, competition, and food supply are difficult to consistently and reliably measure, and we were unable to find studies that reported these measures in the literature on mangrove fishes.

Data analyses

Having summarized where, when, and how fish data have been collected from mangrove habitats, the ensuing discussion is concerned with what has been done with them. Fish abundances were usually analyzed at one of 3 levels: the entire assemblage, 'dominant taxa' (e.g. the 10 most abundant species grouped), or individual species. A measure of the entire assemblage (e.g. total fish density or biomass) was the most commonly used level of analysis (52%), followed by the analysis of dominant taxa (31.2%) and then individual species abundances (16.8%). As most studies aimed to identify patterns of fish use, analyses were focused on examining temporal and spatial variation (Fig. 6a). Fish–habitat correlations were examined less often, and were completely absent from the West African region. Regardless of the focus, the type of data analysis conducted was typically in the form of simple side-by-side comparisons (Fig. 6b). Similarity indices, ANOVA, and ordination techniques were applied with equal frequency among studies with spatial or temporal emphasis, and less often in studies with a fish-habitat focus; the latter investigation type alone utilized multiple linear regression techniques.

Simple data comparisons dominated the literature. Comparisons of fish data by family (38.1%) predominated, probably because this information is presented in species lists (Fig. 7a). Comparing fish groups according to life-history (maturity) stage or as either residents or transients (residency) was also common (23.7 and 19.5%, respectively). Comparisons according to trophic groups and diel period were among the least reported in the database. The characterization and comparison of fishes according to their trophic level can be a valuable tool for revealing their role in system energy flow. The concept of using such functional groups as a basis for site and ecosystem comparison and evaluation has recently been reviewed for coral reefs (Bellwood et al. 2004) and holds promise for application to mangrove systems as well. Evidence is mounting that mangroves primarily serve as daytime refugia for a major component of fishes

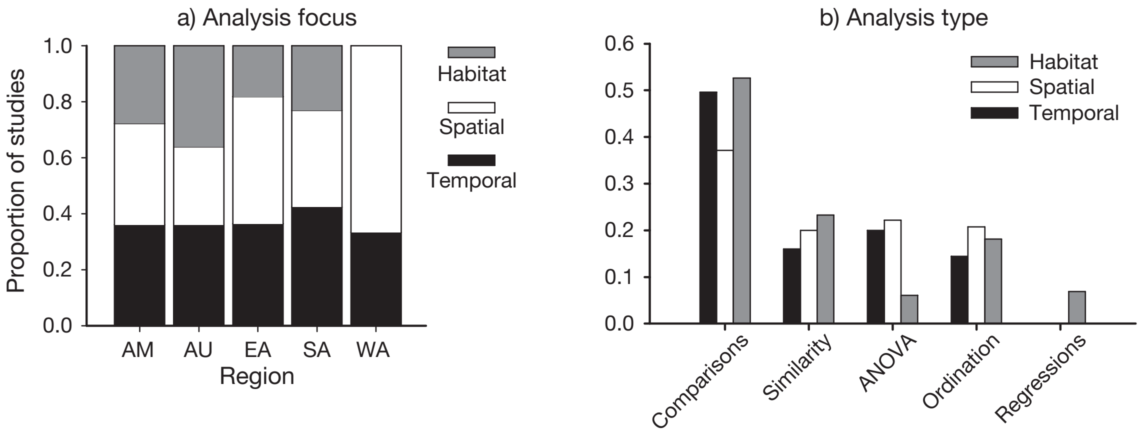

Fig. 6. Data analyses performed within studies of mangrove fishes organized by (a) geographic region and (b) type (i.e. statistical test). Data are organized according to the purpose of analyses: identifying spatial patterns (spatial), identifying temporal patterns (temporal), or exploring fish–habitat interactions (habitat). Non-statistical comparisons of data types (e.g. density) are labeled comparisons. Similarity refers to indices of similarity, diversity, and evenness. Geographic regions abbreviated as in Fig. 4

occupying mangrove shorelines (Rooker & Dennis 1991, Nagelkerken et al. 2000a, Valdés-Muñoz & Mochek 2001). This suggests for some species that fish production attributed to mangroves may not necessarily derive from this habitat alone (Adams et al. 2006). Linkages between mangrove shorelines and the proximity, size, and availability of nocturnal foraging areas, such as seagrass beds or mudflats, deserve greater attention.

SYNOPSIS

This work represents the first attempt to assemble and examine a substantial number of published studies of mangrove fishes. In contrast, previous reviews of the literature on mangrove fishes have been more limited in scope. Thayer & Sheridan (1999) examined the methods and results of less than 12 studies from Florida (USA), while Sheridan & Hays (2003) compiled data from 19 studies that quantified fishes within mangroves and at least one other habitat.

Current limitations

Our review reveals that (1) certain regions, specifically South and Southeast Asia and West Africa, are under-represented in the literature, (2) the majority of surveys were spatially restrictive and/or of short duration, and (3) numerous purported surveys of mangrove fishes failed to sample within mangrove habitats per se. In defense of these studies, most were designed with modest goals in mind: (1) to identify which taxa were present, and (2) to determine their abundances among locations and/or sequential samples. While these studies have been useful in identifying the components and dynamics of various assemblages of mangrove fishes, this type of data provides little information with which to compare and evaluate the

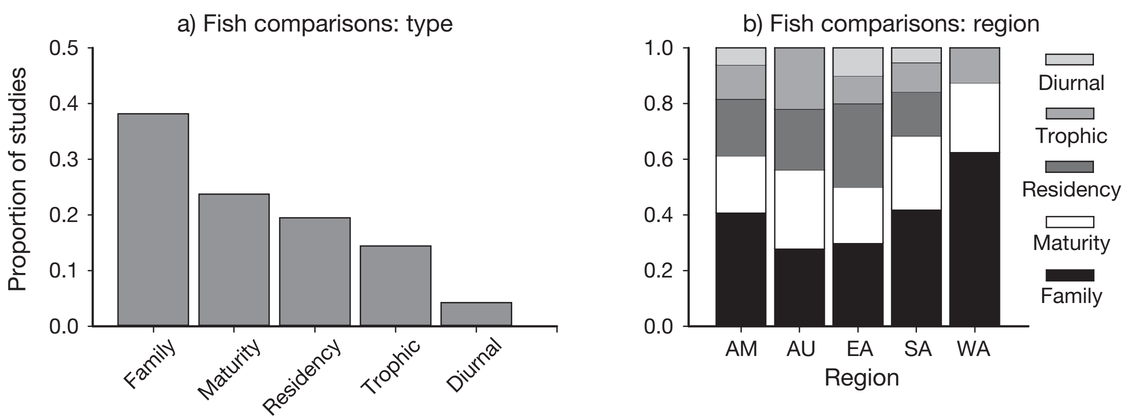

Fig. 7. How fish metrics were grouped for data comparisons (a) among studies, and (b) by geographic region. Geographic regions abbreviated as in Fig. 4

importance of mangrove habitats for ecosystem diversity and productivity.

Where fish–habitat correlations have been examined, most studies performed analyses at the assemblage level using environmental data obtained at the time of sampling. Consequently, there is meagre information on how individual species respond to environmental variability. This is unfortunate, given that recent works suggest that the nature of the relationship between habitat features and fishes is species- and size-specific, and that only with this level of understanding can insight into ecological processes be gained (Benedetti-Cecchi 2003, Cocheret de la Morinière et al. 2004). Furthermore, the type of fish metrics reported did not often include those most desired by decision makers. For example, although simple presence/absence and percentage composition data were commonly reported, size and frequency of occurrence were not, despite the fact that these metrics should be available from any survey that repeatedly samples fishes. The more detailed, difficult-to-collect data needed for mangrove valuation were effectively absent from the database. With possibly 1 exception (i.e. Robertson & Duke 1990b), no study of mangrove fishes recorded adequate numbers over time, numbers at age, size-frequencies, or tag-recapture data needed for the traditional assessment of growth, mortality, or secondary production. As a result, comparisons of EFH or nursery data from studies of mangrove fishes will likely be limited to density or biomass values only. If the USDOC (1996) or Beck et al. (2001) definitions of these terms are to be used to assess the habitat value of mangroves, future efforts must strive to track cohorts of fish over space and time.

Among the most significant conclusions to draw from this review is that surveys of mangrove fishes are not readily comparable. Hence, the findings of any new study may be either bolstered or refuted using selected references from the relevant literature. For example, findings are mixed in studies relating habitat features to assemblages of mangrove fishes with respect to water temperature (Wright 1986, Lin & Shao 1999), salinity (Quinn 1980, Ikejima et al. 2003), and turbidity (Little et al. 1988b, Kimani et al. 1996). Different conclusions regarding the fish assemblage may be reached even when 2 studies have been conducted within the same body of water. For example, Williamson et al. (1994), who sampled with 8 mm mesh beach seine in Raby Bay, Australia, reported, 'the majority of fish captures were either small species or juveniles', while Moreton (1990) — who sampled with 18 mm mesh seines and 100 to 150 mm mesh gill nets — stated, 'most species .... were present as both juveniles and adults' and 'standing-crop estimates for the fishes occurring within the mangroves were amongst the highest recorded values for estuarine areas'.

Future directions

The limitations above are important to consider when planning future studies. Given the history of the literature, it appears likely that future studies will continue to examine its spatio-temporal patterns of mangrove use by fishes. In general, studies that examine fish and habitat features at multiple spatial and temporal scales will be more valuable than those that examine at only one scale. Irrespective of scale, studies that examine both the mean and variance of abiotic and biotic metrics will provide more insight than those that only consider 'static' measures at the time of sampling. Power analysis and/or sampling efficiency evaluation are exceedingly rare in the literature, but are needed for mangrove fishes research to gain the attention it deserves (Ley et al. 1999). It is possible that statistical treatments such as these have been lacking in the literature partly because, at the species-specific level, 'zero-laden' fish abundance datasets are typical and less than desirable for traditional statistical treatments. However, the problem of rarity is widespread in ecological studies (Gaston 1994), including those on coral reef fishes (Jones et al. 2002). Researchers examining species-specific fish abundance data will benefit from the work of Aitchison (1955), Pennington (1983), Lo et al. (1992) and Johnson et al. (1999).

Several scientists are moving the study of mangrove fishes beyond pattern recognition towards more ecologically meaningful landscape-scale approaches, including habitat connectivity, suitability, and the contribution of mangrove habitats in support of adult fish populations (e.g. Pittman et al. 2004, Sheaves 2005, Mumby 2006). However, the need for species- and life-stage-specific information on growth, mortality, and secondary production rates remains. Although sufficient age–length, biomass and size-distribution data exist for several species to generate habitat-specific production estimates, this step has yet to be taken for mangrove fishes. Attaining accurate home ranges and movement rates for mangrove fishes represents an additional and significant challenge towards linking juvenile and adult stocks. Studies that examine habitat quality and availability are also needed to determine what makes some mangroves more important fish habitats than others.

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