

Multiple parasite introduction and host management plan: case study of lutjanid fish in the Hawaiian Archipelago

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ABSTRACT: The bluestriped snapper *Lutjanus kasmira* and the blacktail snapper *L. fulvus* were deliberately introduced in the Hawaiian Archipelago from French Polynesia in the late 1950s to enhance local fisheries. These species rapidly spread all over the Windward Islands, became extremely abundant and, therefore, caused controversial environmental concerns. A comparison of the whole metazoan parasite community of *L. kasmira* and *L. fulvus* was performed between their native ranges in French Polynesia (Moorea Island in the Society Archipelago and Ua Huka in the Marquesas Islands) and their introduced range in O'ahu, Hawaii, USA. We suggest that 8 monogenean species have been introduced with *L. kasmira* and *L. fulvus* into the Hawaiian Archipelago from French Polynesia; 2 other species as well as one nematode should be referred to as cryptogenic. Moreover, experimental mortality conducted on monogeneans found in Polynesia emphasizes the inefficiency of anti-parasite treatment which was performed 50 yr ago, explaining possible parasite introduction. Finally, we discuss the potential threat of exotic parasites to the native fish community in the Hawaiian Archipelago and conclude that the absence of co-evolved hosts prevents parasite transfer from non-indigenous to native fishes as monogeneans are highly specific.

KEY WORDS: Parasite community · Non-indigenous species · *Lutjanus* · Hawaii · Polynesia · Copper sulphate

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INTRODUCTION

Coastal estuarine and marine systems are currently among the most heavily invaded systems in the world (Grosholz 2002) and the rate of biological invasions in those ecosystems has substantially increased in recent years (Ruiz et al. 2000). The introduction of non-indigenous animals and plants has been identified by scientists and policy makers as a major threat to biodiversity in marine ecosystems with each successive invasion having unpredictable negative consequences on the environment, economy and society (McNeely

2001, Bax et al. 2003, Pimentel et al. 2005). Ecological studies of exotic species focus primarily on how invaders directly affect particular resident species. In contrast, little is known about the indirect effects of introduced species on native communities in the wild, including how pathogens may be spread by introduced species. Among the less conspicuous effects of introduced species is the presence of accompanying parasites and diseases (e.g. bacteria, viruses, fungi) that can strike local populations and communities (Thomas et al. 1999, Horwitz & Wilcox 2005, Hudson et al. 2006). The threat to native populations from the introduction

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of exotic parasites is well known (Dobson & Foufopoulos 2001, Grosholz 2002, Prenter et al. 2004, Bondad-Reantaso et al. 2005). For example, introduced parasites have decimated naïve host populations in several cases (Anderson & May 1986, Harvell et al. 1999, Hay et al. 2004, Prenter et al. 2004). The best known example among fish is the decimation of the Aral Sea sturgeon *Acipenser nudiventris* by the monogenean *Nitzschia sturionis*. This parasite was accidentally introduced to the Aral Sea with the Caspian Sea sturgeon *Huso huso* in the 1930s (Dogiel & Lutta 1937). However, parasites remain an underestimated component of total biodiversity (Luque & Poulin 2007), usually because of their small size and cryptic way of life. Thus, the introduction of parasites in a new ecosystem is of concern in a conservation context and remains poorly studied in the wild.

The Hawaiian Islands are among the most geographically and hydrographically isolated in the world and, thus, exhibit a unique reef fish assemblage. This isolation has resulted in some major reef fish taxa being totally absent or poorly represented. Further, unlike other islands in the Indo-Pacific, the Hawaiian Islands lack reef fish species that support valuable commercial and recreational fisheries such as shallow-water groupers and snappers (Oda & Parrish 1981, Coleman et al. 2000). Thus, in the late 1950s, the Hawaiian government introduced various reef fishes to the Hawaiian Islands from French Polynesia to enhance local fisheries.

Among the 11 species intentionally introduced from French Polynesia to the Hawaiian Islands (Randall 1987), only 5 became established (Murphy 1960, Oda & Parrish 1981, Randall & Kanayama 1982, Randall 1987, Randall et al. 1993a): the Marquesan sardine *Sardinella marquesensis*, 3 lutjanid species (blacktail snapper *Lutjanus fulvus*, humpback snapper *L. gibbus* and bluespotted snapper *L. kasmira*) and the bluespotted grouper *Cephalopholis argus*. Between 1955 and 1961, 3200 small (<25 cm) *L. kasmira* were transported from the Society Islands (Moorea, 728 individuals) and the Marquesas Islands (Nuku Hiva, 2472 individuals) to Hawaii (O'ahu only) and 2204 small *L. fulvus* were transported from the Society Islands (2021 individuals), the Marquesas Islands (35 individuals), and the Canton Islands (Kiribati, 148 individuals) to Hawaii (O'ahu only). The distinct aspect of this case study compared with others is that the qualitative and quantitative protocol of introduction is known, whereas for most biological invasions, which are usually unintentional and undesired, such information is lacking.

Since their introduction to the Hawaiian Islands in the 1950s, introduced snappers belonging to the genera *Lutjanus* became extremely abundant (Friedlander et al. 2002, Schumacher & Parrish 2005) and have become the focus of considerable attention in the sci-

entific and recreational community because of their possible effect on local marine communities. It has been suggested that the introduced snappers may adversely affect native fish species through competition for spatial and/or dietary resources (Parrish et al. 2000, Schumacher & Parrish 2005). For example, habitat use patterns of the native yellowtail goatfish *Mulloidichthys vanicolensis* (Family: Mullidae) are very similar to those of introduced *L. kasmira* and asymmetrical competition occurs for shelter (Schumacher & Parrish 2005). In addition to the potential direct threat to native reef fish communities in terms of competition and predation, the introduction of non-indigenous fishes could also lead to the introduction of exotic parasites. The compositions of parasite communities are generally influenced by host ecology and phylogeny. Sympatric and phylogenetically related hosts with similar ecologies should have similar parasite communities (Muñoz et al. 2006). Therefore, transfer of parasites between native and introduced hosts usually concerns hosts that are closely related phylogenetically or ecologically. In the Hawaiian waters, parasite transfers may occur between introduced snappers and native Lutjanidae (phylogenetically related species) as well as native Mullidae (ecologically related species), such as the native syntopic *M. vanicolensis*. Despite the potential threat from the spread of exotic parasites, there is limited information on the parasites of introduced snappers in the Hawaiian Islands with the exception of protozoan (Work et al. 2003) and nematode parasites (Font & Rigby 2000).

Before their release in the Hawaiian Islands, these snappers were bathed in copper sulphate (concentration of 0.4 to 0.8 ppm) to remove their parasites (Fujimura 1957–1958, Randall & Kanayama 1982). In the 1950s, copper sulphate was assumed to be an effective anti-parasite treatment, but unfortunately, subsequent studies have shown that it has a relatively poor ability to control infections. In addition, such treatment remains ineffective against internal parasites. Thus, it is suspected that parasites were released in the Hawaiian Islands with the massive introduction of 5404 lutjanids from Polynesia. Here, we compared the parasite communities of *Lutjanus kasmira* and *L. fulvus* in their native range (i.e. the Society and Marquesas islands) to the parasites on these fishes in O'ahu, Hawaii, where these 2 snappers were introduced 50 yr ago. Then we investigated the potential introduction of parasites into the Hawaiian Archipelago and experimentally evaluated the effectiveness of copper sulphate as a means of removing parasites to explain possible parasite introduction. Finally, we investigated the possible transfer of introduced parasites to the abundant native syntopic *Mulloidichthys vanicolensis*.

MATERIALS AND METHODS

Sites and host collection. A total of 446 fish were collected off the north coast of Moorea Island (17° 30' S, 149° 50' W, Society Archipelago, French Polynesia) in 2 sampling events: (1) in February to April 2006 (99 *Lutjanus kasmira* and 77 *L. fulvus*), and (2) in May to July 2007 (132 *L. kasmira* and 138 *L. fulvus*). Additionally, a total of 85 fish (72 *L. kasmira* and 13 *L. fulvus*) were collected from the Marquesas Islands (8° 57' S, 139° 35' W, near Ua Huka, French Polynesia) in March 2007. Fish were collected by means of a spear gun from both the inner and outer reefs at depths ranging from 5 to 40 m. Immediately upon collection, each fish was individually enclosed within a Ziploc plastic bag. This prevented the loss of ectoparasites, particularly those that were not permanently attached (Grutter 1995). Plastic bags were stored on ice in a cooler until the fish were dissected (within 2 to 6 h).

A total of 226 fish were collected from the Hawaiian Islands (21° 17' N, 157° 53' W, south coast of O'ahu) in 2 sampling events: (1) in April 2006 (66 *Lutjanus kasmira* and 32 *L. fulvus*), and (2) April and May 2007 (88 *L. kasmira* and 40 *L. fulvus*). Because of logistical constraints, we hired a local fisher to catch snappers by means of hook and line and fishing net from both the inner and outer reefs at depths ranging from 10 to 60 m. As soon as fish were on the boat each fish was placed in an individual Ziploc plastic bag and stored on ice until dissection. All snappers sampled in Polynesia and Hawaii were sexually mature and their length measurements overlapped throughout all localities. Gills of an additional 153 native *Mulloidichthys vanicolensis* were also purchased at local fish markets in Honolulu in 2006 and 2007.

Parasite collection. Fish were examined for parasites under a dissecting microscope. Monogeneans were fixed on a slide with a drop of ammonium picrate-glycerine (Malmberg 1957) or with a drop of Berlese fluid. Copepods and isopods were fixed in cold ethanol (70%) and nematodes were fixed in hot ethanol (70%). Leeches and cestodes were flattened alive on a slide by applying a cover slip and then fixed. Parasite species with prevalences greater than 50% are referred to as 'common species,' those with prevalences less than 10% are referred to as 'rare species' and those for which fewer than 5 individuals were found are referred to as 'incidental species.'

Experiments. For the copper sulfate exposure experiments, *Lutjanus kasmira* and *L. fulvus* were caught with hook and line off the north coast of Moorea Island. Fish were kept in 300 l saltwater aquaria. The water within all aquaria was aerated using low-flow air stones and filtered through a charcoal filter. Once each week, two-thirds of the water in each aquarium was

replaced with unfiltered water from Oponuhu Bay in Moorea (salinity 32‰). The aquaria were maintained in a room at 23 to 28°C with natural light and water temperature similar to that from the ocean. Frozen mackerel was added twice daily to each aquarium until the fish stopped eating. Each fish species was kept in separate aquaria with a maximum of 13 fish per aquarium. All fish were kept for at least 30 d in aquaria before any experiment to allow the fish to acclimatise and to increase monogenean intensity. In all of the experiments described below, only the 6 most abundant monogenean species were counted: *Diplectanum fusiforme*, *Euryhaliotrema chrysotaeniae*, *E. spirotubiformum*, *Haliotrema longitubocirrus*, *H. patellacirrus* and *H. sp. conf. anguiformis*. Those species have been selected because of their likely introduction to the Hawaiian Archipelago (see 'Discussion') and their high abundance.

In vitro mortality: Ten *Lutjanus fulvus* and 10 *L. kasmira* were killed and the gills extracted. Gills were then placed in Petri dishes and covered with seawater. Monogeneans were removed from the gills with needles under a dissecting microscope. Each monogenean was immediately placed in an individual 1 ml vial that was randomly filled with one of the following: seawater (control), copper sulphate (0.4, 0.8 or 1.6 µg l⁻¹), formalin (75 mg l⁻¹) or freshwater. The concentrations of copper sulphate used correspond to the minimum (0.4 µg l⁻¹), maximum (0.8 µg l⁻¹) and twice the maximum (1.6 µg l⁻¹) concentrations used to treat fish before their introduction to the Hawaiian Islands 50 yr ago (Randall 1960). Freshwater and formalin were not used in the late 1950s, but are used in the present study in a comparative manner.

Every hour all parasites were stimulated with a thin needle and their reaction was observed. Live monogeneans generally tie themselves into knots upon stimulation, whereas inactive monogeneans were assumed to be dead. Each individual that was assumed to be dead for 2 h was fixed on a slide and identified. The experiment continued until all parasites were dead. The experiment was replicated 4 times using 25 monogeneans of each parasite species from each host fish species (i.e. *Lutjanus fulvus* and *L. kasmira*) in each treatment. Thus, there were a total of 200 individuals of each monogenean species in each treatment for a total of 7200 individuals (25 individuals × 6 species × 4 replicates × 6 treatments × 2 hosts).

In vivo mortality: After 30 d in laboratory aquaria, 15 *Lutjanus kasmira* were transferred to a single aquarium with 0.8 ppm copper sulphate solution. The control group of 10 *L. kasmira* was maintained in single seawater aquarium for the same period. After 24 h, all fish were killed and dissected.

Table 1 (continued)

Parasite species	Moorea (2006–2007)			Ua Huka (2007)			O'ahu (2006)			O'ahu (2007)		
	Prevalence (%)	Intensity (mean no. fish ⁻¹ ± SD)	Range	Prevalence (%)	Intensity (mean no. fish ⁻¹ ± SD)	Range	Prevalence (%)	Intensity (mean no. fish ⁻¹ ± SD)	Range	Prevalence (%)	Intensity (mean no. fish ⁻¹ ± SD)	Range
Digenea												
Bivesiculidae	3	1.7 ± 0.8	1–3	8	1.0 ± 0.0	1–1	nd	nd	nd	nd	nd	nd
Hemiuridae												
<i>Lectichoirim aphareii</i>	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.0 ± 0.0	1–1	1–1
Opaeoelidae	16	1.6 ± 0.9	1–4	nd	nd	nd	nd	nd	nd	nd	nd	nd
<i>Hamacreadium mutabile</i>												
Isopods												
Gnathiidae												
<i>Gnathia</i> sp.	1	2.6 ± 0.5	2–3	nd	nd	nd	3	1.0 ± 0.0	1–1	nd	nd	nd
Leeches												
Piscicolidae	nd	nd	nd	8	1.0 ± 0.0	1–1	nd	nd	nd	nd	nd	nd
Monogeneans												
Capsalidae												
<i>Benedenia bodiani</i>	nd	nd	nd	nd	nd	nd	3	1.0 ± 0.0	1–1	nd	nd	nd
<i>Benedenia lutjani</i>	2	1.0 ± 0.0	1–1	nd	nd	nd	nd	nd	nd	nd	nd	nd
Dactylogyridae												
<i>Euryhaliotrema chrysoetaeniae</i>	30	3.6 ± 3.2	1–13	100	20.5 ± 9.7	9–29	65	7.5 ± 6.4	1–25	67	7.7 ± 7.2	2–28
<i>Euryhaliotrem spirotubiforum</i>	35	5.3 ± 5.4	1–23	100	49.0 ± 50.7	5–112	72	14.3 ± 13.4	1–53	70	15.3 ± 24.1	1–62
<i>Haliotrema patellacirrus</i>	37	3.5 ± 3.2	1–15	70	4.7 ± 0.6	4–5	31	2.2 ± 1.6	1–5	30	1.9 ± 1.7	1–4
<i>Haliotrema longitubocirrus</i>	13	2.0 ± 1.3	1–4	100	29.1 ± 42.7	6–93	75	11.8 ± 10.6	1–43	77	10.7 ± 11.3	1–54
<i>Haliotrema</i> sp. conf. <i>anguiformis</i> 22	2.5 ± 2.0	1–8	1–8	100	66.5 ± 41.1	26–112	72	21.1 ± 20.4	1–79	70	22.3 ± 21.1	1–82
<i>Haliotrema</i> sp. 1	nd	nd	nd	nd	nd	nd	9	2.0 ± 1.0	1–3	7	1.0 ± 0.0	1–1
<i>Haliotrema</i> sp. 2	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Diplectanidae												
<i>Diplectanum fusiformis</i>	9	1.2 ± 0.4	1–2	15	1.0 ± 0.0	1–1	22	1.7 ± 1.1	1–3	20	1.8 ± 0.9	1–3
Microcotylidae												
<i>Lutianicola</i> sp.	nd	nd	nd	nd	nd	nd	12	1.2 ± 0.5	1–2	10	2.0 ± 0.0	2–2
<i>Polylabris</i> sp.	1	1.0 ± 0.0	1–1	nd	nd	nd	nd	nd	nd	nd	nd	ndn
Nematodes												
Anisakidae	2	1.0 ± 0.0	1–1	nd	nd	nd	3	2.0 ± 0.0	2–2	ndn	nd	ndn
Camallanidae												
<i>Spirocamallanus istiblenni</i>	2	4.5 ± 2.7	1–5	nd	nd	nd	42	6.2 ± 4.4	1–14	50	6.8 ± 3.9	2–9
(b) <i>Lutjanus kasmira</i>												
Acanthocephala												
Polymorphida	nd	nd	nd	1	1.0 ± 0.0	1–1	nd	nd	nd	nd	nd	nd
Cestodes												
Tetraphyllidea	10	14.5 ± 12.9	1–50	15	9.0 ± 9.1	1–28	5	8.6 ± 4.5	4–13	7	8.7 ± 6.7	2–18
Trypanorhyncha	1	1.0 ± 0.0	1–1	63	8.1 ± 6.2	1–25	nd	nd	nd	nd	nd	nd

N = 88

N = 66

N = 72

N = 231

Table 1 (continued)

Parasite species	Moorea (2006–2007)			Ua Huka (2007)			O'ahu (2006)			O'ahu (2007)		
	Prevalence (%)	Intensity (mean no. fish ⁻¹ ± SD)	Range	Prevalence (%)	Intensity (mean no. fish ⁻¹ ± SD)	Range	Prevalence (%)	Intensity (mean no. fish ⁻¹ ± SD)	Range	Prevalence (%)	Intensity (mean no. fish ⁻¹ ± SD)	Range
Copepods												
Caligidae												
<i>Caligus</i> sp. 1	62	12.1 ± 4.2	1–16	63	2.0 ± 1.3	1–6	nd	nd	nd	nd	nd	nd
<i>Lepeophtheirus</i> sp.	nd	nd	nd	nd	nd	nd	1	2.0 ± 0.0	2–2	4	1.5 ± 0.8	1–3
Hatschekiidae												
<i>Hatschekia</i> sp.	50	7.5 ± 2.6	1–12	nd	nd	nd	nd	nd	nd	nd	nd	nd
Pennellidae	nd	nd	nd	6	1.0 ± 0.0	1–1	nd	nd	nd	2	1.0 ± 0.0	1–1
Digenea												
Cryptogonimidae	nd	nd	nd	9	2.2 ± 0.9	1–3	nd	nd	nd	nd	nd	nd
Opaeoelidae												
<i>Hamacreadium mutabile</i>	5	2.0 ± 0.8	1–3	nd	nd	nd	nd	nd	nd	nd	nd	nd
<i>Opaeoelus</i> sp.	nd	nd	nd	13	1.0 ± 0.0	1–1	nd	nd	nd	nd	nd	nd
Hemiuridae												
<i>Lecithochirium aphaerei</i>	nd	nd	nd	nd	nd	nd	3	1.0 ± 0.0	1–1	5	1.3 ± 0.5	1–2
<i>Lecithochirium</i> sp.	nd	nd	nd	17	1.7 ± 1.2	1–4	nd	nd	nd	nd	nd	nd
Isopods												
Gnathiidae												
<i>Gnathia</i> sp.	3	1.0 ± 0.0	1–1	nd	nd	nd	nd	nd	nd	nd	nd	nd
Leeches												
Piscicolidae												
Monogeneans												
Capsalidae												
<i>Benedenia lujani</i>	2	1.0 ± 0.0	1–1	nd	nd	nd	nd	nd	nd	nd	nd	nd
<i>Benedenia</i> sp.	nd	nd	nd	1	1.0 ± 0.0	1–1	nd	nd	nd	nd	nd	nd
Dactylogyridae												
<i>Euryhalotrema chrysoaeniae</i>	40	2.3 ± 1.6	1–8	71	9.3 ± 9.2	1–43	72	8.8 ± 6.4	1–27	82	9.4 ± 6.3	1–21
<i>Euryhalotrema spirotubiforum</i>	12	1.3 ± 0.6	1–3	95	35.1 ± 53.6	1–294	84	48.5 ± 33.2	1–145	94	47.1 ± 34.2	2–138
<i>Haliotrema patellacirrus</i>	39	2.7 ± 2.5	1–12	91	15.0 ± 14.7	1–67	77	15.1 ± 14.8	1–64	79	17.1 ± 15.6	1–77
<i>Haliotrema longitubocirrus</i>	16	1.5 ± 0.8	1–4	95	23.2 ± 24.4	1–109	92	35.8 ± 21.7	1–154	93	37.6 ± 27.1	3–109
<i>Haliotrema</i> sp. conf. <i>anguiformis</i> 2	nd	1.5 ± 0.7	1–2	4	1.5 ± 0.7	1–2	nd	nd	nd	nd	nd	nd
<i>Haliotrema</i> sp. 1	nd	nd	nd	9	2.3 ± 1.3	1–4	84	20.3 ± 15.8	1–96	93	19.1 ± 13.8	1–58
<i>Haliotrema</i> sp. 2	nd	nd	nd	78	11.4 ± 10.8	1–43	78	25.5 ± 19.6	2–116	86	27.2 ± 21.5	1–111
Diplectanidae												
<i>Diplectanum fusiformis</i>	46	2.4 ± 1.8	1–8	54	7.3 ± 7.0	1–27	47	6.4 ± 3.2	1–12	49	4.8 ± 5.8	1–24
Microcotylidae												
<i>Lutianicola</i> sp.	1	1.0 ± 0.0	1–1	1	1.0 ± 0.0	1–1	1	1.0 ± 0.0	1–1	nd	nd	nd
<i>Polylabris</i> sp.	5	1.8 ± 0.9	1–4	8	1.0 ± 0.0	1–1	3	1.0 ± 0.0	1–1	5	1.7 ± 1.2	1–3
Nematodes												
Amisakidae												
<i>Amisakia</i> sp.	5	1.5 ± 0.75	1–3	28	2.6 ± 0.9	1–4	3	1.0 ± 0.0	1–1	1	4.0 ± 0.0	4–4
Camallanidae												
<i>Spirocamallanus istiblenni</i>	29	1.7 ± 0.9	1–8	52	4.0 ± 2.8	1–12	71	6.5 ± 5.2	1–28	68	6.2 ± 6.0	1–22
Cucullariidae	nd	nd	nd	8	1.0 ± 0.0	1–1	nd	nd	nd	1	1.0 ± 0.0	1–1

Islands. Monogeneans were the most diverse and abundant parasite group found in French Polynesia and belonged to 4 families. In the Society Islands, *L. fulvus* and *L. kasmira* were both infected by 9 monogenean species (5 common species, 1 rare species and 3 incidental species). All monogenean species (except the rare *Benedenia lutjani*) found in the Society Islands were also found in the Marquesas Islands, although 3 additional undescribed species were only found in the Marquesas Islands. Ancyrocephalid and diplectanid monogeneans found in both locations had higher intensities (up to 27 times higher) in the Marquesas Islands.

The parasite communities of fish from the Hawaiian Islands exhibited lower parasite species richness than in French Polynesia. Although some of the monogenean species found were common to both French Polynesia and the Hawaiian Islands, none of the copepod, isopod, leech and digenean species found in French Polynesia were found in the Hawaiian Islands. Despite this difference in the parasite communities, only 3 parasites that were identified to the species level were found exclusively in the Hawaiian Islands: *Lepeophtheirus* sp., *Benedenia bodiani* and *Lecithochirium aphaei*. Although anisakids, gnathiids, pannelids, tetracanthellids (all larvae stages) and cucullariids were found in fishes from both French Polynesia and the Hawaiian Islands (Table 1), these taxa were only identified to family, making the introduction of species from these families undetectable in this study. Nonetheless, 10 monogenean species and the nematode *Spirocamallanus istiblenni* were found in both the Hawaiian Islands and French Polynesia.

Mulloidichthys vanicolensis from Hawaii had a mean (\pm SD) of 85.3 ± 30.2 monogeneans per host. Due to the method used to collect these fish (i.e. fish were purchased at local fish markets and were not individually bagged upon capture), quantitative assessment may be biased low. However, among the more than 13 000 monogenean individuals observed, none corresponded to species found on the 2 introduced snappers. All monogeneans belonged to the family Ancyrocephalidae and were already described by Yamaguti (1968). They were all morphologically distinct from those on *M. vanicolensis* in Moorea.

Experiments

In vitro mortality

When comparing the copper sulphate treatments of 0.4 and 0.8 ppm to the control (seawater), there was no significant effect of replicate or host species but

there was a significant effect of treatment (Table 2). The mortality of 5 ancyrocephalids and 1 diplectanid by treatment is shown in Fig. 1. Although there was a significant effect of copper sulphate on parasite mortality (Table 2), the difference in survival between control (seawater) and copper sulphate at either 0.4 or 0.8 ppm was relatively minor, as shown in Fig. 1. Copper sulphate at 1.6 ppm (double of the maximum concentration used 50 yr ago) cause noticeably higher mortality than at either 0.4 or 0.8 ppm, but was still very low even after several hours. In contrast, formalin and freshwater treatments caused much higher parasite mortalities, as 90% of the monogeneans died after only 2 h (compared with less than 10% after 2 h for copper sulphate at 1.6 ppm).

In vivo mortality

No significant differences were found in mean parasite intensity between treatments with and without copper sulfate for both the total number of monogeneans and each monogenean species (Mann-Whitney *U*-test, $p > 0.5$). For each treatment, all monogeneans species remained on their host with a prevalence of 100% and, thus, monogeneans diversity was equal between treated and untreated fish. While the experimental design consisted of pseudo-replicated data (replicates should consist of several aquaria with or without treatment, not fishes within 2 separately treated aquaria), it nevertheless provided reliable *in vivo* evidence that copper sulphate is ineffective at removing monogeneans.

Cross-infection

While monogenean intensities on *Lutjanus kasmira* and *L. fulvus* increased by more than 15 times (compared with typical intensity in the field) over the 30 d that the fish were maintained in aquaria, none of the monogenean species found on either *L. kasmira* or *L. fulvus* were found on *Mulloidichthys vanicolensis* at the end of the experiment.

Table 2. Results of Cox regression testing for differences in the mortality of 6 monogenean species (see Fig. 1) by treatment (seawater, copper sulphate 0.4 and 0.8 ppm), host species (*Lutjanus fulvus* and *L. kasmira*), and replicate (4 replicates)

	Beta	SE	<i>t</i> -value	Exponent beta	Wald statistics	p-value
Treatment	0.292	0.051	5.682	1.340	32.285	<0.0001
Host species	0.027	0.033	0.800	1.027	0.640	0.42
Replicate	0.013	0.015	0.844	1.013	0.712	0.39

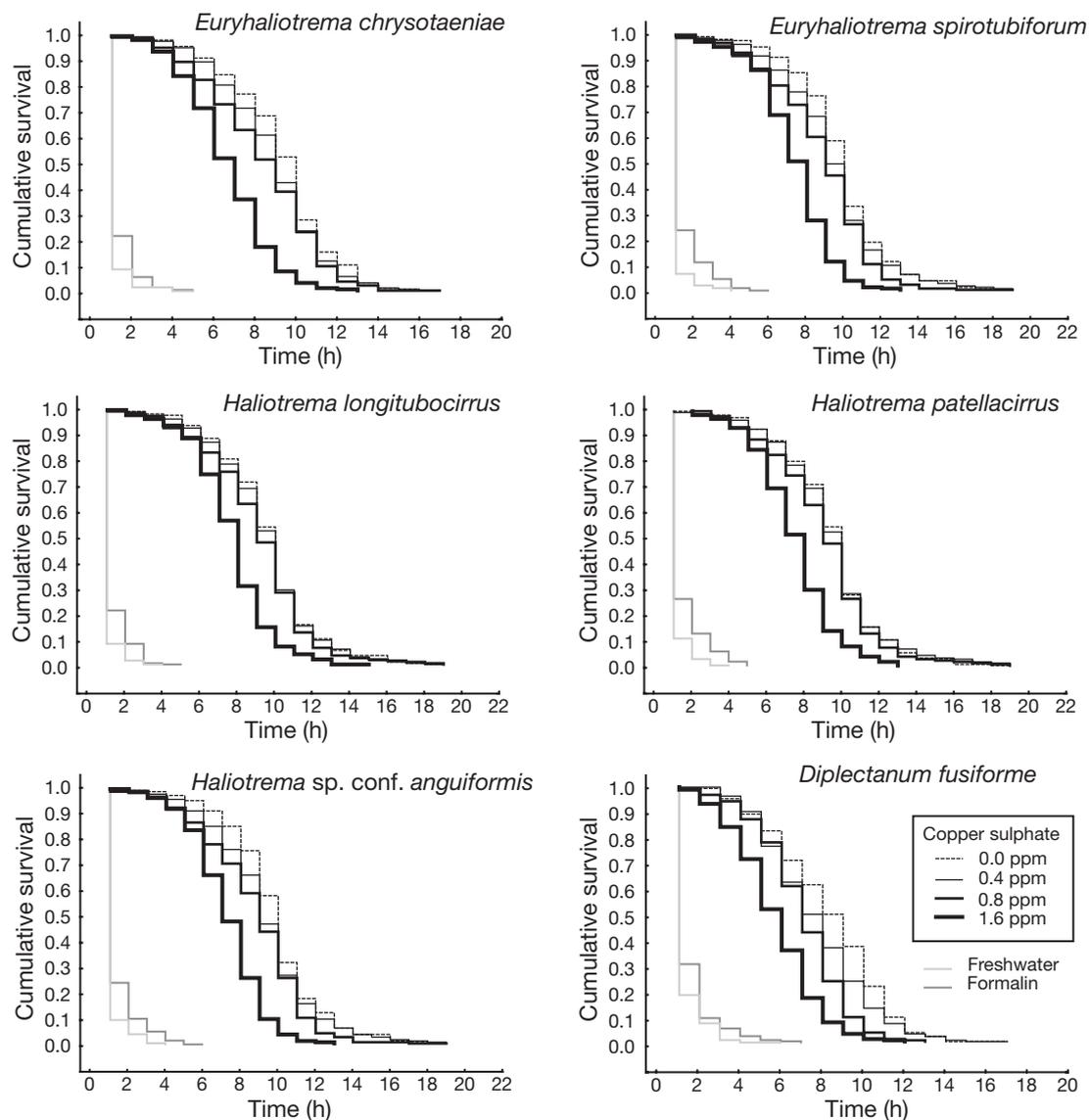


Fig. 1. Cumulative survival curves of 6 monogenean species (5 ancycrocephalids and 1 diplectanid) found in *Lutjanus fulvus* and *L. kasmira*. Six treatments were tested *in vitro*: seawater without copper sulphate and with copper sulphate (0.4, 0.8 and 1.6 ppm), freshwater and formalin (75 mg l^{-1}). A total of 200 parasites were analyzed for each curve (4 equal replicates together)

DISCUSSION

We initially suspected that parasites were released in the Hawaiian Islands with the massive introduction of 5404 lutjanids from Polynesia. The comparison of the whole parasite communities associated with *Lutjanus kasmira* and *L. fulvus* between their native range and their introduced range suggests that (1) most natural parasites were lost, (2) local transfer of parasites from native to introduced fish were scarce, and (3) several parasites were introduced to the Hawaiian Archipelago. Moreover, experimental data confirmed the ineffectiveness of copper sulphate at a concentration of

0.4 to 0.8 ppm as a means of removing parasites, and instead favoured parasite introduction. Finally, a cross-infection experiment and parasitological data supported the hypothesis that the transfer of introduced parasites to the native syntopic *Mulloidichthys vanicolensis* did not occur.

Parasites lost

In the Hawaiian Islands, fish had less diverse parasite communities than in French Polynesia. None of the copepods, isopods, leeches and digeneans found in

Lutjanus kasmira and *L. fulvus* in French Polynesia were introduced with their hosts to the Hawaiian Islands. This loss of parasite species may be due to several factors, including the following: (1) the anti-parasite treatment was applied before introduction (experiments only referred to monogeneans and almost nothing is known about the effectiveness of copper sulfate at 0.4 to 0.8 ppm on other taxa), (2) the lack of appropriate intermediate host species for parasites with complex life cycles, (3) vulnerability to local environmental conditions and predators (e.g. cleaner fish and shrimp) and (4) the inability to maintain a viable population in a low host-density or parasite-density population (see Torchin et al. 2002 for a general discussion).

Parasite transfer from native to introduced fish

The 3 parasite species that were only found on *Lutjanus kasmira* and *L. fulvus* in the Hawaiian Islands (i.e. *Benedenia bodiani*, *Lecithochirium aphareii* and *Lepeophtheirus* sp., Table 1) are assumed to be the result of parasite transfer from native to introduced hosts. Adult *Lepeophtheirus* sp. as well as caligid and penellid larvae generally have low host specificities (Boxshall 1998). Anisakid and tetraphyllidean larvae (which are trophically transmitted) also have low host specificities and may parasitize introduced snappers as paratenic or intermediate hosts. *B. bodiani* is the only native (i.e. species found only in the Hawaiian Islands) capsalid species found on the gills of the introduced snappers in the Hawaiian Islands. Because this species was originally described on the gills of *Bodianus bilunulatus* (Labridae) in the Hawaiian Islands and because only a single individual was found, we suggest that it more probably resulted from a transfer of the parasite occurring in a crowded fishing net. Interestingly, *L. aphareii* has previously been reported in *Aphareus furca* (Lutjanidae) in the Hawaiian Islands (Yamaguti 1970); these fish live in shallower waters than do other deep-bottom snappers (Parrish et al. 2000). Since *L. aphareii* is acquired by its fish hosts through the food that they consume, its presence in *L. fulvus* and *L. kasmira* suggests that these 2 fishes feed (at least occasionally) on the same prey items as *A. furca*, whose diet is unknown at present.

Parasite species that were only found in the Hawaiian Islands had low prevalences (<6%) and intensities (<3 fish⁻¹) in *Lutjanus kasmira* and *L. fulvus* (Table 1). Although introduced hosts were naïve to local parasites, our data suggest that the native parasites have been relatively incapable of infecting the introduced fish species. Thus, the lack of native parasites may have contributed to the successful introduction and

rapid spread of *L. fulvus* and *L. kasmira* in the Hawaiian Islands. It is frequently argued that species are more likely to become invasive when they are released from the pressure of their enemies (i.e. competitors and parasites) in their new territories, as stated by the Enemy Release Hypothesis (Mitchell & Power 2003, Torchin et al. 2003). When introduced organisms are susceptible to native parasites, pressure from their own natural parasite species is generally less important than that from the related indigenous parasite species because hosts may have limited specific defences towards the latter.

Introduction mechanisms

Before their introduction to the Hawaiian Islands in the 1950s, numerous fish were kept in small circular pens in French Polynesia for several weeks (Randall 1960) until they were shipped almost 4500 km on a research vessel. This high density stocking in pens and onboard the boat may have favoured the rapid increase in population density of parasites with a direct life cycle, such as monogeneans (Leong & Wong 1988, Scholz 1999, Johnson et al. 2004, Bondad-Reantaso et al. 2005). After transportation and before their release, potentially heavily infected fish were treated for 19 to 24 h with copper sulphate at a concentration of 0.4 to 0.8 ppm to remove external parasites (Fujimura 1957–1958). Copper sulphate was assumed to be an effective anti-parasite treatment, but unfortunately, subsequent studies have shown that it has a relatively poor ability to control monogenean infections, especially because of their resistant eggs (Thoney 1990, Liang & Leong 1992, Ogawa 1996).

Our experimental results show that copper sulphate was relatively ineffective at killing monogeneans (both ancyrocephalids and diplectanids) that had been removed from their hosts. Although higher concentrations than those used 50 yr ago to treat fish are more effective (e.g. 1.6 ppm resulted in higher mortality in monogeneans separated from their hosts than did 0.4 or 0.8 ppm, Fig. 1), the use of copper sulphate at concentrations known to be effective at killing monogeneans and other parasites is prohibited by the US Food and Drug Administration as these concentrations are also toxic to fish. Copper sulphate is currently used as an algicide only (Hawkins & Griffiths 1987). In contrast, formalin and/or freshwater are much more effective at killing marine monogeneans (Fig. 1) (Fajer-Ávila et al. 2007). If either freshwater or formalin had been used to treat the fish before their release in the Hawaiian Islands, the probability of introducing exotic parasites would have been much reduced. Thus, it is likely that a large number

of parasites (both adults and eggs) were released in the Hawaiian Islands along with their hosts in the 1950s.

Generally, intensity and prevalence increase with host population density (Arneberg et al. 1998). On the other hand, there is also a lower host density threshold below which parasite populations are not able to persist (Lafferty & Kuris 1999, Torchin et al. 2002). After the fish were released in the Hawaiian Islands, host densities were probably relatively low and the host population size was also small. Therefore, any parasite species that were introduced along with their fish hosts may have been vulnerable to the effects of a small host population size; i.e. local extinction for the introduced parasite species could occur. However, fish were introduced to the Hawaiian Islands in large numbers (e.g. 2447 *Lutjanus kasmira* in June 1958), and individuals tended to remain in the area in which they were introduced (Fujimura 1957–1958, Randall 1960). Further, the *L. kasmira* population in the Hawaiian Islands has dramatically increased since its introduction (Oda & Parrish 1981, Randall & Kanayama 1982, Randall et al. 1993b). Such host behaviour and demographic expansion may have favoured the establishment of the exotic monogenean species that were introduced to the Hawaiian Islands with their fish hosts. Moreover, the copper sulphate treatment only affected external parasites, and internal parasites (e.g. the nematode *Spirocamallanus istiblenni*) might have been successfully transported from French Polynesia to the Hawaiian Islands.

Parasite introduction

Our results showed that several monogeneans occurred both in the native and the introduced range of their hosts. However, we are not able to determine whether these parasites were introduced with their fish hosts to the Hawaiian Islands or whether the parasites were already in the Hawaiian Islands at the time the fish were introduced. In the following discussion, we present our hypotheses for several different parasite groups.

Ancyrocephalidae and Diplectanidae

The monogeneans of native reef and shore fishes from the Hawaiian Islands have been relatively well studied, and among the 55 Ancyrocephalinae and the 11 Diplectanidae identified by Yamaguti (1968) none are similar to those found on the introduced species. Observed ancyrocephalids and diplectanids belonging to genera *Euryhaliotrema*, *Haliotrema* and *Diplec-*

tanum have only been reported from lutjanids belonging to the genus *Lutjanus*. No *Lutjanus* spp. naturally occur in the Hawaiian Islands, and lutjanids belonging to the genera *Aphareus*, *Aprion*, *Etelis* and *Pristipomoides* that inhabit deeper water in the Hawaiian Islands have a different parasitofauna that does not include any ancyrocephalids (Yamaguti 1968). Therefore, we suggest that *E. chrysotaeniae*, *E. spiro-tubiformum*, *H. longitubocirrus*, *H. patellacirrus*, *H. conf. anguiformis* and *D. fusiforme* are not native to the Hawaiian Islands. We also suggest that the 2 undescribed ancyrocephalids (*Haliotrema* sp. 1 and sp. 2), which have most of the morphological features that characterise ancyrocephalids from snappers of the genus *Lutjanus* from the China Sea and the Gulf of Mexico (Bychowsky & Nagibina 1971, Zhukov 1976, Kritsky & Boeger 2002), are also non-indigenous in the Hawaiian Islands and have been introduced with Marquesan hosts.

Microcotylidae

The 2 undescribed Microcotylidae found in both French Polynesia and the Hawaiian Islands are morphologically identical, including the fine morphological features of the genitalia and clamps. Given the high degree of host specificity of most microcotylid monogeneans (see Hayward 1996, Yang et al. 2007 for the genus *Polylabris*) and the identical morphologies of both species in French Polynesia and the Hawaiian Islands, it is more likely that these 2 species are non-indigenous in the Hawaiian Islands and have been introduced from French Polynesia. However, in the absence of a formal identification, and because only a few individuals were observed throughout all localities, these 2 monogeneans should be referred to as cryptogenic species sensu Carlton (1996) (i.e. 'a species that is not demonstrably native or introduced').

Spirocamallanus istiblenni

The nematode *Spirocamallanus istiblenni* also needs special consideration. This species was originally described in the Hawaiian Islands (Noble 1966), but occurs in most parts of the Pacific Ocean (Rigby & Font 1997). *S. istiblenni* has been reported in 18 carnivorous fish species of 11 families from 2 orders (Hasegawa et al. 1991, Rigby & Font 1997). Despite its uncertain status in the Hawaiian Islands (i.e. native or introduced) (Font & Rigby 2000), this nematode currently occurs both in French Polynesia and the Hawaiian Islands and parasitises several native fish species,

including Mullidae (*Mulloidichthys* spp. and *Parupeneus* spp.) in the Hawaiian Islands. However, it is not clear whether this species is native to the Hawaiian Islands, is introduced, or may be represented by both native and introduced populations (that may or may not hybridise). Thus, *S. istiblenni* should still be referred to as cryptogenic and further molecular work on this species should be done to provide a more precise answer. Alternately, it may be possible to determine whether this parasite was introduced by examining specimens of native Hawaiian fishes deposited in natural history museums before the Polynesian snapper introduction.

Further, we suggest that 8 monogenean species have been introduced with *Lutjanus kasmira* and *L. fulvus* to the Hawaiian Islands from French Polynesia and this nematode as well as 2 additional monogeneans should be referred to as cryptogenic.

Threat to native communities

Coral reef fish generally become parasitised after recruitment (Rigby & Dufour 1996, Cribb et al. 2000) via the ingestion of prey items that were not consumed during the larval stage or through congeneric contacts, or both. The parasite community of fish species is generally influenced by host ecology and phylogeny. Therefore, sympatric and closely related host species with similar ecologies should have similar parasite communities (Muñoz et al. 2006, 2007). In the Hawaiian Islands, since there are no native snappers of the genus *Lutjanus*, transmission from the introduced species to native other lutjanids (i.e. deep-water snappers) or species with similar ecological relationships are more likely. Therefore, there is some concern that diseases and/or parasites from *L. kasmira* and *L. fulvus* may threaten the existing valuable commercial and recreational handline deep-water snapper (Parrish et al. 2000) and goatfish fisheries. Further, some goatfishes are 'species of greatest conservation need' (Mitchell et al. 2005).

As previously stated, deep-water snappers of the genera *Aphareus*, *Aprion*, *Etelis* and *Pristipomoides* occur in Hawaiian waters. Parrish et al. (2000) stated that *Lutjanus kasmira* is exclusively present at depths significantly shallower than all of the native snappers, except *Pristipomoides filamentosus*, but *L. kasmira* feed near the bottom whereas *P. filamentosus* feed considerably higher up in the water column. Thus, parasite transfer from the introduced snappers to native deep-water lutjanids is highly unlikely, at least for ectoparasites whose mobility is largely determined by their hosts. Moreover, deep-water snappers have a markedly different parasitofauna, excluding

ancyrocephalids, from the snappers found in shallower waters (Yamaguti 1968). In general, the monogeneans species found on deep-sea fishes are largely unrelated to those found on surface-water fishes in the same geographical area (Rohde 1988, 2002). Even though native Hawaiian snappers are not syntopic with introduced snappers and parasite transfer is highly unlikely, we recognize that parasitological data remain to be collected to confirm the absence of such transfer.

Parupeneus multifasciatus, *Mulloidichthys flavolineatus* and *M. vanicolensis* are the most common species of goatfish (Mullidae) on O'ahu. The habitat use patterns of *M. vanicolensis* are very similar to those of *Lutjanus kasmira* (Schumacher & Parrish 2005). In French Polynesia, where species belonging to these 3 genera (i.e. *Lutjanus*, *Mulloidichthys* and *Parupeneus*) naturally occur, *Mulloidichthys* and *Parupeneus* do not have any parasite species in common with *Lutjanus* spp. In the Hawaiian Islands, although these species are all infected with ancyrocephalids belonging to the genus *Haliotrema* (Yamaguti 1968), they have distinct monogenean communities. Ultimately, the introduced diplectanids and ancyrocephalids found on the gills of *Lutjanus* spp. in the Hawaiian Islands appear to be strongly genus-specific, or even species-specific, which fits with the high degree of host specificity that has been observed for monogeneans in general (Sasal et al. 1999, Whittington et al. 2000).

Fortunately, the native snappers and goatfish are both ecologically and phylogenetically distant from the 2 introduced snappers (Allen 1985, Parrish et al. 2000, Schumacher & Parrish 2005). However, some degree of parasite transfer is still possible; e.g. the long-term evolution of the introduced monogeneans may ultimately allow parasite transfer.

Once a pathogen/disease agent or a parasite is introduced and becomes established in the natural environment, there is little or no possibility for eradication of either. Because the introduction of non-native marine organisms is one form of anthropogenic change that can cause irreversible alterations in marine communities, effective management strategies urgently need to be established (Perrings et al. 2005, Schlaepfer et al. 2005, Godwin et al. 2006). These strategies also need to consider the parasites of the introduced non-native marine organisms. Through education and effective management strategies, which include drastic preventive measures (e.g. quarantine, appropriate treatment; Cunningham 1996), the threat of marine invasions can be reduced.

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