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Functional response of goldlined spinefoot rabbitfish *Siganus guttatus* (Siganidae, Perciformes) early juveniles to live zooplankton prey

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Abstract

The rabbitfish *Siganus guttatus* is an important tropical aquaculture species, but fry production is hampered by availability of ideal live feeds. This study investigated the predatory functional response of *S. guttatus* early juveniles on live brine shrimp nauplii (*Artemia franciscana*), rotifers (*Brachionus plicatilis*), and wild copepods. The predation experiment comprised one individual fish of different (small, medium or large) sizes, and either of the three live zooplankton prey at four to six increasing densities in a sealed 1-L plastic bottle with filtered seawater. An experiment was replicated five times, and fish and prey were kept suspended in a plankton roller. Videography and gill raker analysis were done to further understand feeding mechanism. Highest fish consumption rates were on *Artemia* nauplii, but only medium and large size fish showed a Holling's type II model with peak consumption at 15 nauplii mL^{-1} concentration half those regularly provided to the fish in the current rearing practice. The functional response of small fish on *Artemia* was dome-like. Only the large size fish successfully ingested copepods and the functional response was directly proportional. Rotifers were only ingested by small fish that showed an inversely proportional response. The deviations from Holling's models were attributed to fish size, *Artemia* nauplii size, highly evasive behaviour of copepods and the small size of rotifers. This study identified ideal *Artemia* nauplii concentration to *S. guttatus* early juveniles, but evasive prey behaviour of wild copepods and small size of rotifers render these prey types less ideal for early juvenile *S. guttatus*.

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Introduction

Critical to marine fish recruitment and ultimately fish stock, the predatory feeding behaviour of early life stages of many fish species has been recognized as a complex system which requires more detailed study to elucidate its intricacies (Houde and Schekter, 1980; Rao, 2003). For instance, a successful consumption of a prey by a fish larva is achieved if all components of a sequence of predatory behavioural activities (e.g., search, attack, capture, ingestion) will each have high probability of success (Greene, 1983). Predation is generally influenced primarily by the size and/or stages of both predators and prey, and predators are usually larger than their prey (Mullin, 1963; Rao, 2003). However, various morphological (mouth type), physiological (palatability), and behavioural (motion, escape reactions) features explain the vulnerability to predation of prey (Ostergaard *et al.,* 2005). Recently, hydrodynamic properties at the size scale of fish larvae and prey are as important in predation success (China and Holzman, 2014).

The importance of Holling's (1959a,b) functional response models of predation in larval fish predatory behaviour studies has been emphasized (Rao, 2003). Defined as the change in ingestion rate of prey with increasing concentration of prey density, the functional response of a predator may be classified into types I, II, and III (Holling, 1959a,b). The type I or rectilinear response is characterized by a linear increase in consumption rate up to a certain prey concentration where the rate suddenly reaches a plateau and stays at zero with further increases in prey concentration. This is exemplified by filtration rate of filter feeders such as daphniids (Rigler, 1961), and calanoid copepods (Frost, 1972). The type II or exponential response is an initial proportional increase with increasing prey concentration which gradually decreases as "saturation" level of prey concentration is approached; beyond this predation rates remain stationary with further increase in prey concentration as in the type I functional response (Holling, 1959b). These two types of responses have been considered destabilizing to predator-prey interactions because of the capacity of the prey to damp predation rates by simply increasing its density. In addition, at low prey density, predators could drive prey populations to extinction. This contrasts with the type III functional response in which predation rate remains low at low prey concentration and starts to increase at a certain higher prey density. The type III functional response is stabilising to the predator-prey interaction and is characterised by a sigmoid type of curve. Analysis of the functional response of fish larvae is very important because it helps in ascertaining the appropriate amount of live food for larval culture (Rao, 2003).

The goldlined spinefoot rabbitfish *Siganus guttatus* belongs to Family Siganidae and the species is distributed in the tropical eastern Indian and western Pacific Oceans (Iwamoto *et al.,* 2012). Traits such as high reproduction in captivity, herbivory, and tolerance to low dissolved oxygen and 10 to 35 PSU salinity allowed the adults of the species to be successfully reared in hatcheries (e.g., Bagarinao, 1986**;** Duray 1988; Ayson *et al.,* 2014). Rabbitfishes (i.e. mainly *S. guttatus*) global production was 241 tons as of 2007 (Lucas and Southgate, 2012). The species *S. guttatus* is ideal for mariculture because its mature stages can subsists on the lower trophic level of the food chain being principally herbivore and most importantly high market acceptability as food and aquarium species (Lam, 1974; Carpenter and Smith-Vaniz, 2016). However, there is no information available on the functional response of *S. guttatus* postlarvae to prey density (Rao, 2003). The lack of detailed knowledge on aspects of postlarval predatory behaviour may contribute to reasons the rabbitfish aquaculture is yet to take off on a commercial scale (Nash, 1975 cited in Rao, 2003). Still remaining unaddressed is the important question: what is the ideal concentration of live food should be fed to *S. guttatus* postlarvae?

This study aimed to determine the functional response of early juveniles (i.e. postlarvae) *S. guttatus* on different concentrations of live feeds *A. franciscana* nauplii, *B. plicatilis*, and mixed wild copepod populations.

Materials and methods

Experimental live prey

Newly hatched *Artemia franciscana* nauplii (Ocean Star International, Inc. Snowville, UT. 84336 USA) and live *Brachionus plicatilis* mature rotifer individuals were obtained from live feed rearing tanks of a siganid hatchery. Copepods were collected along with wild zooplankton at the coast near the laboratory. A 1-m mouth diameter conical plankton net of 100 µm mesh size was towed horizontally at a speed of 1 m s^{-1}. The plankton net has a closed cod-end which minimizes damage to the animals (Omori and Ikeda, 1984; Sameoto *et al.,* 2000). Tow duration was at least 3 minutes to capture more zooplankton, but not longer to avoid damage of animals due to overcrowding (Metillo *et al.,* 2015). After the tow, plankton net was retrieved, and captured zooplankton inside the cod end was gently filtered through 1000 µm mesh sieve to remove gelatinous mesozooplankton that feed on copepods, while collecting the filtrate with zooplankton size less than 1000 µm using a clean container. The container with zooplankton was diluted with 1µm-filtered seawater to avoid cannibalism. Several net tows were made to collect enough zooplankton. Animals were brought to the wet laboratory, aerated, and fed with the chlorophyte *Nannochloropsis* sp. to avoid starvation and cannibalism. Zooplankton samples were labeled as mixed copepod prey since copepods comprised 85 to 95% of the entire <1000 µm zooplankton collected, The most abundant were calanoid copepods of the genera *Paracalanus* cyclopoid copepods *Oncaea* and *Corycaeus* and harpacticoid copepod *Euterpina* were also common. Gastropod and bivalve veligers were also occasionally present.

Fish, experimental set up and procedures

Feeding experiments were conducted at a siganid hatchery facility with access to freshwater (deep well), brackish water (15 PSU), and sand-filtered seawater (33 PSU) supply, and a direct access to the sea from the shore. Prior to the experiment, predation chambers made of 1L polyethylene bottles were cleaned and rinsed well with 1µm-filtered seawater. These plastic bottles are translucent that allow light to penetrate inside the bottle. All laboratory materials (white dipper, 500 ml plastic beakers, and Pasteur pipettes) were thoroughly rinsed to eliminate detergent residues and other contaminants that may influence experimental animals.

Siganus guttatus early juveniles used in the experiment were categorized into small (7.7-12.3 mm Total Length (TL)), medium (21-25 mm TL), and large (26-45 mm TL) (see mean TL values in Table 1). In order to ensure greater postlarval survival during the feeding experiments, juvenile fish used in this study were from young, 4-5 years old, brood stock (Gorospe *et al.,* 2011).

Three types of live feeds (*A. franciscana*, *B. plicatilis*, and mixed copepods) were used in this study (see Table 1 for mean body lengths). These were provided at at different concentrations. *A. franciscana* were given at 5, 10, 15, 20, 30, and 60 (animals mL^{-1}), *B. plicatilis* at 10, 30, 50, 60, and 70 (animals mL^{-1}), and copepods at 5, 10, 15, and 20 (animals mL^{-1}). The concentrations of *A. franciscana* and *B. plicatilis* include the usual density of prey (30 *A. franciscana* nauplii per mL^{-1}; 50 *B. plicatilis* adult individuals mL^{-1}) given to *S. guttatus* fish larvae in the hatchery. Since we did not find any literature citing ideal prey concentration of copepods for early juveniles of *S. guttatus*, our copepod prey concentrations are similar to those for *A. franciscana* considering sizes of copepods (500 to 700 µm) are very similar to nauplii of *A. franciscana* (600 to 850 µm).

The concentration of prey, control 1 (fish only) and control 2 (prey only) were replicated five times. Live feed (*A. franciscana*, *B. plicatilis,* and copepod) stock abundance was estimated by counting three 1ml (average computed) aliquot under a stereomicroscope. These values were then used to compute for the desired volume of live feed stock using the equation $C_1V_1 = C_2V_2$, where C_1 and V_1 mean initial concentration and volume, respectively while C_2 and V_2 are the desired concentration and volume. One litre of sand-filtered seawater was added up to the bottle's neck.

An experiment commenced after one *S. guttatus* early juvenile was placed in a bottle with live prey. Bottle lids were then tightly secured ensuring no leaks, and then bottles with live feed and fish were loaded into a plankton wheel (Malugao *et al.,* 2015) and rotated for 1 h. After 1 h juvenile fish were obtained by filtering the contents of plastic containers through 100 μm sieve. Fish and excess live feed were immediately anaesthetized in ice and preserved in 10% formalin.

Mean values (± standard deviation) of salinity (35.00 ± 0.00 to 35.10 ± 0.00) and temperature (28.52 °C ± 0.48 to 28.72 °C ± 0.74) were kept the same before and after feeding experiments. Respective mean initial and final dissolved oxygen values (in mgL^{-1} ± standard deviation) during the experiments involving each prey type were: 4.11 ± 0.12 and 3.56 ± 0.13 for *A. franciscana*; 4.21 ± 0.16 and 3.63 ± 0.20 for *B. plicatilis*; and 4.36 ± 0.40 and 3.50 ± 0.05 for mixed copepods.

Preserved siganid early juveniles were removed carefully from the container using forceps, rinsed with filtered seawater to remove excess formalin, and individual total length measured using a caliper. Viewed under a stereomicroscope, mouth gape and number of gill rakers on the first pair of gill arch were recorded for every individual fish.

The gut of each fish was dissected out, its percentage fullness estimated, opened lengthwise with fine needles under a Motic (SMZ-168 Series) stereomicroscope, and all prey items in the gut were counted and recorded. In experiments using copepods as prey, each food item in the stomach of the fish was examined under stereo- and compound microscopes, and all ingested prey items were counted and identified based on general body shape and the features of the different appendages were then matched to photographs, descriptions and taxonomic keys of Scott (1909), Wilson (1942, 1950), Grice (1962), Tanaka (1969), Mulyadi (2004), and Razouls, de Bovée, Kouwenberg, and Desreumaux (2011), Metillo (2012). All prey items were also preserved in 5% borax-buffered formalin.

Feeding behaviour filming

The feeding behaviour arena was in an aquarium containing filtered seawater, and with a dimension of 30.48 cm x 10.16 cm x 20.32 cm with lines drawn on one of the broad side of the aquarium as reference grid lines. Live prey (i.e. *A. franciscana*, *B. plicatilis* and mixed copepods) at concentrations similar to those of the functional response experiment was separately prepared into the aquarium. A single fish was then introduced inside the aquarium marking the start of the fish feeding video recording using a Nikon COOLPIX, 16 MP digital camera. The footage was ensured to capture the early juvenile fish pursuit, attack, and handling of the prey. The video was processed using the GoPro Studio software.

Data analysis

The non-parametric Kruskal-Wallis single factor analysis of variance (ANOVA) was computed to test the null hypothesis that fish predation (= ingestion) rates and gut fullness between prey densities (treatments) were equal, while treatment means were compared using the non-parametric Mann-Whitney *U* test (Zar, 1984). The functional response curves of the *S. guttatus* early juveniles were described from the relationship between ingestion rate and prey density. Curve fitting was performed using polynomial regression with replication, and slopes were compared using analysis of covariance followed by a Tukey's test to determine significant differences between slopes (Zar, 1984). All statistical analyses were conducted using the computer program SPSS version 11 (SPSS, 2002).

Results

Mouth gape and gill raker number of S. guttatus early juveniles

Analysis of the mouth gape measurements showed a linear relationship with total body length (Fig. 1a). In contrast, number of gill rakers in the first pair of gill arch depicted a parabolic relationship with body length (Fig. 1b).

The number of gill rakers peaked at 25 to 30 mm total length, then declined at >30 mm total lengths.

Table 1. Predator (early juveniles *S.guttatus*) and prey sizes in the functional response experiments.

Experiment	Predator total length	Prey total length
	(mean ± SD mm)	(mean ± SD mm)
Large *S. guttatus* VS *A. franciscana* nauplii	27.50 ± 2.64, n = 20	0.53 ± 0.05, n = 25
Medium *S. guttatus* VS *A. Franciscana* nauplii	22.93 ± 1.28, n = 20	0.50 ± 0.09, n = 25
Small *S. guttatus* VS *A. Franciscana* nauplii	10.92 ± 0.73, n = 20	0.53 ± 0.09, n = 25
Large *S. guttatus* VS mixed Copepod	27.65 ± 2.99, n = 20	0.17 ± 0.02, n = 25
Small *S. guttatus* VS *B. plicatilis*	9.45 ± 0.31, n = 20	0.10 ± 0.04, n = 25

Functional response of S. guttatus early juveniles to A. franciscana

Predation rates were significantly different among *A. franciscana* prey densities (H = 15.30, df = 4, p < 0.005). Predation rates of large size fish reached first maximum mean value of 8264.4 prey predator^{-1} hour^{-1} at 15 ml^{-1} prey density (Fig. 2a), and the curve showed maximum predation rates remaining constant beyond 15 ml^{-1} prey density.
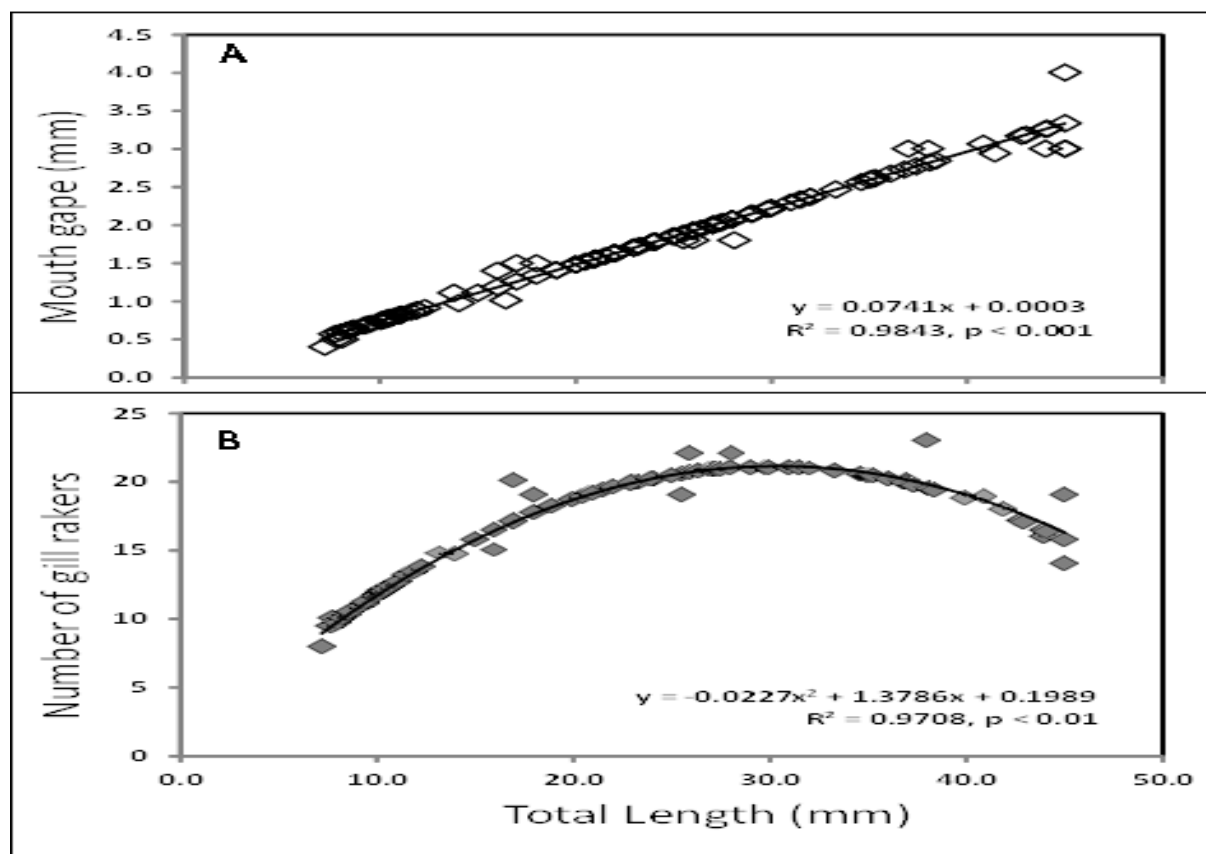

Fig. 1. Mouth gape (a) and number of gill rakers on the most anterior pair of gill arches in the different sizes of *Siganus guttatus* early juveniles fed different types of prey (nauplii of *Artemia franciscana*, mixed zooplankton, and rotifer *Brachionus plicatilis*.

The lowest predation rate of 1492.2 prey predator^{-1} hour^{-1} was observed at prey concentration of 5 ml^{-1}. The functional response curve had a statistically significant fit with the Holling's Type 2 model (X^2 = 863.5, p < 0.000). Similarly, the mean predation rates of medium size fish varied significantly with prey density (H = 10.75, df = 4, p < 0.05). The functional response curve shown was also curvilinear that peaked at 15 ml^{-1} prey density with a maximum average of 6994 prey ingested by a fish in one hour

(Fig. 2b). The lowest predation rate recorded was 2333 prey predator^{-1} hour^{-1} at the prey concentration of 5 ml^{-1}. The functional response curve of medium size fish to *A. franciscana* prey density also had a statistically significant fit with Holling Type 2 model ($X^2 = 445.7$, $p < 0.000$.
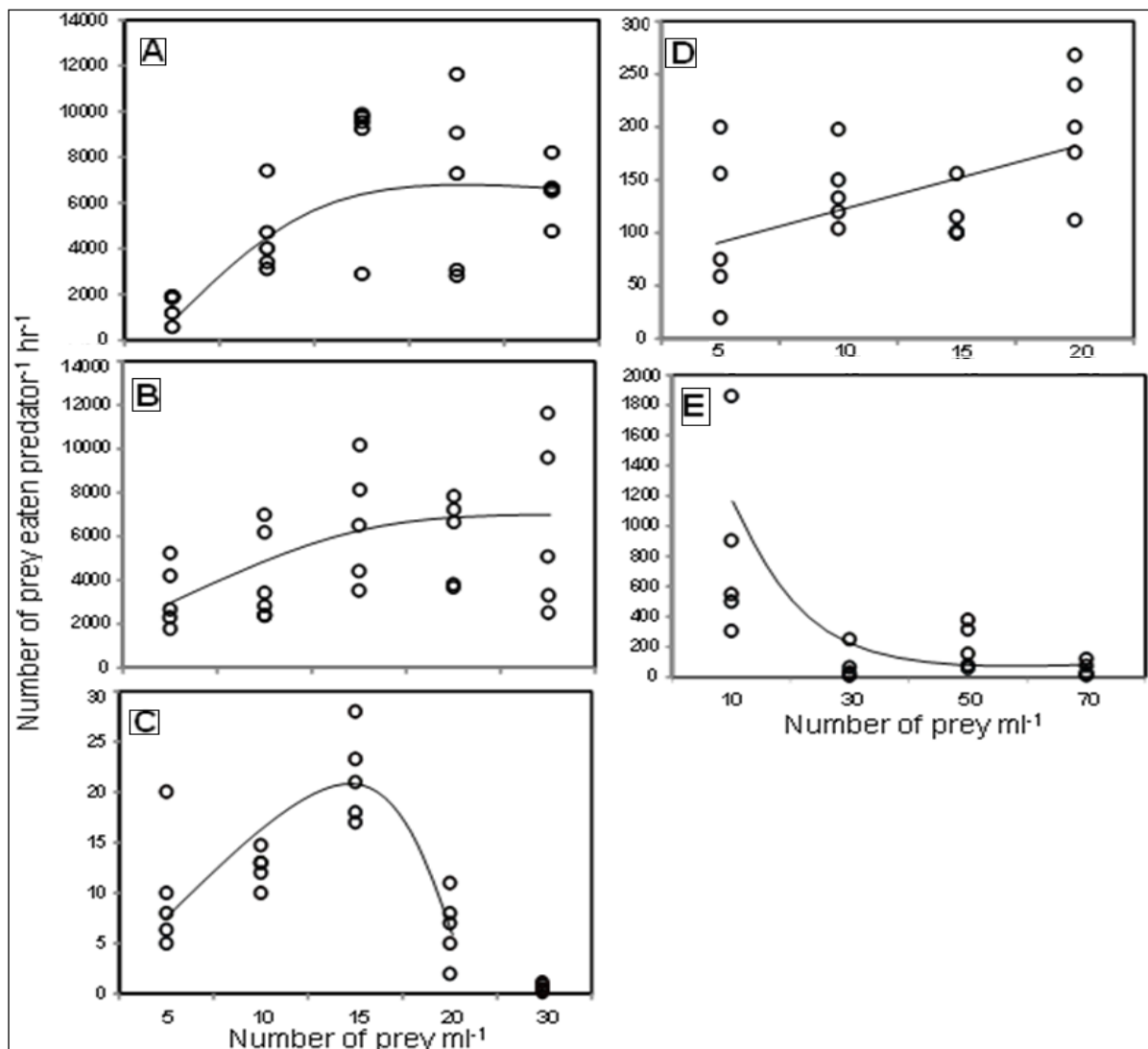
Fig. 2. Functional response of *Siganus guttatus* early juvenile predators on different preytypes. Number of *Artemia franciscana* nauplii prey eaten by large (a), medium (b), and small (c) *S. guttatus* early juveniles at different prey concentrations. Number of mixed copepod prey (d) eaten by large *S. guttatus* early juveniles at different prey concentrations. Number of *Brachionos plicatilis* prey (e) eaten by small *S. guttatus* early juveniles at different prey concentrations.

Although mean predation rates of small size fish varied significantly with prey density ($H = 13.75$, df = 4, $p < 0.04$), number of ingested prey was much lower than those shown by the two larger fish. The peak in predation rate was still at prey concentration of 15 ml^{-1}, but maximum average ingestion was only 22.3 prey predator^{-1} hour^{-1} (Fig. 2c). Mean predation rates drastically dropped at 20 prey ml^{-1} to 7 prey predator^{-1} hour^{-1} and fish ingested very few prey at the maximum prey density of 30 ml^{-1}. The functional response of predator to prey density was dome-like and had no statistically significant fit with Type 2 Holling's model ($X^2 = 0.054$, $p < 0.974$).

Functional responses of S. guttatus early juveniles to mixed copepods and B. plicatilis
Only the large size *S. guttatus* early juveniles ingested the mixed copepod prey. Although the trend of

average values was increasing, predation rate on copepod prey was not significantly different between copepod concentration treatments ($H = 5.33$, df = 4, $p > 0.14$). The lowest mean predation rate of 77.5 prey predator[-1] hour[-1] was observed at the lowest prey concentration, and the highest predation rate value of

184 prey predator[-1] hour[-1] was obtained at the highest prey concentration (Fig. 2d). The linear functional response of *S. guttatus* juveniles on increasing copepod concentration did not fit any of the Holling's models ($X^2 = 1.70$, $p < 0.637$).
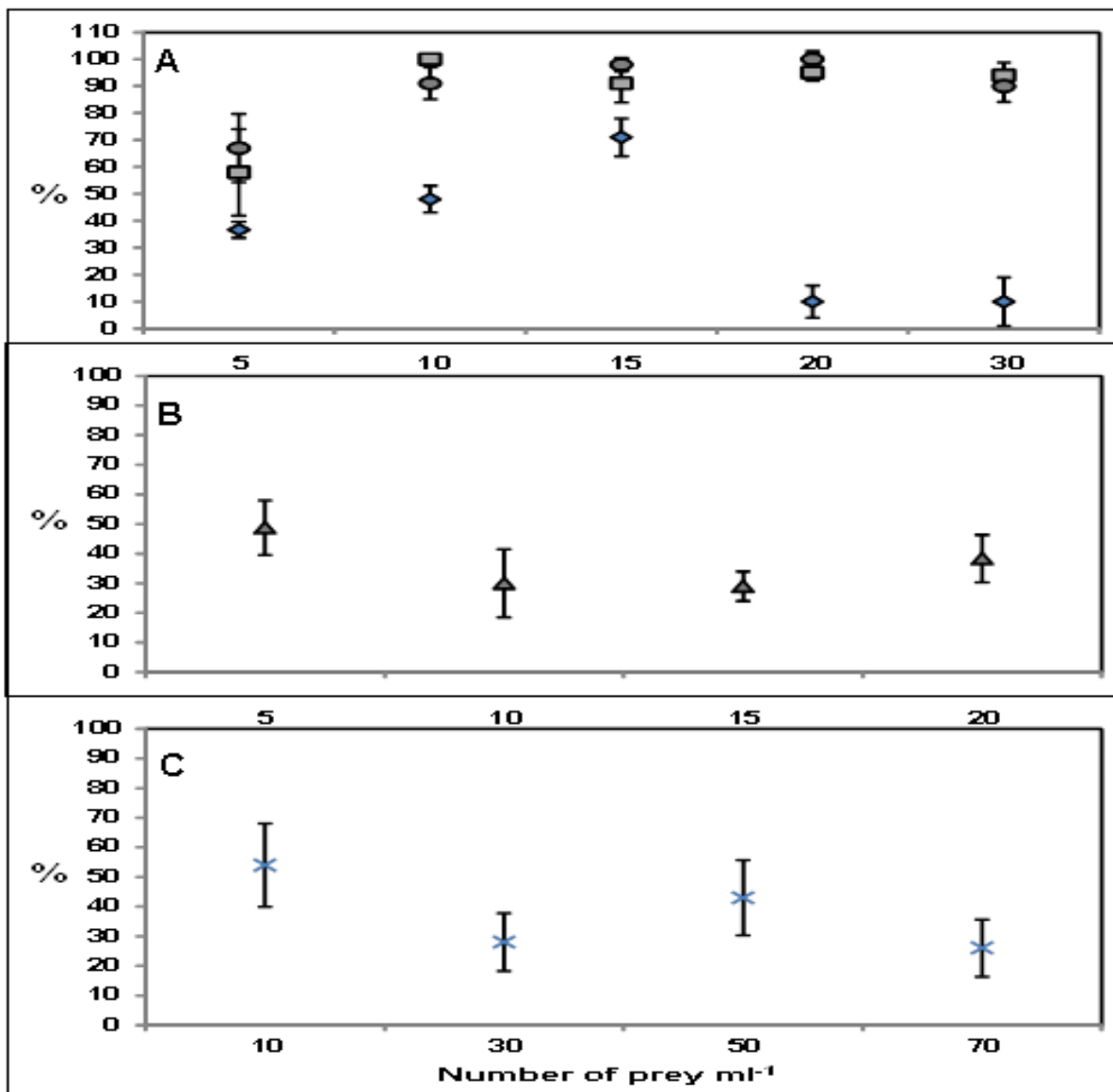
Fig. 3. Mean gut fullness in *Siganus guttatus* early juveniles in all functional response experiments with three different prey types. (a) small (solid diamond), medium (solid square) and large (solid circle) *S. guttatus* ingesting *Artemia franciscana* nauplii at different prey concentrations. (b) Large (solid triangle) *S. guttatus* ingesting mixed copepods. (c) *S. guttatus* ingesting the rotifer *Brachionos plicatilis*. Error bars = standard error.

Only the small fish ingested the rotifer *B. plicatilis*. The average predation rate of small *S. guttatus* early juveniles on different concentrations of the rotifer *B. plicatilis* varied highly significantly with prey concentration ($H = 12.82$, df = 4, $p < 0.006$).

Predation rate appeared to decrease with increasing prey concentration with the highest mean value of 824.2 prey predator[-1] hour[-1] at the lowest prey concentration of 10 individual rotifers per ml (Fig. 2e). The lowest average predation rate was 51.6 prey

predator^{-1} hour^{-1}recorded at the highest prey concentration. The functional response curve shown did not match any of the Holling's model types (X^2=1.48, p < 0.477), but showed an inversely proportional curve.

Gut fullness of S. guttatus early juveniles in all functional response experiments

Percentage gut fullness of the large size fish varied highly significantly among *A. franciscana* treatments (H = 12.92, df = 4, p < 0.005) (Fig. 3a). The lowest mean gut fullness was observed at the lowest prey concentration and the highest (100%) was first reached at 15 ml^{-1} prey density and maximum gut fullness remained the same for the rest of the prey concentrations. Similarly, gut fullness in medium size fish varied significantly among *A. franciscana* treatments (H = 15.20, df = 4, p < 0.003), and 100% gut fullness was first achieved at 15 ml^{-1} prey density and remained similar for the other prey densities (Fig. 3a). Gut fullness in small size fish varied significantly across treatments (H = 7.18, df = 4, p < 0.05) but the highest value was only 80% at prey concentration of 15 ml^{-1}, and dropped to only 10 to 20% for the other highest prey concentrations (Fig. 3a). Fish gut fullness was not significant among copepod prey density (H = 4.87, df = 4, p > 0.18). Gut fullness values were lower than those fish fed with *A. franciscana* nauplii (Fig. 3b). The gut fullness of fish larvae varied significantly among different *B. plicatilis* prey concentration treatments (H = 8.86, df = 4, p < 0.03), and decreased with increasing prey density (Fig. 3c).

Feeding behaviour

The feeding mechanism of *S. guttatus* early juveniles observed from video-recordings was similar at different *A. franciscana* prey concentrations. There was no clear difference in fish capture speed on *A. franciscana* prey despite fish size variation. However, when fed with 30 *B. plicatilis* individuals ml^{-1}, fish feeding was short-lived because fish abruptly stopped feeding. Between *A. franciscana* and mixed copepod as live prey, fish fed longer with the former compared to when offered with the latter type of prey. But

among the three live preys, *B. plicatilis* incited the shortest feeding duration. Fish performed a series of thrusting body movement towards the prey and mouth suction feeding, but copepod prey evaded by a darting movement away from fish. The fish had to be very quick for a successful capture of a copepod prey. Furthermore, all early juvenile siganids were often observed to feed only on suspended or swimming live prey. Live prey that settled on the bottom of the aquarium was no longer eaten. All types of live prey given to fish were observed to have settled in approximately 10 minutes. The higher the concentration of live prey, the longer it takes for live prey to settle. The fish are very aware of its environment as they can easily detect any moving object which can trigger the fish to swim to a corner away from the moving object.

In terms of detection of prey, as soon as a single live prey was approximately 10 mm away (i.e. reactive distance), the fish opens its mouth and, by bucco-pharyngeal suction-feeding mechanism, suck and ingest the prey (Fig. 4.). However, due to the absence of modeling software, speed of larval response to prey was not quantified (i.e., visually estimated to be 2/10th of a second). The search for prey was short if concentration is high. Fish were stationary most of the time in abundant prey. If live prey was relatively less dense due to settling, the fish barely moved.

Discussion

The linear relationship of mouth gape with total body length is expected since increase in mouth size is isometrically related with body size of *S. guttatus*. In contrast, the parabolic relationship between fish body length and the number of gill rakers in the first pair of gill arch revealed a peak at 25 to 30 mm fish length, then declined at >30 mm. This is an important finding because >25 mm long *S. guttatus* is already regarded as young fish and can be weaned from particulate food (Duray, 1998). This study shows that early juveniles of *S. guttatus* within 25 to 30 mm still have more gill rakers that can capture particulate food, but juveniles beyond 30 mm in length can already be fed brown macroalgae (Kohno *et al.*, 1986).

The functional responses by large and medium *S. guttatus* early juveniles to increasing *A. franciscana* nauplii concentration were all curvilinear matching a Holling Type II functional response. The exponential curve shows an increasing predation rate phase at low prey concentration until a stable maximum rate was achieved. In addition, medium and large fish showed comparable maximum mean consumption rate on *A. franciscana* nauplii. This study identified ideal *A. franciscana* nauplii prey concentration to *S. guttatus* early juveniles at 15 prey mL^{-1}, a value half the prey density that is regularly given to juvenile *S. guttatus* in the hatchery.
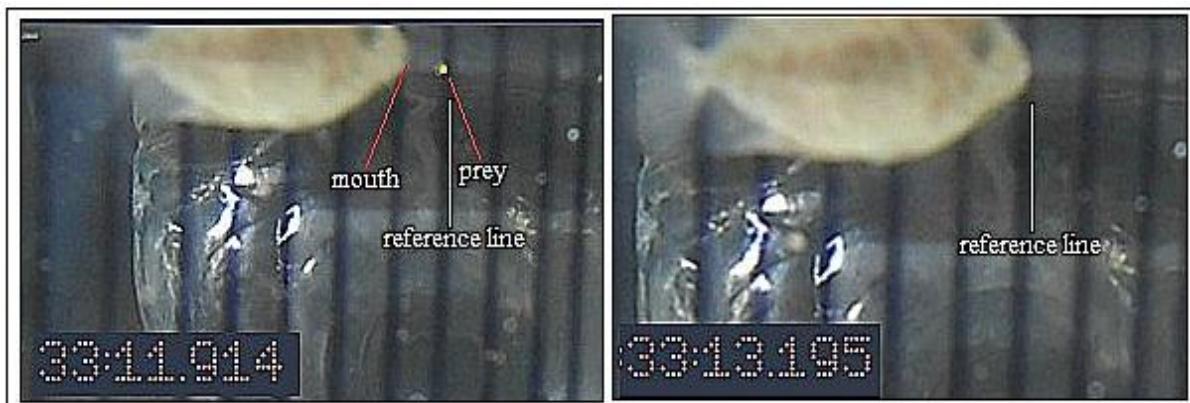
Fig. 4. Reactive distance and feeding speed of large *S. guttatus* early juvenile. (1 grid = 10mm; time = second:millisecond).

A Holling Type II functional response curve is commonly observed among invertebrate predators (Holling, 1965). However, the curve has also been reported in larval fish feeding experiment (Houde and Schekter, 1980). This type of functional response has been attributed to prey vulnerability that varies according to prey types and their escape abilities (Drenner *et al.,* 1978), predator hunger and feeding physiology (Yen, 1983), aggregative behaviour of both prey and predator (Folt, 1985), and temperature (Fulton, 1983). In this study, *A. franciscana* nauplii were most ideal as prey for medium and large *S. guttatus* early juveniles. The higher ingestion rates in these fish size categories may also be attributed to the motion introduced by the plankton roller we used during the feeding experiment. It is speculated that these water movements increase rates of encounter and successful capture by the larvae. The increased encounter rate between predator and prey due to water movements has been reported (Rothschild and Osborn, 1988; Kils, 1992).

In contrast, the functional response of small *S. guttatus* did not fit to any of Holling's models as it showed a parabolic or dome-like curve, although the fish still showed a peak predation rate at 15 mL^{-1} prey density. This finding for the small fish *S. guttatus* can be attributed to being an ineffective predator for *A. fransiscana* nauplii in the context of prey density and feeding biomechanics. We believe that at 15 mL^{-1} prey concentration the small fish have reached a saturation point with their small stomachs already filled up.

The one hour experimental period was not enough for the fish to empty their stomach explaining the sudden drop in predation rates. The small fish may have suddenly stopped ingesting prey as their stomachs are already full at prey concentrations > 15 mL^{-1}. Apart from gut fullness, the decrease in predation rate beyond 15 mL^{-1} may also be attributed to confusion of the predator to high density of *A. franciscana* nauplii as reported by Gulbrandsen (2001).

Predation rates for wild mixed copepods and *B. plicatilis* also did not match any of the Holling's types of functional response. Evasive prey behaviour of wild copepods and small size of *B. plicatilis* render these prey types less ideal for early juvenile *S. guttatus*. The

low predation rates on copepods and only by large *S. guttatus* early juveniles may indicate low capture efficiency for adult calanoid copepods (Graeb *et al.*, 2004). Low predation rates have been associated with the extremely agile and fast swimming attributes of adult calanoid copepods (Yen, 1982; Greene and Landry, 1985; Ohman, 1988).

The high frequency of this prey type from gut content analysis in many fish larvae may be attributed to eating younger calanoid stages with weak escape motility (not tested in the present study) or moribund adult calanoid copepods. Feeding of *B. plicatilis* by the small size *S. guttatus* only is expected (Dhont *et al.*, 2013). Being small requires small prey as well (Conceição *et al.*, 2010). Thus, evasive prey behaviour of wild copepods and small size of *B. plicatilis* render these prey types less ideal for early juvenile *S. guttatus*.

The observed feeding behaviour of juvenile *S. guttatus* when offered with the rotifer prey *B. plicatilis* was short-lived feeding, i.e. fish suddenly halted then completely stopped moving. When fed with mixed copepod, feeding was relatively longer than that with *B. plicatilis*. *A. franciscana* feeding was the longest duration among live prey – even much longer in higher concentrations. Our present results are consistent with the findings that *S. guttatus* >8 mm total length would prefer *Artemia* sp. nauplii over *B. plicatilis* (Hara *et al.*, 1986).

Predation may not be limited by prey ingestion and handling time considering the very short duration associated with these processes. Again, prey morphology and escape tactics/behaviour may partly explain variability in predation rates. Gerritsen and Strickler (1977) noted that although their model predicts that increased swimming speeds of a cruising invertebrate predator would mean increased encounter rate with its prey, this does not necessarily cause increased prey ingestion rates. This is so because in real situations prey escape abilities may reduce their chance of being ingested after encounters with predators.

Conclusion

We conclude that predatory functional response of medium and large early juveniles of *Siganus guttatus* matches type II of Holling's model when fed with *Artemia franciscana* nauplii. However, small early juveniles fed *A. franciscana* nauplii and *Brachionus plicatilis*, and large fish fed wild copepods did not show any of the three types of Holling's functional response models. Our results further showed that the ideal *A. franciscana* concentration as live feed is 15 per mL, which is half those regularly provided to the fish in the current rearing procedure. We also recommend that early *S. guttatus* juveniles of 25 to 30 mm total length should still be fed with particulate food that may include both artificial feeds and live zooplanktonic food.

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