

# Host introduction and parasites: a case study on the parasite community of the peacock grouper *Cephalopholis argus* (Serranidae) in the Hawaiian Islands

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**Abstract** The peacock grouper (*Cephalopholis argus*) was intentionally introduced to the Hawaiian coastal waters 50 years ago to enhance the local fisheries. Following introduction, this species spread rapidly and became extremely abundant. A comparison of the metazoan parasite community of *C. argus* was performed between its native range (Moorea Island, French Polynesia) and its introduced range (Oahu and Big Island, Hawaii). Polynesian groupers were infected with a highly diversified parasite community whereas Hawaiian groupers exhibited a depauperate ensemble of parasite species, *C. argus* having lost most of the parasites common in their native range. Interestingly, the grouper has not acquired new parasites present in Hawaiian waters. This study provides the first field evidence of significant parasite release in a wild but previously introduced fish in coral reefs and is discussed in relation to the Enemy-Release Hypothesis which has never been assessed in those ecosystems.

## Introduction

Coastal estuarine and marine systems are currently among the most heavily invaded systems in the world (Grosholz

2002). Historically, they have received less attention than terrestrial and freshwater ecosystems (Grosholz 2002), a fact especially evident in tropical insular systems (Coles and Eldrege 2002). The mechanisms of establishment of nonindigenous species in new ecosystems are widely unknown and present a fundamental challenge to ecologists and evolutionary biologists worldwide. Nevertheless, the idea that parasites may play a role in determining the success of invasion has been proposed (Torchin et al. 2003). It has been frequently argued that species are more likely to become invasive when they are released from the pressure of their natural enemies (i.e., competitors and parasites). Empirical support for this hypothesis (the Enemy-Release Hypothesis, ERH) comes from observations across a broad range of taxa which exhibit, on average, fewer parasites in their introduced range than in their native range (Mitchell and Power 2003; Torchin et al. 2003, respectively, for plants and animals). Several studies have compared parasite load between introduced and native fishes and generally supported the ERH. Data only concern inland freshwater fishes (Kennedy and Pojmanska 1996), Lessepsian migrants (Diamant et al. 1999), ornamental fishes (Kim et al. 2002), reared fishes (Carvajal et al. 1998), and anadromous salmonids (Poulin and Mouillot 2003). However, marine ecosystems are relatively understudied and very few parasitological comparisons have focused on coral reef ecosystems.

In parallel with terrestrial life, marine organisms show a general increase in diversity towards the tropics with coral reefs having the greatest species diversity. Numbers of metazoan parasite species also increase towards the equator both in the Atlantic and Pacific Oceans (Rohde 1984). Although parasite biodiversity in coral reef has not been thoroughly evaluated, data generally show that parasite biodiversity in these ecosystems is very high, reaching

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more than two to ten times the number of fish species (Rohde 1976; Lester and Sewell 1989; Cribb et al. 1994). Main parasite groups (Monogenea, Digenea, Cestoda, Nematoda, Acanthocephala, Copepoda, and Isopoda) appear to be well represented. The trend of increasing species richness in coral reefs is best documented for metazoan parasites of marine fishes (Rohde and Heap 1998). However, no comparative parasitological studies have been carried out for wild-introduced fishes in coral reef ecosystems and yet these ecosystems harbor an extraordinary concentrated diversity of parasites. Thus, introduction of coral reef fish allows opportunity to assess how the ERH could be generalized to ecosystems with highly diversified parasite communities. In such a parasitological context, coral reef fish may not escape from their natural parasites and may not prevent native parasite transfer in their introduced range. This trend is commonly observed in many other ecosystems (Torchin et al. 2002, 2003; Torchin and Mitchell 2004).

The Hawaiian Islands are among the most geographically and hydrographically isolated in the world and exhibit an unusual reef fish assemblage. Their high endemism rate (up to 29% for reef and shore fishes, Randall 1987) makes them particularly vulnerable to biological invasions (Carlton 1987). Because of the lack of highly commercially valuable fish species such as groupers and snappers (Oda and Parrish 1981), the Bureau of Commercial Fisheries of Hawaii developed a program of fish introduction in order to enhance local fisheries in the late 1950s. Among the species introduced intentionally from French Polynesia, only five successfully established in Hawaii (Randall and Kanayama 1982; Randall 1987): The Marquesan sardine (*Sardinella marquesensis*), three lutjanid species (*Lutjanus fulvus*, *Lutjanus gibbus*, and *Lutjanus kasmira*), and a grouper (*Cephalopholis argus*). The peacock grouper (*C. argus*) is a widely distributed grouper (from the Red Sea to South Africa and east to French Polynesia and the Pitcairn group, including northern Australia). Two thousand three hundred eighty-five small individuals (none of them exceeded 25 cm) were transported from Moorea (Society archipelago) to Hawaii (Oahu and the Big Island) in 1956 and 1961. Fish were treated before their release with copper sulfate (concentration of 0.4–0.8 ppm during 19–24 h) in order to remove parasites (Fujimura 1957–1958). The species rapidly spread all over the Windward Islands and became abundant, especially around the Big Island (Randall 1987). The originality of this case study is that the qualitative and quantitative protocol of introduction is known, whereas most biological invasions, being unintentional and undesired, lack such information.

The aim of this work was to compare the whole metazoan parasite community of the introduced peacock grouper (*C. argus*) between its native range (Moorea Island,

French Polynesia) and its introduced range (Oahu and Big Island, Hawaii) where the species was voluntarily introduced 50 years ago. As no fish larger than 25 cm were brought to Hawaii, we sought to estimate the consequences of such a choice in terms of parasite introduction.

## Materials and methods

### Sites and host collection

One hundred sixty-seven fish were caught in March–April 2005. A total of 94 fish were sampled on the north coast of Moorea Island (17° 30' S, 149° 50' W, Society archipelago, French Polynesia), the source of the introduction. Among the 73 Hawaiian fish, 25 were from Kaneohe bay (21° 29' N, 157° 47' W, north coast of Oahu) and 48 were from the west coast of the Big Island (19° 59' N, 155° 50' W), near Puako. All fish were speared on the outside slope of the barrier reef, at a depth ranging between 15 and 30 m. Each fish was individually and immediately enclosed within skimpy plastic bag underwater at the point of capture until dissection. It prevents any loss of ectoparasites, particularly those that are not permanently attached (Grutter 1995).

### Parasite collection

Standard length (SL) and total length (TL) of *C. argus* were measured to the nearest millimeter. Both total (W) and eviscerated weight (We) were measured to the nearest gram. Fulton's condition index (*K*) is believed to be a good indicator of general well-being of a fish (Bolger and Connolly 1989) and was calculated as:

$$K = We / SL^3 \quad (1)$$

$$We = K \cdot SL^3 \quad (2)$$

All of the parts of the fish were examined for parasites under a binocular microscope. Parasites were counted and fixed for identification. Monogeneans were fixed with a drop of ammonium picrate–glycerine mixture on a slide, following the method of Malmberg (1957), or with a drop of Berlese fluid. Copepods and isopods were fixed in cold ethanol (70%) and nematodes in hot ethanol (70%). Leaches and cestodes were observed alive and flattened by coverslip pressure. Parasite identification was carried out according to Rigby and Font (1997), Lo et al. (1998), Whittington et al. (2001), and Chervy (2002). Epidemiological indices (prevalence, abundance, and mean intensity) were used according to Bush et al. (1997). Global

prevalence and global mean intensity referred to prevalence and mean intensity, respectively, based on all parasites species (i.e., irrespective of taxonomic group).

### Experiment

Fish were killed, with gills extracted and placed in seawater; copepods, isopods, and monogeneans (*Caligus* sp. adults, *Caligus* sp. larvae, *Hatschekia* sp., *Gnathia* sp., and *Benedenia* sp., respectively) were delicately removed with needles under stereomicroscope and immediately and randomly placed in individual vials with 15-mL seawater (35‰, control), copper sulfate solutions (0.8 ppm which corresponded to the maximum concentration used 50 years ago), or desalted water (7–10‰). Thus, a total of three treatments were tested and 25 individuals of each species were used per treatment. Every hour, all parasites were stimulated with thin needle and reaction was observed. Inert individuals were considered as dead and then fixed to confirm their specific identification. Experiment continued during 24 h, even if all parasites did not die. A total amount of 375 parasites was therefore analyzed in vitro for mortality.

### Analyses

**Epidemiological analyses** As no fish larger than 25 cm (TL) was brought to Hawaii (Randall and Kanayama 1982), fish were separated in two groups, one with individuals smaller than 25 cm and one with individuals larger than 25 cm. For each parasite taxon, Fisher's exact test and Mann–Whitney *U* test were performed to compare prevalence and mean intensity, respectively, between these two size groups within each locality. A Mann–Whitney *U* test was also conducted between the two groups in order to compare global mean intensity and generic richness (number of parasite genera per fish) within each locality. We used null model analysis to test whether the introduction of 2,385 small (i.e., smaller than 25 cm) or 2,385 large fish (i.e., larger than 25 cm) was different than expected under a null model (under the assumption of randomly translocated fish, irrespective of their size). A Monte Carlo approach was performed by generating populations of 2,385 individuals by randomly selecting individual hosts from Moorea with replacement, irrespective of their size, and the specific number of parasites associated was calculated. This procedure was repeated to yield a distribution of 10,000 populations (null distribution). Moreover, we generated 10,000 populations of 2,385 fish individuals from small and 10,000 populations of 2,385 fish individuals from large individual hosts from Moorea. Finally, we determined the specific probability value of the number of potentially introduced parasites with small or large fish assemblage in the null model distribution. In order to take into account

small interannual fluctuations and to obtain a more general view of parasitism, data provided by Lo et al. (1998) and based on an annual survey of *C. argus* in Moorea between October 1994 and October 1995 were also considered in a second null model analysis.

**Experiment analyses** We performed a Cox regression model (Cox 1972) which is the most widely used regression method for analyzing survival data in epidemiology. This unparametric survival regression model is based on hazard function. We performed therefore Cox regression model stratified by parasite species to detect effects of treatments on in vitro survival of parasites.

**Fish condition analyses** Correlations between individual epidemiological values (specific number of parasites per fish, total number of parasites per fish, number of external parasites, number of internal parasites, taxonomic richness) and Fulton's condition index were estimated with Pearson correlation coefficient and tested with associated *r* test. According to Eq. 2, least-square linear regression was calculated between eviscerated weight and standard length. *t* test was performed to compare the regression slope (Fulton's condition index) between Polynesian and Hawaiian fishes.

## Results

### Parasite diversity

All Polynesian fish investigated (global prevalence 100%,  $n=94$ ) were infected with a highly diverse parasite community: Annelida, Cestoda, Copepoda, Isopoda, Monogenea, and Nematoda (Table 1). Fish had a mean intensity of  $11.1 \pm 13.2$  parasites per host (mean  $\pm$  SD). Those species for which prevalence was lower than 5% and or less than five fish individuals were observed are referred to as infrequent. However, Hawaiian fish only exhibited cestode larvae (plerocercoid tetraphyllids and encysted trypanorhynchs) and unidentified fragments of Nematoda (apparently different from *Spirocamallanus istiblenni*; Table 1). Only 5% (four fish out of 73) of Hawaiian fish was infected and the mean intensity was only  $1.0 \pm 0.0$  parasites per host (only a unique individual parasite per infected host). Hawaiian fish were totally free of ectoparasites (skin, nostril, gills, and mouth).

### Relationship between parasites and host size

TL of speared fish was on average  $29.5 \pm 5.8$  cm (mean  $\pm$  SD) in Polynesia (range 14–39 cm,  $n=94$ ) and  $32.6 \pm 7.5$  cm

**Table 1** Epidemiological values of parasite species found in *C. argus* in Polynesia ( $N=94$ ) and Hawaii ( $N=73$ )

Parasite species		Prevalence (%)	Abundance (mean±SD)	Intensity (mean±SD)	Minimum–maximum
<b>Polynesia</b>					
Monogenea					
<i>Benedenia epinepheli</i>	<i>G</i>	38	1.8±3.9	4.4±5.3	2–30
Cestoda					
Tetraphyllidea (plerocercoid)	<i>I</i>	46	6.6±11.7	14.4±13.8	1–54
Trypanorhyncha (larvae) <sup>a</sup>	<i>E</i>	1	0.01±0.10	1.0±0.0	1–1
Nematoda					
<i>Spirocamallanus istiblenni</i> <sup>a</sup>	<i>I</i>	2	0.03±0.23	1.5±0.7	1–2
Crustacea					
Copepods					
<i>Caligus</i> sp. (adult)	<i>M</i>	58	1.9±2.8	3.1±3.1	1–15
<i>Caligus</i> sp. (copepodite and chalimus)	<i>G</i>	46	1.7±2.4	3.6±2.2	2–8
<i>Hatschekia</i> sp.	<i>G</i>	7	0.2±0.6	2.2±0.8	2–4
Isopods					
Corallanidae <sup>a</sup>	<i>N</i>	2	0.02±0.14	1.0±0.0	1–1
<i>Gnathia</i> sp. (praniza)	<i>G</i>	35	1.2±2.5	3.4±3.1	2–16
Hirudinea					
Piscicolidae <sup>a</sup>	<i>G</i>	4	0.05±0.27	1.2±0.5	1–2
<b>Hawaii</b>					
Cestoda					
Tetraphyllidea (plerocercoid)	<i>I</i>	3	0.03±0.16	1.0±0.0	1–1
Trypanorhyncha (larvae)	<i>E</i>	1	0.01±0.12	1.0±0.0	1–1
Nematoda					
Fragments	<i>I</i>	3	0.03±0.16	1.0±0.0	1–1

<sup>a</sup> Infrequent Polynesian species (those which prevalence is lower than 5%)

*E* encysted in the visceral cavity, *G* gills, *I* stomach and intestine, *M* mouth, *N* nostril

in Hawaii (range 19–47 cm,  $n=73$ ). Considering the low epidemiological values for fish in Hawaii, only fish from Polynesia were used to test if there was a relationship with parasites. When the two size groups were compared (<25 and >25 cm, see “Materials and methods” for details), prevalence of tetraphyllidean plerocercoids and *Benedenia* sp. was significantly higher in large fish (Fisher’s exact test, one-tailed  $p<0.001$  for both parasites) whereas differences were not significant for *Gnathia* sp., *Caligus* sp. (both adult and larvae), and *Hatschekia* sp. (Fisher’s exact test, one-tailed  $p>0.05$ ). Because of a high variability between fish (i.e., high SD), no significant difference in intensity (Mann–Whitney,  $p>0.05$ ) between the two specified groups was found for the genera *Benedenia*, *Gnathia*, *Caligus* (larvae and adult), or *Hatschekia* (insufficient data to perform a Mann–Whitney *U* test). Differences for tetraphyllidean plerocercoids were significant (Mann–Whitney,  $W=287$ ,  $n_1=14$ ,  $n_2=29$ ,  $p=0.029$ ). Mean global intensity and generic diversity were significantly higher for Polynesian fishes larger than 25 cm (Mann–Whitney,  $W=1,747$  and  $W=1,725$ , respectively,  $n_1=47$ ,  $n_2=47$ ,  $p<0.001$ ) and small Polynesian fishes remain naturally poorly infected (Fig. 1). Those results are consistent with data found by Lo et al. (1998) on main parasitic taxa found on *C. argus* in Moorea.

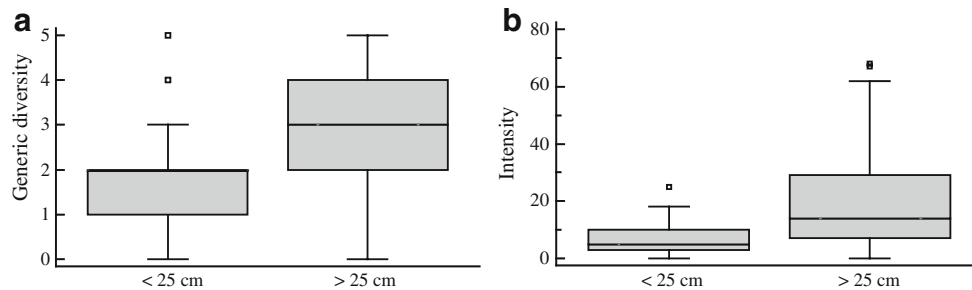
Considering null model, the introduction of 2,385 small or 2,385 large fish was significantly different than expected under the assumption of randomly translocated fish ( $p<0.001$ ). Data provided by Lo et al. (1998) also supported these differences. Thus, the introduction of small host individuals has probably limited introduction of parasites. The number of introduced parasites would have potentially been tripled if large individuals had been introduced.

#### Relationship between parasites and host condition index

No significant correlation was found between any epidemiological values and Fulton’s condition index in Moorea (*r* test,  $df=94$ ,  $p>0.05$  for all relationships). Hawaiian fishes exhibited a significantly higher Fulton’s condition index than fishes from Moorea (*t* test,  $t=9.5$ ,  $df=163$ ,  $p<0.001$ ; Fig. 2). Exclusion of the 11 larger Hawaiian fishes, whose sizes exceed the largest Polynesian fishes, did not affect this result (*t* test,  $t=10.9$ ,  $df=152$ ,  $p<0.001$ ).

#### In vitro mortality

Cox regression model stratified by parasite species revealed overall differences between species ( $p<0.001$ ). When considering copper sulfate treatments (0.8 ppm) and control



**Fig. 1** Mean **a** generic diversity (number of parasite genus per fish) and **b** intensity (number of parasites per fish) between small (total length <25 cm) and large (total length >25 cm) *C. argus* in Moorea.

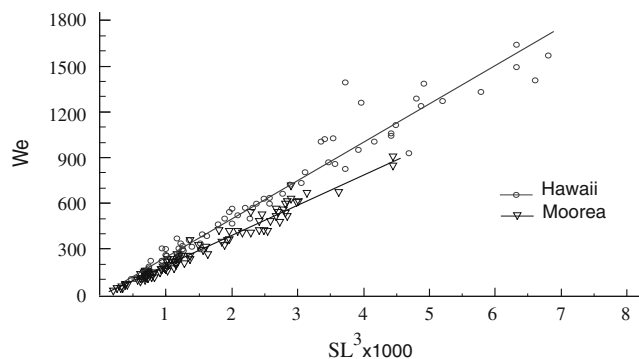
(seawater, 35‰), Cox regression did not reveal significant effect of treatment on parasite mortality ( $p > 0.5$ ), emphasizing in vitro ineffectiveness of treatment performed 50 years ago against ectoparasites. In contrast, desalted water exhibited significant and obvious effect on parasite mortality ( $p < 0.001$ ).

## Discussion

Data reveal that the Polynesian population exhibited a more diverse parasite community than did the introduced population. However, Moorea is a single locality among the broad geographic range of *C. argus* and additional studies at different sites are required to determine whether parasite communities in fish from Hawaii are depauperate compared to those in fish throughout their native range.

### Loss of natural parasite community

In Hawaii, *C. argus* have lost most of the parasites they presumably had in Moorea and exhibited very low epidemiological values. There are numerous nonexclusive



**Fig. 2** Least-square regression line between eviscerated weight ( $We$ , g) and cube of standard length ( $SL^3$ ,  $10^{-4}$  cm) for Hawaiian (round) and Polynesian (triangle) *C. argus*. Regression slopes are equal to Fulton's condition index

ways by which parasites might have been lost (see Torchin et al. 2002 for a general discussion) or not found. Main hypotheses are reviewed below and discussed in view of our results.

1. During their accumulation and their transportation, the high-density stocking may have favored the development of some parasites. However, upon arrival in Hawaii, the fish were treated with copper sulfate (0.4–0.8 ppm during 19–24 h (Fujimura 1957–1958) to remove external parasites (Randall 1960). Considering that parasites of *C. argus* are predominantly external, effective treatment would have significantly limited the introduction of parasites. Unfortunately, in vitro experiment suggests that performed treatment was ineffective on the main external parasite species found in Moorea and is not currently used any more (Thoney 1990). Thus, it might have not prevented introduction of parasites. Another treatment, such as desalted water, would have been more effective.

2. There is a lower probability of successful introduction of parasites with complex life cycles because all host species involved in the life cycle must be present. However, *Benedenia epinepheli*, caligids, gnathiids, and hatchekiids have direct life cycles and low host specificity and occur over a wide biogeographic range. Thus, one might expect them to have tolerated new environmental conditions. Nevertheless, these parasites were not maintained in Hawaii on *C. argus*.
3. In general, only a few host individuals are introduced (and as a consequence only a limited number of parasites), minimizing the probability of parasite introduction. In their native ranges, *C. argus* appear to become initially infected at about 20-cm length and only small fishes were captured and introduced (i.e., smaller than 25 cm, Randall and Kanayama 1982). Such a practice might have by itself reduced potential introduction of parasites in a significant manner. Because a succinct knowledge of the parasitofauna of an introduced species (relationship between parasitism

and host size) can significantly decrease risk of parasite introduction and considering complexity, effectiveness, hazard, secondary effects, and cost of parasitic treatments, this prominent point should not be ignored when species are voluntarily introduced. However, it is likely that introduced fish allowed translocation of several parasites but they did not maintain until today. In contrast to these data, parasite species are sometimes assumed to have established from a very limited number of displaced individuals (Torchin et al. 2002). However, very few are known about the minimum number of introduced parasites that can lead to establishment in the wild and is mostly case specific. Biotic and abiotic underlying factors remain widely unknown. Epidemiological values (i.e., intensity and prevalence) generally increase with host population density (Arneberg et al. 1998) and parasites are not able to persist below a low host density threshold (Torchin et al. 2002). Thus, after introduction, parasites would have been vulnerable in small host populations (571 individuals in 1956 and 1,814 in 1961). Predation by cleaner fish may also have contributed to parasite limitation, as *Labroides phthirophagus* found in Hawaiian waters (Randall 1958) feeds specifically on *Benedenia* spp., gnathiids larvae, and caligids (Youngbluth 1968; Grutter 2002), the most common ectoparasites found on *C. argus*.

#### Lack of native parasite transfer

In agreement with previous studies on a wide range of taxa, species have, on average, fewer parasites in their introduced range than in their native range (Torchin et al. 2002; Poulin and Mouillot 2003). However, the almost total lack of native parasite transfer from natives to exotic fish after 50 years is unusual and of particular interest. As previously stated, Hawaiian waters lack native groupers, except for *Epinephelus quernus* which lives deep in the Windward Islands and rarely overlaps with *C. argus* and the infrequent and threatened giant grouper *Epinephelus lanceolatus*. Yamaguti (1968, 1970) has described three monogeneans and four digeneans in the endemic grouper *E. quernus*, but none of these parasites were found on *C. argus* in Hawaii. The parasite community of marine fish is generally influenced by host ecology and phylogeny. Therefore, sympatric and phylogenetically related hosts with similar ecologies should have similar parasite communities (Muñoz et al. 2007). However, the two native groupers are both ecologically (Heemstra and Randall 1993) and phylogenetically (Craig and Hastings 2007) distant from *C. argus* and monogeneans are usually very host specific.

Since its introduction, this grouper has spread all over the Windward Islands, became abundant, and has integrated into new and complex food webs, eating a wide variety of fishes and invertebrates (Randall and Brock 1960). Like in all marine ecosystems, most of these prey items could be infected with acanthocephalans, cestodes, digeneans, or nematodes (Marcogliese 2002, 2007) but this predator remains uninfected. Nonetheless, most of these parasites are often considered to be generalists, lacking host specificity for both intermediate and definitive hosts (Marcogliese 2002). On the one hand, extreme biogeographic isolation and absence of adapted parasites in Hawaiian waters might explain such a lack of local transfer (Adamson and Caira 1994; Hoberg and Klassen 2002). Such an absence of adapted natural enemies (i.e., competitors, predators, and parasites) is commonly suggested to explain vulnerability of tropical insular systems to invasion (Coles and Eldregge 2002; Hutchings et al. 2002). On the other hand, despite the presence of numerous generalist and ubiquitous parasites (Lewis 1967; Yamaguti 1968, 1970), *C. argus* is not infected, not even as a paratenic host. Underlying mechanisms are still unknown. Genetic analyses on this grouper have indicated extremely reduced effective population size (Planes and Lecaillon 1998). Such a bottleneck might have contributed to select resistant individuals. The nematode *S. istiblenni* needs special consideration. This heteroxenous species was originally described from Hawaii but occurs in most parts of the Pacific (Rigby and Font 1997). *S. istiblenni* has been reported in 18 carnivorous fish species of 11 families from two orders (Rigby and Font 1997). Despite its uncertain status in Hawaii (i.e., native or introduced; Font and Rigby 2000), this nematode currently occurs both in Polynesia and the Hawaiian archipelago but infests *C. argus* only in the former locality. Perhaps its allopatric distribution led to different host specificity, integrating different trophic webs. Alternately, *S. istiblenni* may occasionally infest *C. argus* in Hawaiian waters but sample size is not large enough to observe this nematode.

Although some data support parasite accumulation in exotic inland and anadromous fishes, this process can be particularly slow (i.e., over centuries or millennium; Guégan and Kennedy 1993; Torchin et al. 2003). The most probable explanation is that, during the last 50 years, this grouper has not had sufficient time to acquire parasites from native species. However, it is likely that a long-term switch from natives to exotic and naive host will occur.

#### Effect of parasite loss on host introduction outcome

While parasites can regulate wildlife populations (Scott and Dobson 1989; Tompkins and Begon 1999), empirical studies demonstrating effects of macroparasites on wild host

population dynamics in marine systems are relatively scarce (Finley and Forrester 2003). However, parasites are suspected to affect the outcome of invasions in marine systems (Torchin et al. 2002). As suggested by the ERH, detrimental effects of parasites are strongly minimized by costly defenses (Colautti et al. 2004) and release from parasites allows reallocation of energetic resources to other functions which might give a competitive advantage over natives (i.e., high demographic success and/or large body size) and may contribute to the successful introduction (Torchin et al. 2002).

Most parasites found in Moorea can be pathogenic in a confined environment (Ogawa et al. 1995; Rigby 1997; Jones and Grutter 2005). Lesser effects are expected in the wild but parasites still impose an energetic cost upon their hosts (Sheldon and Verhulst 1996; Rigby et al. 2002). Despite the potential pathogenicity of parasites observed in Moorea, no correlation was found between parasitism and fish health (Fulton's condition index *K*). The effect of parasites on host condition could be more subtle and/or hosts are able to compensate for the energetic cost of parasites in the wild. If so, the direct effect of substantial parasite release may have contributed to the successful introduction of *C. argus* in Hawaii. The comparison is consistent with expectations of the ERH, but an experimental approach would be needed to test this hypothesis and assess the contribution from parasite release to the successful introduction of this grouper in the Hawaiian archipelago.

Ultimately, other numerous biotic and abiotic factors and interactions (i.e., biotic resistance; intrinsic host behavior, robustness, or demography; nutritive effectiveness, etc.) should not be ignored (Mills et al. 2004) as they may have largely contributed to the successful introduction and rapid spread of *C. argus* all over the Windward Islands. The fact that Hawaiian fish exhibit significantly higher Fulton's condition index and reach larger size is more likely due to their local conditions rather than direct effect of parasite loss.

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