Why Are Lionfishes (*Pterois*, Scorpaenidae) So Rare In Their Native Ranges?

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ABSTRACT

Rarity in tropical and subtropical coral reef fishes is an important ecological and biogeographical concept that has received little attention until recently. These studies have emphasized the relative lack of information about the processes that limit the distributions or abundances of rare species. This lack of information extends even to assumptions about ecological processes acting upon life history traits that may vary significantly from what might be seen in common species. Lionfishes (genus *Pterois*, family Scorpaenidae) of the Indo-West Pacific region are typically uncommon or rare throughout most of their native ranges. Two species, however, *Pterois volitans* and *P. miles*, both invasive species in the Caribbean and Gulf of Mexico, are anything but rare. Since their introduction to the western Atlantic region, both species, but especially *P. volitans*, have exploded in terms of patterns of distribution, colonization rates, and abundance. Shifts in the behavior of these lionfishes are apparent, as well, and the success of these invasive species is causing major negative impacts already. How and why these species have become successful within the western Atlantic is the subject of considerable research. The how and why of their rarity within their native ranges has drawn less attention. In this paper, we present the preliminary results of various surveys conducted within the western and central Pacific over the last thirty years in an attempt to understand patterns of lionfish (*P. volitans*, *P. antennata*, and *P. radiata*) abundance, distribution, habitat association and behavior.

KEY WORDS: Abundance, behavior, distribution patterns, habitat use, life history, species range

Por qué los Peces León (*Pterois*, Scorpaenidae) Son Tan Raros en Sus Rangos Nativos?

La rareza en los peces arrecifales de las zonas tropicales y subtropicales es un importante concepto ecológico y biogeográfico que ha recibido poca atención hasta hace poco tiempo. Estos estudios han resaltado la falta de información acerca de los procesos que limitan la distribución y la abundancia de las especies raras. Esta falta de información se extiende incluso a las suposiciones sobre los procesos ecológicos que actúan sobre las características de la historia de vida que pueden variar perceptiblemente con respecto a las características de una especie común. El pez león (género *Pterois*, familia Scorpaenidae) de la región del Pacífico Indico Occidental es típicamente poco frecuente o raro a lo largo de la mayor parte de su distribución natural. Dos especies, sin embargo, *Pterois volitans* y *P. miles*, ambas especies invasoras en el Caribe y el golfo de México, son todo menos raras. Desde su introducción a la región atlántica occidental, ambas especies, pero especialmente *P. volitans*, han estallado en términos de sus patrones de distribución, sus tazas de colonización y de abundancia. Los cambios en el comportamiento de estos peces son evidentes, y el éxito de estas especies invasoras ya está causando impactos negativos importantes. Cómo y por qué estas especies han sido tan exitosas en el Atlántico occidental es un tema que ha sido objeto de numerosas investigaciones. Sin embargo, el cómo y por qué de su rareza dentro de sus rangos naturales, ha recibido menos atención. En este trabajo presentamos los resultados preliminares de los muestreos conducidos en el Pacífico occidental y central durante los últimos treinta años en un intento por entender los patrones de distribución, asociación con el hábitat, abundancia y comportamiento del pez león (*P. volitans, P. antennata,* y *P. radiata*).

PALABRAS CLAVE: Abundancia, comportamiento, patrones de distribución, uso del hábitat, historia de la vida, rango de la especie

Pourquoi les Poissons Lions (*Pterois*, Scorpaenidae) Sont-ils Assez Rare dans Leurs Aires de Répartition?

La rareté des poisons coralliens tropicaux et subtropicaux est un concept écologique et biogéographique important qui n'a pas retenu l'attention jusqu'à récemment. Ces études ont souligné le manque relatif d'information sur les processus qui limitent la distribution et l'abondance des espèces rares. Ce manque d'information s'applique même aux hypothèses liant les processus écologiques aux traits d'histoire de vie et qui pourraient varier significativement de ce qui est observable pour les espèces communes. Les poissons lions (genre *Pterois*, famille des Scorpaeniae) de la région Indo-Pacifique Ouest sont peu communs ou rares dans toutes leurs aires de répartition natives. Cependant, deux espèces, *Pterois volitans* et *P. miles*, qui sont des espèces envahissantes aux Caraïbes et dans le Golfe du Mexique, sont loin d'être rares. Depuis leur introduction dans la région Atlantique Ouest, les deux espèces, et en particulier *P. volitans*, ont explosé en termes de dispersion, de vitesse de colonisation, et d'abondance. Des modifications de comportement de ces poissons lions sont également observées, et le succès de ces espèces envahissantes est déjà la cause d'impacts négatifs importants. Comment et pourquoi ces espèces ont réussi dans l'Atlantique Ouest est sujet de recherches considérables. Comment et pourquoi ils sont rares dans leurs aires de répartition natives a attiré moins d'attention. Dans cet article nous présentons les résultats préliminaires de plusieurs études qui ont été réalisées dans le Pacifique Ouest et Central durant les trente dernières années afin de tenter d'expliquer les aires de distribution, l'abondance, la relation avec leur habitat et le comportement des poissons lions (*P. volitans*, *P. antennata*, and *P. radiata*).

MOT CLÉS: L'abondance, les aires de distribution, le comportement, traitement du habitat, traits d'histoire de vie , répartition des espèces

INTRODUCTION

Two species of lionfishes, *Pterois volitans* and *P. miles* (Scorpaenidae) are successful invaders of the western Atlantic following their relatively recent introductions into the region. Both species have established populations along the southeastern coast of the United States as far north as North Carolina, and individuals have been observed or collected seasonally as far north as New York (Courtenay 1995,Whitfield et al. 2002, 2007, Meister et al. 2005, Ruiz-Carus et al. 2006), while *P. volitans* has been found in the Bahamas, Bermuda, Cuba, the Gulf of Mexico, and in the Caribbean as far west as Belize and the Yucatan, and south as Venezuela (Semmens et al. 2004, Snyder and Burgess 2007, Morris et al. 2008, Lasso-Acalá and Posada 2010). The rapid dispersal of both species within their respective invasive ranges is impressive as are their abundances at certain localities (Whitfield et al. 2007, Green and Côté 2009), with *P. miles* believed to be less common than *P. volitans* (Hamner et al. 2007), while populations of the latter species have exploded to seemingly "biblical" proportions in the Bahamas and elsewhere in the region. This pattern of abundance contrasts sharply with what little is known about lionfish distribution and abundance patterns within their native ranges. There, these showy and easily identified fishes are seemingly uncommon or rare, perhaps because of their behavior. Individuals often shelter in holes or under structure during daylight hours but become more active as sunset and nighttime approach (Myers 1999), yet intensive directed searches for them in habitats with these characteristics often fail to detect these species. So, perhaps they are uncommon or even rare variously within their respective ranges.

Rarity has two expressions: low abundance and restricted geographic range (Gaston 1994, 1998). Rarity may be caused by one or more of the following factors that include relationships between body size and range size or abundance, specialized habitat requirements and resource availability, environmental adaptations resulting from range size variability at higher latitudes, poor ability to exploit marginal habitat or other resources, poor mobility, low reproductive effort and poor recruitment (Gaston 1994, Jones et al. 2002). To confound matters further, sampling of rare species is often difficult because they are cryptic, are at low densities, or because sampling methodologies are inadequate or inappropriate (Andrew and Mapstone 1987, Jones et al. 2002). Tropical and subtropical scorpionfishes (Scorpaenidae and Synanceiidae) have life history traits that include a high degree of habitat specificity in many species, strong site fidelity because of poor mobility of adults or behavioral patterns, such as ambush or stealthy -hunting behavior, and long larval life but possible poor recruitment. How these might contribute towards rarity remains to be examined in great detail (Donaldson Unpubl. data).

Here, we focus upon abundance of three species of *Pterois* found in tropical, subtropical and warm temperate inshore habitats within the western and central Pacific, and present preliminary results of a meta-analysis of three types of survey data. This analysis is meant to provide a baseline for comparisons between their native and invasive ranges.

METHODS

Underwater visual survey data from various localities in the western and central Pacific were extracted from published accounts, technical and environment reports, or unpublished data sets of the authors and are representative of effort conducted over the last 30 years (Table 1). Survey methods included the use of belt transects, timed-swim transects, and GPS timed-swim transects (P.L. Colin and T.J. Donaldson Unpubl. manuscript). The latter two methods allow for more intensive searches within complex habitats, but such searches may not have been employed. Most of these surveys were conducted during daylight hours, although some were made just prior to sunset or in darkness. Here, no effort was made to standardize transect lengths for each of these three sampling methods. Rather, we chose to illustrate qualitatively how effective each might be in detecting lionfishes while deferring a more quantitative analysis until later (Donaldson In prep.). Data examined here include locality, species identity, and abundance. Observations of behavior used to characterize habitat use, foraging, and social group structure are summarized here but will be addressed in more detail elsewhere (Donaldson In prep.).

RESULTS

Data from 1,156 transects (Table 2), including 685 belt, 392 timed-swim, and 79 GPS timed-swim transects (Table 3) indicate that lionfishes are seen rarely in their native ranges, at least during daylight hours when the majority of the surveys examine here were conducted. *Pterois volitans* (n = 53) and *P. antennata* (n = 51) were seen most commonly compared to *P. radiata* (n = 11). *Pterois volitans* was recorded from a variety of habitats, ranging from structurally- complex coral reefs to boulder fields on coral pavement, patch reefs and coral bommies, sand and rubble flats, and large structures or man-made debris. Although observed singly at many localities, at five survey sites on Guam individuals were observed in small social groups that shared shelter, such as coral pillars, holes and artificial structures. Repeated visits to three of these sites during the course of other studies found the same patterns of sociality and shelter use. At one of these sites, a large anchor block (ca. 8 m^2) with a mooring line and buoy, all overgrown heavily with algae and set at a 25 m depth upon a sand-silt flat within Cocos Lagoon, five *P. volitans* were resident. Individuals there were observed hunting prawn-associated gobies (Gobiidae) on the adjacent lagoon floor when not resting at the block or hunting damselfishes (Pomacentridae) that were very abundant there. The smaller *Pterois antennata* and *P. radiata* were reported from a narrower range of habitats, however, with *P.*

antennata occurring amongst corals, often in more protected habitats, while *P. radiata* occurring under rocks and in holes in hard coral pavement in exposed reef bench and lower spur and groove habitats. Pairs of *P. antennata* were found at two sites on Guam and one at Tulamben, Bali (Indonesia), while *P. radiata* were always observed singly.

A preliminary comparison of abundance for each survey method (Table 4) indicates that belt transects accounted for the most observations of all lionfish species (n = 62), compared to timed - swim (n = 40) and GPS timed-swim (n = 13) transects, but proportionally (number of lionfishes observed/number of transects x 100%) lionfishes were found on 16.5% of GPS timed-swim transects compared to 10.2% on timed-swim and 9.1% on belt transects.

DISCUSSION

Why are Lionfishes so Rare in Their Native Ranges?

The results of this preliminary study indicate that three species of lionfishes are relatively rare at various localities and habitats surveyed within the western and central Pacific. In an attempt to explain these patterns, or at least suggest where further study is needed, we now examine causal factors of rarity as they might relate to lionfishes. These include sampling artifacts, the relationship between body size, range size and abundance, poor mobility, specialized habitat requirements and resource availability, low reproductive effort, poor recruitment, and predation.

Lionfishes are visually conspicuous on reefs and estimates of their abundance at any given locality or habitat type might be obtained easily provided that they are observed in the open. Lionfishes in their native ranges display cryptic behavioral patterns in habitat use and are most active nocturnally, however. Thus, abundance estimates might be unreliable because sampling methods may be appropriate only for more common species (Andrew and Mapstone 1987). While the low number of encounters with lionfishes on belt, timed-swim and GPS timed-swim transects reported here may be an artifact of sampling during daylight hours, similar sampling artifacts would also be a factor in the western Atlantic yet, both *Pterois volitans* and *P. miles* may be observed easily during daylight hours at localities where they are firmly established (e.g. Whitfield et al. 2007, Green and Côté 2009, Lasso-Acalá and Posada 2010; photograph in Maljković and Van Leeuwen 2008). Therefore, the results given here have utility in establishing patterns of abundance of lionfishes within their native ranges and these may be used in subsequent comparisons with invasive populations in the western Atlantic.

Table 1. Visual survey data from published literature, technical and environmental reports, and unpublished data used in a meta-analysis of lionfish distribution and abundance in the western and central Pacific.

Locality	Source
Guam, Mariana Islands	Jones et al. (1974), Amesbury et al. (1977b, 1993, 1995,), Chernin et al. (1977), Eldredge (1979), Tsuda and Donaldson (2004), Tsuda et al. (2004), (2004), Tsuda *et al.* (2004), Wilkins et al. (2004), Smith *et al*. (2005a, 2009, 2010), Donaldson and Rongo (2006), Donaldson *et al*. (2010), Donaldson (Unpublished data), this paper
Northern Mariana Islands (limestone) (Rota, Saipan and Tinian)	Doty and Marsh (1977), Amesbury *et al*. (1979), Randall *et al*. (1988), Smith et al. (1989)
Northern Mariana Islands (volcanic)	Eldredge et al. (1977)
Palau Islands	Birkeland et al. (1976), Randall et al. (1978), Maragos et al. (1994), Donaldson (1996, 2002, Unpublished data)
Southwest Palau Islands	Donaldson (1996, Unpublished data)
Yap-Ulithi, Federated States of Micronesia (FSM)	Amesbury et al. (1975, 1977a), Tsuda (1978), Tsuda et al. (1978), Orcutt et al. (1989)
Chuuk (Truk), FSM	Tsuda et al. (1975), Amesbury et al. (1977c, 1978, 1982)
Pohnpei (Ponape), FSM	Tsuda et al. (1974), Smith et al. (2005)
Kosrae, FSM	Eldredge et al. (1977), U.S. Army Corps of Engineers (1989), Donaldson and Maragos (2007)
Kwajalein Atoll, Marshall Islands	Jones and Randall (1973)
Majuro Atoll, Marshall Islands	Amesbury et al. (1975)
Christmas Island, Line Islands, Kirabati	Donaldson (Unpublished data)
Canton Atoll	Grovhoug and Henderson (1978)
American Samoa (Tutuilla, Manu'a Is., Rose Atoll, Swains Reef)	Birkeland et al. (1987), Donaldson (Unpublished data)
Santa Isabella, Solomon Islands	Donaldson (Unpublished data)
Russell Islands, Solomon Islands	Donaldson (Unpublished data)
Tablas and Boracay Is., Visayas, Philippines	Donaldson (Unpublished data)
Tulamben, Bali, Indonesia	Donaldson (Unpublished data)
Pulao Mejagan, Bali, Indonesia	Donaldson (Unpublished data)
Maumere, Flores, Indonesia	Ulbicki, M. (1996)

Table 2. Visual survey effort at selected western and central Pacific localities (n = 1,156 transects).

Locality	Transect type and number			
	Belt	Timed Swim	GPS Timed Swim	Total
Guam, Mariana Islands	259	19	35	313
Northern Mariana Islands (limestone)	47	0	0	47
Northern Mariana Islands (volcanic)	0	14	0	14
Palau Islands	37	74	29	140
Southwest Palau Islands	0	135	0	135
Yap-Ulithi, FSM	29	52	0	81
Chuuk (Truk), FSM	52	0	0	52
Pohnpei (Ponape), FSM	20	1	0	21
Kosrae, FSM	69	56	0	125
Kwajalein Atoll, Marshall Islands	7	0	0	7
Majuro Atoll, Marshall Islands	3	0	0	3
Christmas Island, Line Islands, Kiribati	21	3	0	24
Canton Atoll	2	0	0	2
American Samoa	33	0	0	133
Santa Isabella, Solomon Islands	0	21	0	21
Russell Islands, Solomon Islands	0	9	0	9
Tablas and Boracay Is., Visayas, Philippines	0	0	15	15
Bali, Indonesia	0	8	0	8
Maumere, Flores, Indonesia	6	0	0	6
Total	685	392	79	1,156

Table 3. Lionfishes (*Pterois* spp) observed on visual survey transects (belt, timed-swim and GPS timed-swim, pooled) at selected western and central Pacific localities (n = 1,156 transects).

Locality	Species		
	P. antennata	*P. radiata*	*P. volitans*
Guam, Mariana Islands	24	10	34
Northern Mariana Islands (limestone)	3	0	0
Northern Mariana Islands (volcanic)	1	0	2
Palau Islands	3	0	5
Southwest Palau Islands	0	1	3
Yap-Ulithi, FSM	0	0	0
Chuuk (Truk), FSM	0	0	1
Pohnpei (Ponape), FSM	0	0	0
Kosrae, FSM	1	0	6
Kwajalein Atoll, Marshall Islands	0	0	0
Majuro Atoll, Marshall Islands	0	0	0
Christmas Island, Line Islands, Kiribati	1	0	1
Canton Atoll	8	0	0
American Samoa	0	0	0
Santa Isabella, Solomon Islands	0	0	0
Russell Islands, Solomon Islands	0	0	0
Tablas and Boracay Is., Visayas, Philippines	1	0	0
Bali, Indonesia	7	0	0
Maumere, Flores, Indonesia	2	0	1
Total	51	11	53

Table 4. Number of lionfishes (*Pterois* spp) observed in visual surveys by transect type at selected western and central Pacific localities (n = 1,156 transects).

Transect type	Species			Total
	P. antennata	*P. radiata*	*P. volitans*	lionfishes
Belt (n = 685)	33	1	28	62
Timed-swim (n = 392)	13	8	19	40
GPS timed-swim (n = 79)	5	2	6	13
Total individuals	51	11	53	115

Among benthic shorefishes, body sizes of lionfishes are relatively modest compared to many moray eels (Muraenidae), groupers (Serranidae), snappers (Lutjanidae), sweetlips (Haemulidae), parrotfishes (Labridae: Scarinae), etc. While the relationship between body size and range size remains to be examined quantitatively, many lionfish species enjoy broad distributions within the Indo-West Pacific region (Myers 1999). The pattern of broad geographic distribution but low abundance at any given locality is consistent for a number of species, particularly predators (e.g. *Cheilinus undulatus*, Labridae; see Sadovy et al. 2003). The relationship between body size and abundance may be highly variable for reef fishes. Species with body sizes comparable to lionfishes, e.g. emperors (Lethrinidae) and smaller groupers (Serranidae), both predatory species, may be highly abundant compared to lionfishes within their native ranges (Donaldson Unpubl. data). Thus, body size may not explain rarity of the latter fishes.

Adult lionfishes might have poor mobility within their native ranges where extremely deep water may often separate even neighboring islands from one another, but their larvae are not limited in their ability to disperse. Scorpionfish larvae display morphological adaptations and life history specializations that promote dispersal via ocean currents (Leis and Carson-Ewart 2000). Thus, lionfishes have the capacity to disperse widely as larvae within their native ranges and this need not limit their abundance at any given locality.

While the three lionfish species examined here show some variation between species in habitat preference, these habitats are not specialized and their appears to be no great limitation upon their availability. (Donaldson Unpubl. data). *Pterois volitans* appears to be especially variable in its use of habitat.

Low reproductive effort might limit abundances of lionfishes within their native ranges but more studies are needed.

Recruitment dynamics of lionfishes in their native range are not well known but it is possible to speculate upon the existence of mechanisms that might also regulate recruitment. These include the existence of highly specific habitat or microhabitat types that favor recruitment but is in short supply, or more likely, stochastic effects that prevent larvae from settling out. Both the Pacific and Indian ocean basins are extremely large in area compared to the western Atlantic, and while currents may carry larvae between localities, the distribution of suitable sites for recruitment may be dispersed enough to prevent high levels of recruitment at any given locality (especially "oceanic" islands).

Predation rates upon lionfishes might limit their abundance within their native ranges. Relatively few predators of lionfishes have been identified, however, and data are largely lacking from both their native and invasive ranges. Predation upon lionfish adults and larger juveniles has been reported for groupers in the Caribbean (Serranidae: Epinephelinae; Maljković and Van Leeuwen 2008), and moray eels (Muraenidae; Rogers and Donaldson Unpubl. manuscript). We are unaware of descriptions of predation upon larvae and small juveniles (ca. < 10 mm TL) in their native ranges. Predation upon larvae and small juveniles doubtless occurs, however, and this might contribute significantly to recruitment limitation.

Why are Lionfishes so Successful and Common in the Western Atlantic?

With respect to the tropical, subtropical and warm temperate western Atlantic, it might be more useful to examine those factors that might promote rapid population growth and distribution, behavioral and ecological differences, and plasticity in life history traits. Given that many of the factors that could limit lionfish abundance and promote rarity in the Indo- West Pacific are likely to operate in the western Atlantic, three factors draw our immediate attention: mobility, reproductive effort and success, and predation.

Adult lionfishes appear to have remarkable mobility in shallow waters of the western Atlantic and seem successful at moving between localities. Disturbingly, observations made from submersibles of lionfishes swimming at depths greater than 300 m (e.g. Meister et al. 2005, Whitfield *et* al. 2007) suggest that deeper waters along the continental shelves of both North and South America will not be a barrier to their dispersal. Larval lionfishes are able to cross deep oceanic barriers, just as in the Indo-West Pacific, but relatively few of these exist within the western Atlantic compared to the Indo-West Pacific. From a regional perspective, the degree of connectivity between localities within the western Atlantic is likely greater than that throughout much of their native ranges, thus promoting greater dispersal and rates of dispersal, and in turn higher levels of recruitment and greater abundances locally.

Reproductive effort of lionfishes within their native ranges might be limited by various intrinsic life history traits operating in relation to certain extrinsic factors, but low local population abundances at any given locality could certainly limit opportunities to reproduce often and successfully. Courtship and spawning has been described for *P. volitans* and *P. radiata* (Fishelson 1975, see Thresher 1984), but reproductive effort has not been quantified nor related to population size within their native ranges. In contrast, higher abundance levels at localities within the western Atlantic would promote increased social interaction between individuals, and thus increased opportunities to mate. Increased mating opportunities could promote increased recruitment locally but also regionally if connectivity between localities is high and rates of recruitment are high as well.

Finally, some effort has been directed towards determination of what preys upon lionfishes and focus has been directed towards larger predators such as groupers (Maljković and Van Leeuwen 2008). We suggest that most predation upon lionfishes, when it occurs, will be upon larval and post-larval fish once potential predators emulate their Indo-Pacific counterparts and learn how to prey upon them.

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LITERATURE CITED

Amesbury, S.S., R.T. Tsuda, W.J. Zolan and T.L. Tansay. 1975a. Limited current and underwater biological surveys of proposed sewer outfall sites in the Marshall Island District. Darrit-Uliga-Dalap Area, Majuro Atoll. University of Guam Marine Laboratory Technical Report No. 23. 30 pp.

Amesbury, S.S., R.T. Tsuda, R.H. Randall, C.E. Birkeland, and F.Cushing. 1976. Limited current and underwater biological survey of the Donitsch Island sewer outfall site, Yap, Western Caroline Islands. University of Guam, Marine Laboratory Technical Report No. 24. 30 pp.

Amesbury, S.S., R.T. Tsuda, R.H. Randall, and C.E. Birkeland. 1977a. Marine biological survey of the proposed dock site at Colonia, Yap. University of Guam Marine Laboratory Technical Report No. 35. 22 pp.

Amesbury, S.S., C. Birkeland, M. Chernin, R. Clayshulte, F. Cushing, J. Day, R. Dickinson, J. Eads, L.G. Eldredge, D. Hamel, S. Hedlund, L. Kock, J.A. Marsh, Jr., C. Neubauer, S. Neudecker, R.H. Randall, and R.T. Tsuda. 1977b. Marine environmental baseline report Commercial Port, Apra Harbor, Guam. University of Guam Marine Laboratory Technical Report No. 34. 96 pp.

Amesbury, S.S., J.A. Marsh, Jr., R.H. Randall, and J.O. Stojkovich. 1977c. Limited current and underwater biological survey of proposed Truk tuna fishery complex, Dublon Island, Truk. University of Guam Marine Laboratory Technical No. 36. 49 pp.

Amesbury, S.S. 1978. Studies on the biology of the reef fishes of Guam, Part I: Distribution of fishes on the reef flats of Guam. Part II: Distribution of eggs and larvae of fishes at selected sites on Guam. University of Guam Marine Laboratory Technical Report No. 49. 65 pp.

Amesbury, S.S., R.N. Clayshulte, T.A. Determan, S.E. Hedlund, and J.R. Eads. 1978. Environmental monitoring study of airport runway expansion site, Moen, Truk, Eastern Caroline Islands. Part I: Baseline study. University of Guam Marine Laboratory Technical Report No. 51. 86 pp.

Amesbury, S.S., D.R. Lassuy, R.F. Myers, and V. Tyndzik. 1979. A survey of the fish resources of Saipan Lagoon. University of Guam Marine Laboratory Technical Report No. 52. 85 pp.

Amesbury, S.S., M.W. Colgan, R.F. Myers, R.K. Kropp, and F.A. Cushing. 1981. Biological monitoring study of airport runway expansion site, Moen, Truk, Eastern Caroline Islands Part B: Construction Phase. University of Guam Marine Laboratory Technical Report No. 74. 125 pp.

Amesbury, S.S., R.N. Clayshulte, G.R. Grimm, and G. Plucer-Rosario. 1982. Biological monitoring study of airport runway expansion site, Moen, Truk, Eastern Caroline Islands. University of Guam Marine Laboratory Technical Report 81. 60 pp.

Amesbury, S.S., P.R. Chirichetti, and J. Dutka-Gianelli. 1995. Andersen Air Force Base Marine Resources Preserve: Baseline Study of Marine Resources. University of Guam Marine Laboratory Technical Report No. 102. 165 pp.

Amesbury, S.S., R.T. Tsuda, R.H. Randall, A.M. Kerr, and B.D. Smith. 1993. Biological communities in Tumon Bay, 1977-1991. University of Guam Marine Laboratory Technical Report 99, 70 pp.

Andrew, N.L. and B.D. Mapstone. 1987. Sampling and the description of spatial pattern in marine ecology. *Oceanography and Marine Biology* 25:39-89.

Birkeland, C.E., R.T. Tsuda, R.H. Randall, S.S. Amesbury and F. Cushing. 1976. Limited current and underwater biological surveys of a proposed sewer outfall site on Malakal Island, Palau. University of Guam Marine Laboratory Technical Report No. 25. 59 pp.

Birkeland, C.E., R.H. Randall, R.C. Wass, B. Smith, and S. Wilkins. 1987. Biological resource assessment of the Fagatele Bay National Marine Sanctuary. NOAA Technical Memorandum NOS MEMD, 3, 232 pp.

Donaldson, T.J. 1996. Fishes of the remote Southwest Palau Islands: a zoogeographical perspective. *Pacific Science* **50**:285-308.

Donaldson, T.J. 2002. High islands vs low islands: a comparison of patterns of species richness, diversity and similarity of fishes from the Palau Islands. *Environmental Biology of Fishes* **65**:241-248.

Donaldson, T.J., and T. Rongo. 2006. Coral Reef Investigations at the Guam National Wildlife Refuge, Ritidian Unit. University of Guam Marine Laboratory Technical Report No. 117.vi + 54 pp.

Donaldson, T.J., J.E. Maragos, M. Luckymis, S. Palik, and O. Nedlick. 2007. Coral and fish surveys at Kosrae Island, July-August 2006, Federated States of Micronesia: a Preliminary Report. Report to the Kosrae Conservation and Safety Organization, Kosrae, Federated States of Micronesia. 36 pp.

Donaldson, T.J., B.D. Smith, and L. Chau. 2010. Marine biological survey of Oscar and Papa Wharves, Inner Apra Harbor, Guam. Report to AECOM, Inc., Bloomfield, New Jersey USA. 38 pp.

Doty, J.E. and J.A. Marsh, Jr. 1977. Marine survey of Tanapag Harbor, Saipan: The power barge *Impedance*. University of Guam Marine Laboratory Technical Report No. 33. 147 pp.

Eldredge, L.G., R. Dickinson, and S. Moras. 1977. Marine survey of Agat Bay. University of Guam Marine Laboratory Technical Report No. 31. 251 pp.

Eldredge, L.G. 1979. Marine biological resources within the Guam seashore study area and the War in the Pacific National Historical Park. University of Guam Marine Laboratory Technical Report No. 57. 75 pp.

Eldredge, L.G., B.R. Best, M.I. Chernin, R.K. Kropp, R.F. Myers, and T.L Smalley. 1979. Marine environmental survey of Okat, Kosrae. University of Guam Marine Laboratory Technical Report No. 63. 101 pp.

Eldredge, L.G., R.T. Tsuda, P. Moore, M. Chernin, and S. Neudecker. 1977. A natural history of Maug, Northern Mariana Islands. University of Guam Marine Laboratory Technical Report No. 43. 87 pp.

Fishelson, L. 1975. Ethology and reproduction of the pteroid fishes found in the Gulf of Aqaba (Red Sea), especially *Dendrochirus brachypterus* (Cuvier) (Pteroidae, Teleostei). *Publ. Staz. Zool. Napoli* 39, Supplement: 635-656.

Gaston, K.J. 1994. *Rarity*. Chapman & Hall, London, United Kingdom.

Gaston, K.J. 1998. Rarity as double jeopardy. *Nature (London)* **394**: 229 -230.

Green, S.J. and I.M Côté. 2009. Record densities of Indo-Pacific lionfish on Bahamian coral reefs. *Coral Reefs* **28**:107.

Grovhoug, J.G. and R.S. Henderson. 1978. Distribution of inshore fishes at Canton Atoll. Pages 99-157 in: S.V. Smith and R.S. Henderson, (eds.) *Phoenix Islands Report, 1: An Environmental Survey of Canton Atoll Lagoon 1973*. *Atoll Research Bulletin* **221**.

Jones, G.P., M.J. Caley and P.L. Munday. 2002. Rarity in coral reef fish communities. Pages 81-101 in P.F. Sale (ed.) *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. Academic Press, San Diego, California USA.

Jones, R.S. and R.H. Randall. 1973. Kwajalein missile range: Environmental survey, Meck Island, and North Loi. University of Guam Marine Laboratory Environmental Survey Report no. 9. 40 pp.

Jones, R.S., R.H. Randall, and R.D. Strong. 1974. An investigation of the biological and oceanographic suitability of Toguan Bay, Guam as a potential site for an ocean outfall. University of Guam Marine Laboratory Technical Report No. 11. 97 pp.

Kulbicki, M. 1996. First observations on the fish communities of fringing reefs in the region Maumere (Flores, Indonesia). *Atoll Research Bulletin* **437**:1-21.

Lasso-Acalá, O.M. and J.M. Posada. 2010. Presence of the invasive red lionfish, *Pterois volitans* (Linnaeus, 1758), on the coast of Venezuela, southeastern Caribbean Sea. *Aquatic Invasions* **5**(1): 853-859.

Leis, J.M. and D.S. Rennis. 2000. Scorpaenidae (Scorpionfishes, Stonefishes). Pages 226-235 in: J.M. Leis and B.M. Carson-Ewart (eds.). *The Larvae of Indo-Pacific Coastal Fishes*. Brill, Leiden.

Maljković, A., T.E. Van Leeuwen and S.N. Cove. 2008. Predation on the invasive red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), by native groupers in the Bahamas. *Coral Reefs* **27**: 501.

Maragos, J.E., C. Birkeland, C. Cook, K. Des Rochers, R. Di Rosa, T.J. Donaldson, S.H. Geermans, M. Guilbeaux, H. Hirsh, L. Honigman, N. Idechong, P.S. Lobel, E. Mathews, K.J. McDermid, K.Z. Meier, R. Myers, D. Otobed, R.H. Richmond, B. Smith and R. Smith. 1994. Marine and coastal areas survey of the Main Palau Islands, Part 2: Rapid Ecological Assessment Synthesis Report. Corial, Honolulu and The Nature Conservancy, Honolulu, Hawaii USA. 125 pp.

Meister, H.S., D.M. Wyanski, J.K. Loefer, S.W. Ross, A.M. Quattrini and K.J. Sulak. 2005. Further evidence for the invasion and establishment of *Pterois volitans* (Teleostei: Scorpaenidae) along the Atlantic coast of the United States. *Southeastern Naturalist* **4**:193-206.

Myers, R.F. 1999. *Micronesian Reef Fishes, 3rd ed*. Coral Graphics, Barrigada, Guam, USA.

Myers, R.F. and T.J. Donaldson. 2003. The fishes of the Mariana Islands. *Micronesia* **35-36**: 594-648.

Orcutt, A.M., R. Cordy, P.J. Rappa, and B.D. Smith. 1989. *Yap Proper Coastal Resource Inventory*. Sea Grant Extension Service, University of Hawaii, Honolulu, Hawaii USA. 356 pp.

Randall, R.H., C. Birkeland, S.S. Amesbury, D. Lassuy, and J.R. Eads. 1978. Marine survey of a proposed resort site at Arakabesan Island, Palau. University of Guam Marine Laboratory Technical Report No. 44. 73 pp.

Randall, R.H., S.D. Rogers, E.E. Irish, S.C. Wilkins, B.D. Smith, and S.S. Amesbury. 1988. A marine survey of the Obyan-Naftan reef area, Saipan, Mariana Islands. University of Guam Marine Laboratory Technical Report No. 90. 62 pp.

Ruiz-Carus, R., R.E. Matheson Jr., D.E. Roberts Jr., and P.E. Whitfield. 2006. The western Pacific red lionfish, *Pterois volitans* (Scorpaenidae), in Florida: evidence for reproduction and parasitism in the first exotic marine fish established in state waters. *Biological Conservation* **128**:384-390.

Sadovy, Y., M. Kulbicki, P. Labrosse, Y. Letourner, P. Lokani, and T.J. Donaldson. 2003. The humphead wrasse, *Cheilinus undulatus*, Rüppell 1835 (Labridae): synopsis of a threatened and poorly known species. *Reviews in Fish Biology and Fisheries* **13**:327-364

Semmens, B.X., E. Buhle, A. Salomon and C. Pattengill-Semmens. 2004. A hotspot of non-native marine fishes: evidence for the aquarium trade as an invasion pathway. *Marine Ecology Progress Series* **266**: 239-244.

Smith, B.D., R.H. Randall, S.S. Amesbury, E.E. Irish and C.R. Wylie. 1989. A marine survey of the Apanon coastal environment, Talakhaya area, Rota, Mariana Islands. University of Guam Marine Laboratory Environmental. Survey Report No. 22. 71 pp.

Smith, B.D., S. de C. Wilkins, and T.J. Donaldson. 2005a. Environmental Impact of the Cooling Water Intake Structure, Tanguisson Power Plant, Section 316b Study, Phase I, A Screening Analysis. University of Guam Marine Laboratory Technical Report No. vi + 62 pp.

Smith, B.D., T.J. Donaldson, A. Edward, and A.M. Kerr. 2005b. Marine Biological Survey of Coral Reef Communities at Dekehtik (Takatik) Island for the Proposed Pohnpei Airport Runway Extension Project. University of Guam Marine Laboratory Technical Report No. 115. viii + 131 pp.

Smith, B.D., T.J. Donaldson, T. Schils, A. Reyes, K. Chop, and K. Dugger. 2009. Marine Biological Survey of Inner Apra Harbor, Guam. University of Guam Marine Laboratory Technical Report No. 126. iv + 41 pp.

Smith, B.D., T.J. Donaldson, and L. Chau. 2010. Marine biological surveys of selected sites adjacent to naval lands in Guam, Mariana Islands. Report to AECOM, Inc., Bloomfield, New Jersey USA. 131 pp.

Snyder, D.B. and G.H. Burgess. 2007. The Indo-Pacific red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), new to the Bahamian ichthyofauna. *Coral Reefs* **26**: 175.

Thresher, R.E. 1984. *Reproduction in Reef Fishes*. TFH Publications, Neptune City, New Jersey USA. 399 pp.

Tsuda, R.T. (ed.). 1978. Marine biological survey of Yap lagoon. University of Guam Marine Laboratory Technical Report No. 45. 162 pp.

Tsuda, R.T., R.H. Randall, and J.H. Chase. 1974. Limited current an biological study in the Tuanmokot Channel, Ponape. University of Guam Technical Report No. 15. 58 pp.

Tsuda, R.T., S.S. Amesbury, S.C. Moras and P.P. Eeeman. 1975. Limited current and underwater biological survey at the Point Gabert wastewater outfall on Moen, Truk. University of Guam Technical Report No. 20; 39 pp.

Tsuda, R.T., M.I. Chernin, J.O. Stojkovich, D.R. Lassuy, & B.D. Smith. 1978. Marine environmental studies of selected sewer outfall sites in the Yap Central Islands and on Falalop Island, Ulithi Atoll, Yap Outer Islands. University of Guam Marine Laboratory Technical Report No. 46. 101 pp.

Tsuda, R.T. and T.J. Donaldson. 2004. Cumulative and secondary impacts: Seawalker, ScubaBob and the Fish Eye Underwater Observatory, Piti and Cocos Lagoon, Guam. University of Guam Marine Laboratory Technical. Report 108. x + 85 pp.

Tsuda, R.T., J.L. Holbrook, H.R. Wood, T.J. Donaldson, and B.D. Smith. 2004. Biological and chemical survey of the Lower Pago River, estuary, near-shore reef channel and adjacent reef flat, Pago Bay, Guam. University of Guam Marine Laboratory Technical Report No. 109. 66 pp.

U.S. Army Corps of Engineers. 1989. Kosrae coastal resource inventory. Environmental Resources Section, U.S. Army Engineer District, Honolulu, Hawaii USA. 187 pp.

Whitfield, P.E., T. Gardner, S.P. Vives, M.R. Gilligan, W.R. Courtenay, Jr., G.C. Ray, and J.A. Hare. 2002. Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America. *Marine Ecology Progress S*eries **235**: 289-297.

Whitfield, P.E., J.A. Hare, A.W. David, S.L. Harter, R.C. Munoz and C.M. Addison. 2007. Abundance estimates of the Indo-Pacific lionfish *Pterois volitans*/*miles* complex in the Western North Atlantic. *Biological Invasions* **9**:53-64.

Wilkins, S.DeC., B.D. Smith and T.J. Donaldson. 2004. Environmental impact of the cooling intake structure, Cabras Power Plant Secion 316B study, Phase 1. University of Guam Marine Laboratory Technical Report No. 111. 43 pp.