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Research Article

Laboratory assessment of feeding-behavior interactions between the introduced Pacific white shrimp *Litopenaeus vannamei* (Boone, 1931) (Penaeidae) and five native shrimps plus a crab species in Thailand

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Abstract

The Pacific white shrimp *Litopenaeus vannamei* (Boone, 1931) is native to the Pacific coast of Central and South America. This species was first introduced to Thailand in 1998 for aquaculture and as a replacement for *Penaeus monodon* Fabicius, 1798 because of problems with disease outbreaks and poor growth performance of the latter. Escapes of cultured *L. vannamei* to the wild were detected recently; however, little is known about the effects of the escape of cultured shrimps on the local ecosystems. In this laboratory study, the feeding behavior of *L. vannamei* was examined and compared with that of five native shrimps and a native crab species to determine the behavioral interactions and potential for food competition. With regards to palatability of the five native shrimp species, *L. vannamei* was non-selective, consuming the first piece of meat encountered. When all species were tested separately, *Litopenaeus vannamei* consumed its food faster than the native shrimps. In paired one-on-one contests, *L. vannamei* was much more aggressive in competing for food than the native shrimp species. When paired with the native crab species, *Charybdis affinis, L. vannamei* lost 100% of the contests and the crab sometimes killed and ate the shrimp. Due to its behavioural dominance in feeding contests with native shrimps, *L. vannamei* pose a serious threat to native shrimp species should it become fully established in marine waters of Thailand.

Key words: Pacific white shrimp, introduction, aquaculture, escape, interspecific competition, food selection

Introduction

Aquaculture is an important source of low-cost protein; however, it is also a major pathway for introducing aquatic non-indigenous species (Gutierrez and Reaser 2005; Galil et al. 2011). The introduction or escape of non-native aquatic species to the wild can pose serious ecological and economic threats (Craig 1992; Moyle and Light 1996; Gutierrez and Reaser 2005). In particular, introduced non-native species may prey upon or compete with native species, alter community structure and functioning, and spread pathogens (Craig 1992; Moyle and Light 1996; Gutierrez and Reaser 2005; Chavanich et al. 2006; Chavanich et al. 2009). There is evidence that shrimp species, such as the Pacific white shrimp *Litopenaeus vannamei* (Boone, 1931), introduced for aquaculture purposes have established populations outside their native ranges (Briggs et al. 2004; Liao and Chien 2011). Other examples include *Penaeus monodon* Fabicius, 1798 introduced in Nigeria and *Penaeus merguiensis* de Man, 1888 introduced in Fiji and the Mediterranean Sea (Gundermann and Popper 1975; Liao and Chien 2011).

The Pacific white shrimp, *Litopenaeus vannamei* (Boone, 1931), is native to the Pacific coast of Central and South America (Perez Farfante and Kensley 1997). This species was first introduced to Asia for experimental culture between 1978 and 1979 (Briggs et al. 2004) and then to Thailand in 1998 for aquaculture and as a replacement for *P. monodon*, which had disease problems and grew poorly (Briggs et al. 2004). Since then, *L. vannamei* has been widely grown in culture because of its fast growth, tolerance to high densities, and high disease resistance (Briggs et al. 2004). Escapes of cultured *L. vannamei* to the wild have been recently detected (Senanan et al. 2007). Escaped *L. vannamei* has also been detected in Hawaii (Balboa et al. 1991), Vietnam (Chavanich et al. 2010), and the southern Gulf of Mexico (Wakida-Kusunoki et al. 2011).

A worrying discovery is the high occurrence of Taura Syndrome Virus (TSV) recently observed in subadult *L. vannamei* caught from the Bangpakong River (Senanan et al. 2009, 2010). The detection of TSV suggests the intentional release of diseased *L. vannamei* from farms to the river (Senanan et al. 2009, 2010). In addition to possible disease transmission, little is known about the effects of the escape of cultured shrimps on the structure and functioning of marine ecosystems of Thailand (Panutrakul et al. 2010; Senanan et al. 2010). Recently, Panutrakul et al. (2010) showed that *L. vannamei* can survive outside their native range, and may compete for food with native species. Monitoring surveys in the Bangpakong River revealed that the proportion *L. vannamei* in the wild panaeid shrimp catches increased from 0.005 in 2005 to 0.16 in 2006, and the percentage of nets containing *L. vannamei* increased from 16% in 2005 to 100% in 2006 (Panutrakul et al. 2010). Senanan et al. (2008) also observed evidence of gonadal development of escaped *L. vannamei*. Thus, the escapees appear to have become established in the wild (Senanan et al. 2008, 2010; Panutrakul et al. 2010).

In this study, the feeding behavior of *L. vannamei* was examined under laboratory conditions and compared with those of native shrimps and a crab to evaluate the behavioral interactions and the possibility for food competition between the non-native and native species. This study comprised four parts: 1) interspecific competitive feeding trials; 2) investigation of feeding rates; 3) investigation of time required to detect food; and 4) feeding preference of the non-native species.

Materials and methods

Experimental species and study site

The introduced white shrimp, *Litopenaeus vannamei*, was obtained from shrimp farms. Specimens of five native shrimp species (*Penaeus monodon*; *P. merguiensis*; *Metapenaeus tenuipes* Kubo, 1949 *M. ensis* (De Haan, 1844 [in De Haan, 1833–1850]); and *M. brevicornis* (H. Milne Edwards, 1837 [in Milne Edwards, 1834–1840])) and a native crab (*Charybdis affinis* Dana, 1852) were collected by using a push-net at the mouth of the Bangpakong River, Chachoengsao Province, a location where individuals of *L. vannamei* escaping from farms were found. The native crab, *Charybdis affinis* was selected for testing because it is abundant in the area where the shrimp escapees were detected, which means it might compete for food with *L. vannamei* and might also prey upon the shrimp. All animals were transferred to the wet laboratory at the Angsila Marine Station, Chulalongkorn University, in Chon Buri Province for acclimation and use in laboratory experiments.

Acclimation and experimental conditions

After collection, conspecific individuals were kept and acclimated in separate 30 × 60 × 30-cm, aerated, glass aquaria for two weeks prior to the start of the experiments. The shrimps and crabs were kept in sea water at ambient temperatures (29 ± 1°C) and salinity (30 ± 0.5). The concentration of dissolved oxygen (DO) was measured periodically during the experiments. The animals were fed with fresh shrimp and/or fresh squid meat twice a day until two days before the start of each experiment. Preliminary results showed that *L. vannamei*, the native shrimps, and the native crab fed equally well upon fresh shrimp meat (*Metapenaeus affinis*) and fresh squid meat. All animals were used only once in an experiment to avoid a confounding effects of prior experience. The experimental trails all used aquaria with no substrate on the bottom. Water used in the experiments was also exchanged for each repetition of each treatment.

Experimental designs

Food preference

Panutrakul et al. (2010) analyzed the stomach contents of *L. vannamei* and the native shrimp species and found overlapping diets of phytoplankton, crustacean appendages, zooplankton, and detritus. Some studies also reported that *L. vannamei* and other penaeid shrimps are carnivores and may exhibit cannibalistic behavior (Thomas 1980; Boddeke 1983; Zhang et al. 2010). To determine whether any of the native shrimps was unpalatable to *L. vannamei*, it was simultaneously offered approximately equal amounts (0.5 g) of fresh meat from the five native shrimp species. The trials were repeated ten times. The aquarium received one *L. vannamei* and one piece of fresh meat from each of the five native shrimp species. Before the experiment, all food items were placed in the center of the aquarium and then one *L. vannamei* was introduced into a corner of the aquarium. The first shrimp meat grasped and eaten was recorded. A chi-square test was used to determine whether *L. vannamei* selected the meat of any species more often than the others.

Feeding rates and feeding habits of *L. vannamei* and native shrimps

To determine the feeding rates of *L. vannamei* and the native shrimp species, a piece of fresh shrimp meat (*Metapenaeus affinis*) (approximately 0.5g) was given to each shrimp species. The animals were fasted for two days prior to the experiment. In each experiment, the time to consume the entire piece of meat by each individual was recorded. Six trials (representing the six species of shrimps), each with ten repetitions, were conducted.

Another experiment was conducted to examine the time required for individuals of each species to detect and find food items. In the aquarium, the food item was placed in the middle of the tank. Immediately after, one individual of one of the five native species or *L. vannamei* was released at the corner of the aquarium. The time needed the individual shrimp to find the food was defined as the time between release into the aquarium until shrimp grasped and began to consume the food. For each shrimp species, the trials were repeated ten times. The water was exchanged with each repetition. A one-way ANOVA followed by Tukey's all-pairwise comparisons was used to test differences in mean feeding rate and mean duration for food searching between the six shrimp species.

Food competition

Food competition trials between introduced white shrimp *L. vannamei versus* each of the five native shrimps and the crab species were conducted in a pairwise fashion. In each trial, the aquarium received one individual of *L. vannamei* and one individual of either native shrimp species or native crab species. The individuals were introduced at the opposite ends of the aquarium. A piece of fresh squid meat (approximately 0.5g) was immediately placed in the middle of the aquarium. The behavior of animals was then recorded with a video camera. An individual that collected and consumed the food item first was considered to have out-competed the other animal.

To investigate whether or not the sizes of shrimps and crabs influenced food competition success, the tested animals were divided into three size classes on the basis of carapace length (shrimp) and carapace width (crab): small (approximately 4 cm and 2 cm for shrimp and crab, respectively), medium (approximately 8 cm and 4 cm, respectively), and large (approximately 11 cm and 6 cm, respectively). We did not test specimens of different sizes against each other, thus, there were 18 treatment (six species, three sizes) combinations with 10 repetitions each.

In addition, a density experiment was conducted to determine whether or not different numbers of each shrimp species influenced the outcome of the food competition. *Litopenaeus vannamei* and *P. monodon* were selected for this experiment. *Penaeus monodon* was used in the experimental trials because the results from the previous 1:1 ratio food competition experiment showed that *P. monodon* was more aggressive than the other native species. All shrimps used in the experiment were approximately 8 cm in carapace length. Five treatments and ten replicates were conducted. Each aquarium received one of the following five density ratios (*L. vannamei* to *P. monodon*), namely, 1:1, 2:1, 3:1, 1:2, and 1:3. For each repetition, the individuals were introduced at the opposite ends of the aquarium at the same time. A piece of fresh squid meat (approximately 0.5g) was then placed in the middle of the aquarium. The species that reached and consumed the food first was considered a winner in that trial.

Results

We used 310 individuals of *L. vannamei*, 140 of *P. monodon*, 60 of each of the other four native shrimp species, and 40 of the native crab species in the experiments.

The results of the preliminary food preference experiment showed that *L. vannamei* consumed the meat of all native shrimps equally ($\chi^2 = 0.53$, df = 4, $P = 0.97$), and simply selected the food item it reached first (Figure 1).

There was a significant difference between shrimp species in time required for finding and detecting food items (ANOVA, $F_{6,60} = 2.634$, $P < 0.025$). P*enaeus monodon* and *L. vannamei* detected food at the same rate and significantly faster than the other four species, which did not differ between them (Figure 2).

The feeding rate also significantly differed (ANOVA, $F_{6,60} = 2.398$, $P < 0.038$) between the

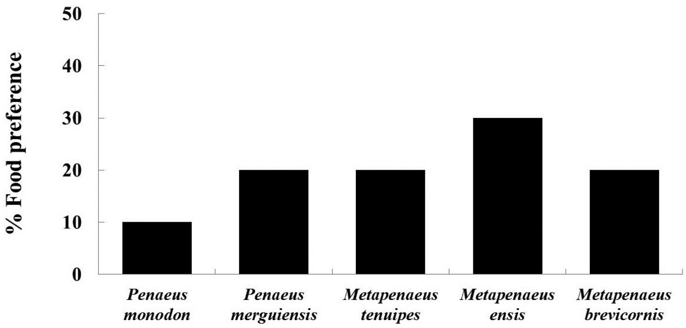

Figure 1. Percentage of different food items (fresh shrimp meat) chosen by *L. vannamei.*

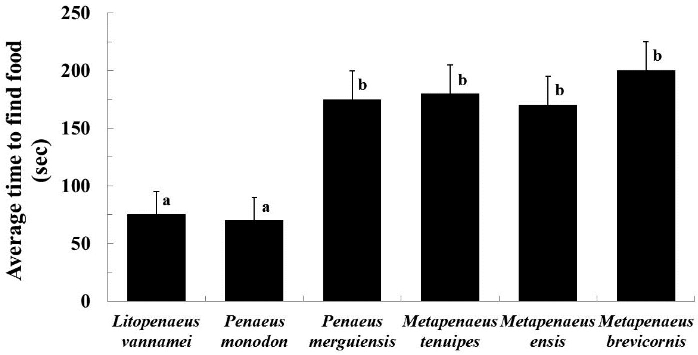

Figure 2. Average times required for each shrimp species to find food plus 1 SE. Letters above each histogram designate the times that differ significantly between species ($P < 0.05$).

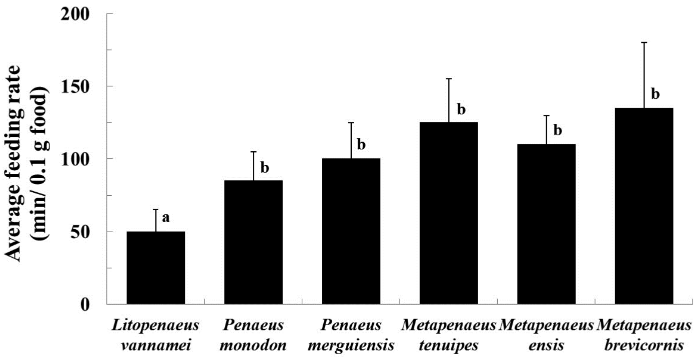

Figure 3. Average feeding rates of six different shrimp species plus 1 SE. Letters above each histogram designate the feeding rates that differ significantly between species ($P < 0.05$).

shrimp species (Figure 3). *Litopenaeus vannamei* consumed the food faster than the five native shrimp species, which did not differ among themselves.

The results of the food competition experiment among the introduced *L. vannamei*, the native shrimps, and the native crab species showed that *L. vannamei* found the food first (winning 70% to 100% of the time) than the native shrimp species regardless of size class used (winning 70% to 100% of the time) (Figure 4). When *Penaeus monodon* was paired against *Litopenaeus vannamei*, we noted *P. monodon* usually crawled on the bottom while *L. vannamei* swam, and tended to feed on vertical and suspended substrates. However, even though the offered food was placed on the bottom, *L. vannamei* still obtained the food before *P. monodon*. In contrast, *L. vannamei* lost 100% of the time when paired with the native crab *Charybdis affinis* regardless of size class used.

In the density experiments, the relative density had an influence on the outcomes of the trials (Figure 5). When the density and ratio of *L. vannamei* to *P. monodon* was (1:1) or when there were more of the former species, *L. vannamei* typically (80 to 100% of the time) encountered

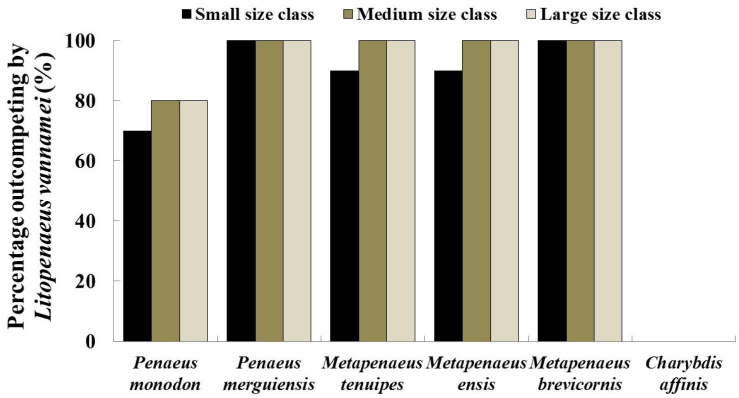

Figure 4. Percentage of *L. vannamei* outcompeting native shrimp and crab species for food in three size classes.

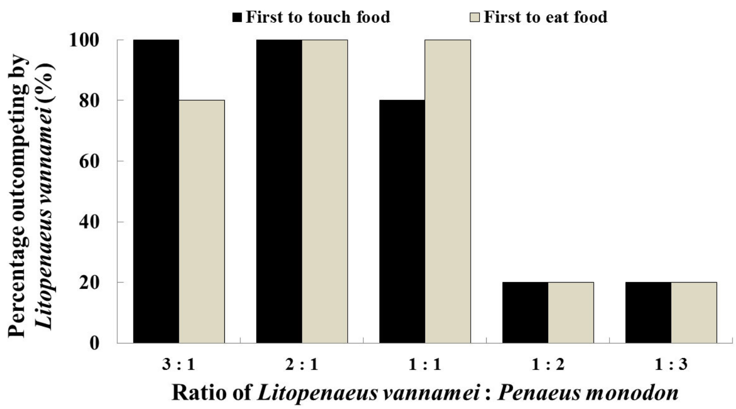

Figure 5. Percentage of *L. vannamei* outcompeting *P. monodon* in five different density ratios.

and ate the food first. However, when the number of *P. monodon* was greater than the number of *L. vannamei*, the frequency of *L. vannamei* winning was reduced to 20% (Figure 5).

Discussion

This study showed that *L. vannamei* fed on the meat of native shrimps without obvious preference. From a predation standpoint, this result indicates the meat of the native shrimps does not contain substances that would deter the white shrimp feeding upon them. While only shrimp meat was tested, this result should not be a surprise because much broader studies indicate that penaeid shrimps in general, and including *L. vannamei*, are carnivores that consume a wide array of invertebrates such as polychaetes, molluscs, and crustaceans (Thomas 1980; Boddeke 1983; Panutrakul et al. 2010; Zhang et al. 2010). Indeed, most cultured penaeid shrimps are opportunistic feeders and also may exhibit cannibalistic behavior (Thomas 1980; Boddeke 1983). *Litopenaeus vannamei* shows an aggressive feeding behavior when food sources are limited (Moss and Moss 2006). A degree of aggressiveness in food and habitat competition may also vary depending on species, sizes, and sexes (Moss and Moss 2006).

The results from the feeding experiments and food competition trials showed that *L. vannamei* was faster than all the native shrimp species except for *P. monodon* in detecting prey and it consumed the food more quickly than all five native species. In pairwise competitions with the five native species, *L. vannamei* individuals successfully found and consumed the food first. Other studies have shown that the ratio of species might influence the outcomes of feeding contests (Jensen et al. 2002; MacDonald et al. 2007). Consistent with this hypothesis, and excepting the one to one of each species trials, it was the numerically more abundant species that won nearly all of the feeding competitions. How this might affect feeding interactions under field conditions is hard to predict because competition for food requires the resource be in limited supply.

When presented with prey on the bottom, and one *L. vannamei* against one *P. monodon*, the swimming species *L. vannamei* usually won against the the benthic *P. monodon*. It is important to note, however, that the arena (aquarium) was small and in a larger setting, *L. vannamei* might not be able to detect prey on the bottom as quickly as a benthic species. Regardless, *L. vannamei* is an opportunistic feeder that can adapt well to changes in diet composition (Gamboa-Delgado et al. 2003). Moreover, there was broad diet overlap between *L. vannamei* that escaped from farms and local shrimp species: the main prey items of all species being phytoplankton, appendages of crustaceans, and vegetal matter (Panutrakul et al. 2010).

When *L. vannamei* competed for food against the native crab *Charybdis affinis*, the crab won all of the contests; moreover, it sometimes caught and consumed the non-native shrimp. In Thailand, *C. affinis* is a common species and widely distributed in the Gulf of Thailand, including areas where the shrimp escapees were detected (Naiyanetr 1998; Senanan et al. 2010). Thus, the native crab species may prey upon *L. vannamei* in the wild and perhaps could assist in controlling the populations once *L. vannamei* becomes fully established.

In the present study, the density of the shrimp individuals used in the experiment had an influence on the outcome of competition for food. With the exception of the one:one encounters, the species with the greater number won the food challenge. This suggests the feeding success was strictly density-dependent. We did not observe any incidences when one species took away the food obtained first by the other individual. While behavioral dominance was clearly shown in a laboratory setting, the application to a field setting is less clear. For competition to have an effect on one or both species, a resource (food) must be in short supply and evidence of food limitation one way or the other is lacking.

Propagule pressure is one of the key factors influencing the success of invading species (Williamson 1996; Ruiz et al. 2000). Increasing the propagule pressure may enhance the establishment of an invasive population (Ruiz et al. 2000). Senanan et al. (2007) reported an increased frequency of encountering *L. vannamei* in Bangpakong estuary, perhaps reflecting an increase in propagule pressure because the frequency of escapes is increasing. That some of these animals are escapees is based on the medium to large (average 85 mm TL) sizes of *L. vannamei* being found in the Bangpakong estuary. The release of the white shrimp from culture can occur during water exchange, pond cleaning, harvests, flooding incidents, or intentional release (Senanan et al. 2007; Chavanich et al. 2010).

From the previous and present studies, there is a potential risk of a negative impact of the introduced white shrimp on native species and the invaded ecosystems (Senanan et al. 2007, 2010; Panutrakul et al. 2010). The white shrimp, behaviorally, was dominant when competing for prey items and any increase in white shrimp numbers may well result in a decrease in abundance of one or more native species. It currently is unknown whether existing predators of native shrimps would also prey upon the non-native white shrimp. The laboratory experiment suggests the common native crab *Charybdis affinis* was able to capture and eat the non-native shrimp and there is no reason to suppose other shrimp predators would avoid the white shrimp. In a best-case scenario, the non-native white shrimp will become naturalized in the shrimp community by partially displacing some of the native shrimps. In a worst case scenario, the non-native shrimp could drive one or more species to local extinction.

Liao and Chien (2011) suggested that culturing *L. vannamei* in inland areas would have less ecological risk than that rearing them in coastal areas. The inland culture would lead to no or low incidents of escapes of cultured shrimp into the wild. The choice of culture locations is important because aquaculture operations using *L. vannamei* is expected to grow in Thailand and other Southeast Asian countries. Thus, preventive measures such as strengthening the government control of introduction of non-native species and establishing a monitoring program for detecting the establishment and spread of *L. vannamei* are needed (Chavanich et al. 2010; Liao and Chien 2011).

Overall, the results of this laboratory study showed that *L. vannamei* was non-selective with respect to palatability of the five native shrimps as food. The white shrimp was behaviorally dominant when competing for food one-on-one with the native shrimp species. Thus, the non-native white shrimp could become a serious threat to native shrimps if it becomes established (begins reproducing successfully) in non-native habitats. However, more studies are needed to provide insights into the interactions between the introduced white shrimp and native shrimp species and into the ecosystem-wide consequences of this introduction.

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