

Research Article

Cite this article: Caasi OJC, Gosselin LA, Juinio-Meñez MA (2023). Size-dependent predation on juvenile sandfish, *Holothuria scabra* by seagrass-associated crabs. *Journal of the Marine Biological Association of the United Kingdom* **103**, e84, 1–13. <https://doi.org/10.1017/S0025315423000735>

Received: 21 March 2023
Revised: 8 September 2023
Accepted: 17 September 2023

Keywords:

Crab predation; *Holothuria scabra*; prey size selection

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Size-dependent predation on juvenile sandfish, *Holothuria scabra* by seagrass-associated crabs

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Abstract

High mortality of juvenile *Holothuria scabra* in seagrass nursery areas has been attributed to predation. In this study, laboratory and field experiments were conducted to determine the effect of the size of two seagrass-associated crabs, *Thalamita crenata* and *Dardanus megistos*, on the survival of juvenile sandfish at different sizes (1–10 g). Small juvenile sandfish (1–2 g) offered in field trials were more preferred by small *Thalamita* and large *Dardanus*. Non-lethal damage caused by both crabs were also evident, indicating differences in the mode of attack and consumption. The incidence of non-lethal wounds in medium and large juveniles in the laboratory indicate higher incidences of unsuccessful attacks by the crabs. Differences in consumption rate may be related to cheliped morphology and handling techniques, and activity patterns affecting encounter rates. Mortality rates of juvenile sandfish due to *T. crenata* (CW: 4.30–7.05 cm) ranged from 10–43%, while those by *D. megistos* (SL: 0.90–2.3 cm) was even higher at 34–53% after 24 h trials. This is the first report that a hermit crab *D. megistos* is a significant predator of juvenile sandfish. Results provide new insights on crab–soft-bodied prey interactions in tropical seagrass areas. These are also important considerations in stock restoration and ocean-based culture. Given that juveniles (≤ 10 g) are very vulnerable to predation by these common crab species, growing sandfish to larger sizes is essential prior to release in the field.

Introduction

Predation is a major factor affecting prey populations in marine macro-benthic communities. Predators may feed indiscriminately or selectively depending on prey availability, with many potential factors contributing to selection patterns that may be observed (Sih and Moore, 1990). In many aquatic species, body size can be a contributing factor for both predator and prey, directly influencing the outcomes of predator–prey interactions (Gribben *et al.*, 2020), especially in earlier life stages where mortality is more apparent (Palmer, 1990; Gosselin and Qian, 1997). In addition, changes with ontogeny in both predator and prey become more evident with size, with prey exhibiting more robust escape responses while predators increase gape size (Scharf *et al.*, 2000). Thus, predator–prey relationships are important in evaluating foraging success among species.

Holothuria scabra, or sandfish, is a holothurian found in seagrass areas endemic to the Indo-Pacific region. During earlier stages, juveniles in the wild settle on seagrass leaves as grazers (Mercier *et al.*, 2000a) before shifting as deposit-feeders onto sand as they grow (Mercier *et al.*, 2000b). It is among the most commercially valuable sea cucumber species processed as *trepan* (Hamel *et al.*, 2001; Conand, 2005). With the rise of global demand and value of *trepan*, coupled with unsustainable fishery practices and overharvesting, the wild populations of this species have been drastically reduced, resulting to its inclusion in the IUCN red list as an endangered species (Hamel *et al.*, 2013). Given the high market demand and price, the culture of this sea cucumber has been explored to increase production and for restoration of depleted populations in many countries (Purcell *et al.*, 2012; Juinio-Meñez *et al.*, 2013). The use of ocean-based nursery systems has been employed for sandfish juveniles following their hatchery-rearing phase to attain the recommended release size of ≥ 3 g (Purcell and Simutoga, 2008; Juinio-Meñez *et al.*, 2012a, 2017), whereas the establishment of grow-out systems in seagrass areas are commonly used for rearing sandfish up to sexual maturity and harvest (Eriksson, 2012). While culture techniques for juvenile production are well-developed (Agudo, 2006; Duy, 2010), high mortality remains a major bottleneck in sea cucumber restocking or grow-out production, mainly due to predation (Bell *et al.*, 2005; Robinson and Pascal, 2012).

Many known predators of sandfish, such as fishes, seastars, crustaceans, and gastropods, are found in seagrass areas where juveniles are commonly released (Francour, 1997; Dance *et al.*, 2003; Pitt and Duy, 2004a; Ceccarelli *et al.*, 2018). Crustaceans are known sea cucumber predators, of which 14% are crabs (Francour, 1997). The crenate swimming crab, *Thalamita crenata* has been reported to feed intensively in many sandfish grow-out areas (Lavitra *et al.*, 2009, 2015; Hair *et al.*, 2016; Altamirano *et al.*, 2017; Ceccarelli *et al.*, 2018). A recent report by Eeckhaut *et al.* (2020) has shown that small *T. crenata* (Carapace Width, CW: 5 cm) were able to cause lesions among juvenile sandfish ≤ 100 g in pens in less than two

weeks. Some hermit crabs have also been suggested to feed on sea cucumbers (Kropp, 1982), but studies on their predation on juvenile sandfish are lacking. The white-spotted hermit crab, *Dardanus megistos*, is a decapod crustacean commonly found in intertidal reef flats. It is known to feed on fishes and a variety of invertebrates in the intertidal zone, such as bivalves, polychaetes, several species of echinoderms (reviewed in Martin, 2012) and gastropods, mainly to obtain their shells (Ribeiro *et al.*, 2017). The species is described to be an omnivorous generalist (Ingle and Christiansen, 2004) and opportunistic predator or scavenger (Lancaster, 1988). *Dardanus megistos* has been observed to feed on juvenile sandfish (Dumalan *et al.*, 2014, unpubl. data); however, whether this species is a significant predator of sandfish juveniles has not been systematically evaluated. Given the widespread distribution of these species, investigation on the potential effects of size-related factors on juvenile sandfish survival is warranted. No study has explored whether crabs selectively choose juvenile sandfish based on size or the relative threat of different crab species on juvenile sandfish survival.

Crabs are known to feed on shelled prey selectively (Arnold, 1984; Hughes and Seed, 1995; Ray-Culp *et al.*, 1999; Smallegange and Van der Meer, 2003), including conspecifics (Fernandez, 1999). Feeding in crabs is reported to be influenced by claw effectivity and chela size limits (Pickering and Quijón, 2011). Depending on a certain diet, generalist and specialist portunid crabs differ in claw structure. Meanwhile, heterochely was observed for predatory hermit crabs (Caine, 1975). Predation is often size-dependent where both advantages and constraints may arise from encounter up to consumption (Woodward and Warren, 2007). Size-dependent mortality of juvenile sandfish in field enclosure studies suggest that vulnerability to predation decreases with size (Purcell and Simutoga, 2008; Purcell, 2009) and although 3 g is a minimum size suggested for juvenile sandfish for release, larger sizes (>20 g) may have improved survival (Battaglione *et al.*, 1999; Pitt and Duy, 2004a). Studies on predation by *T. crenata* have provided initial mortality estimates of juvenile sandfish in field experiments using pens (Lavitra *et al.*, 2015; Eeckhaut *et al.*, 2020), impacting sandfish rearing operations. The present study examined predation by two species of crabs as a function of crab and juvenile sizes, focusing on 1–10 g juvenile sandfish that have been reared in the hatchery.

Size-scaling experiments with sandfish juveniles and crab predators, *T. crenata* and *D. megistos* were used in both in the field and the laboratory to test (1) whether crabs consume juvenile sandfish at different rates based on size of the crab, and (2) if there is preference, whether the preferred prey size varies as a function of the size of the crab. In addition, the relative predation threat of the two crab species was evaluated. The results of this study provide implications to sandfish restocking and ocean-based culture and insights into the predation by crabs on soft-bodied prey such as juvenile sandfish.

Materials and methods

Source of juvenile sandfish and crabs

Holothuria scabra juveniles used in the experiments were from a single batch produced from wild broodstock collected within the Bolinao – Anda reef complex in Pangasinan, Philippines. The broodstock were induced to spawn following the methods modified from Agudo (2006) used at the University of the Philippines' Marine Science Institute (UPMSI) Bolinao Marine Laboratory (BML) hatchery. Juvenile sandfish used in the study were hatchery-reared for ~40 d and reared in an ocean-based floating hapa system for ~60 d to attain different-sized individuals. Juveniles were then transported to the hatchery for sand-

conditioning (Juinio-Meñez *et al.*, 2012b) which lasted for two weeks prior to use in experiments.

Crenate swimming crabs (*T. crenata*) and white-spotted hermit crabs (*D. megistos*), hereafter referred as *Thalamita* and *Dardanus* respectively, were purchased from fishermen in Bolinao, Pangasinan prior to the experiment. Only undamaged male crabs in the late inter-molt stage were utilized to avoid morphological and behavioural differences, sex-specific feeding responses (Ebersole and Kennedy, 1995; Mascaro *et al.*, 2003), or possible sex-related variations (Barbeau and Scheibling, 1994). Collected crabs were brought back to the BML hatchery and allowed to acclimate in an individual partition ($L \times W$: 25 × 30 cm) within 400-l tanks provided with continuous aeration and flow-through seawater. Each crab was fed with fish *ad libitum*, and any residual food was removed in each tank after 24 h. Crabs were then starved for 48 h before experimentation to standardize conditions among individuals and were only used once to ensure independence in the experiments.

Two crab sizes were used in the experiments, small and large, mainly differentiated by weight. In addition, *Thalamita* sizes (Table 1) were quantified using differences in carapace widths (CW), measured as the distance between the two most distal marginal teeth (Barbeau and Scheibling, 1994). For experiments using *Dardanus*, specimen measurements were done following the methods of Ribeiro *et al.* (2017) where shell aperture length (SAL), width (SAW), and shield length (SL) were measured (Table 2). CPCe ver. 4.1 (Kohler and Gill, 2006), a software that determines dimensions utilizing user-based assigned endpoints, was used in all crab measurements.

Predator confirmatory tests

Initial feeding trials were conducted at the BML outdoor hatchery to confirm whether the crabs consume juvenile sandfish. Sand-bedded (~5 cm depth) circular basins ($d = 44$ cm) were used as an arena to test feeding by crabs. Eight individuals of each crab species were used in the experiments; these were starved for 48 h prior to use and were acclimated in respective tanks for 24 h. After predator acclimation, five juvenile sandfish (3.45 ± 1.33 g, mean \pm STD) were then offered to individual *Thalamita* (CW: 4.8–6.3 cm; 50.12 ± 6.35 g) and *Dardanus* (SL: 1.2–1.7; 164.16 ± 28.45 g) crabs by scattering the juveniles around each basin. The juveniles were placed in each basin at 3 pm, when the juveniles are known to be actively foraging and emerged on top of the sediment (Sinsona and Juinio-Meñez, 2018). After 24 h, the number of juveniles consumed was determined.

Prey size preferences by crabs in the field

Sandfish size preferences of each crab species size class were examined in the field within enclosures. The enclosures, made from mesh nets (mesh size: 4 mm) and bamboo stakes, were constructed within the Victory Sea Ranch, Bolinao, Pangasinan ($16^\circ 23'05.78''$ N, $119^\circ 58'10.78''$ E). Each enclosure was ~1.6 m in diameter and 0.8 m deep, with an area of 2 m². Enclosures were placed in a suitable area of a shallow subtidal flat where seagrass is sparse, to ensure that the enclosures were securely placed in a

Table 1. The total weight, shell, and claw measurements (mean \pm SD) of the two size classes of *Thalamita* used in the study

Size class	Weight (g)	Carapace width (CW) (cm)	Left claw length (CL) (cm)
Small	39.38 \pm 1.77	5.26 \pm 0.80	2.79 \pm 0.31
Large	65.71 \pm 9.76	6.64 \pm 0.61	4.05 \pm 0.51

Table 2. The total weight, shell, and claw measurements (mean \pm SD) of the two size classes of *Dardanus* used in the study

Size class	Weight (g)	Shell aperture length (SAL) (cm)	Shell aperture width (SAW) (cm)	Shield length (cm)	Claw length (CL) (cm)	
					L claw	R claw
Small	44.13 \pm 11.34	4.51 \pm 1.39	2.75 \pm 1.34	0.90 \pm 0.47	1.76 \pm 0.72	1.22 \pm 0.43
Large	101.86 \pm 12.08	8.99 \pm 0.83	5.09 \pm 1.52	2.10 \pm 0.39	2.59 \pm 0.61	1.82 \pm 0.67

relatively flat substratum. The entire bottom mesh of the net was then buried within approximately 15 cm of sand to provide a natural substratum to the enclosed predator and prey (Figure 1B). Shell debris and benthic animals were removed from within each enclosure by handpicking to prevent possible interferences in the experiment. Each enclosure was covered with a mesh net to prevent the escape of predator or prey, and to prevent the entry of other potential predators. Temperature and light were measured using HOBO™ pendant loggers deployed in a haphazardly selected enclosure. During field trials, tide levels over a 24 h period ranged from -0.07 to 0.68 m and 0.11 – 0.69 m in trials using *Thalamita* and *Dardanus*, respectively (Supplementary Figure S1). Tide data during experimental trials were retrieved using the software WXTIDE32 4.7 (Informer Technologies Inc., 2002). Average water temperature across trials was $30.95 \pm 2.72^\circ\text{C}$ and daytime maximum light intensities at the field site ranged from 2473–23,642 lux. No rainfall was recorded during any of the field trials.

Crabs that have been acclimated and starved in the hatchery were then transferred into individual polyethylene net cages ($L \times W \times H$: $24 \times 16 \times 11$ cm) prior to transport to the field. Crabs were held inside cages within their respective enclosures for 6 h to acclimate before the start of the experiment (Figure 1A).

Juvenile sandfish were weighed on the day of their release within enclosures. Sandfish juveniles were allowed to expel excess water, and then blotted dry on paper towels before weighing to the nearest 0.1 g.

The experimental design was: 2 crab species \times 2 size classes per crab species \times 10 replicate crabs per size class, and each crab was

offered 14 juvenile sandfish (7 juvenile sandfish per sandfish size class). The two juvenile sandfish size classes were: Small (1.57 ± 0.46 g) and Large (5.22 ± 0.82 g). Juveniles were transferred into each enclosure to acclimate for 6 h, after which crabs in each enclosure were released from their acclimation cages. The experiment lasted 24 h, after which the proportion of different sizes of juvenile sandfish consumed (number per size group) and its associated biomass were measured.

Juvenile sandfish were retrieved the following day by thoroughly scouring the sediment for 1–2 h, and handpicking juveniles found within each pen (Figure 1C). Since enclosures had a closed bottom, nets were also removed to locate juveniles that could not be found near the top layer of the sediment.

Prey size preferences by crabs in the laboratory

Laboratory trials were conducted to test whether crabs would exhibit prey size preferences in controlled conditions as well as to evaluate predator and prey behaviours related to crab consumption rates. Choice feeding trials were conducted at the BML hatchery using twelve blue rectangular polyethylene tanks ($L \times W \times H$: $150 \times 90 \times 40$ cm) supplied with continuous aeration and flow-through seawater. Each tank had a sand bed of previously cleaned and dried sediment (5 cm depth) as substrate. Water levels within each tank were maintained at 30 cm to prevent predators from escaping. To monitor light intensity and temperature within the tanks, a HOBO™ logger was placed in a haphazardly selected control tank. Mean temperature in trials

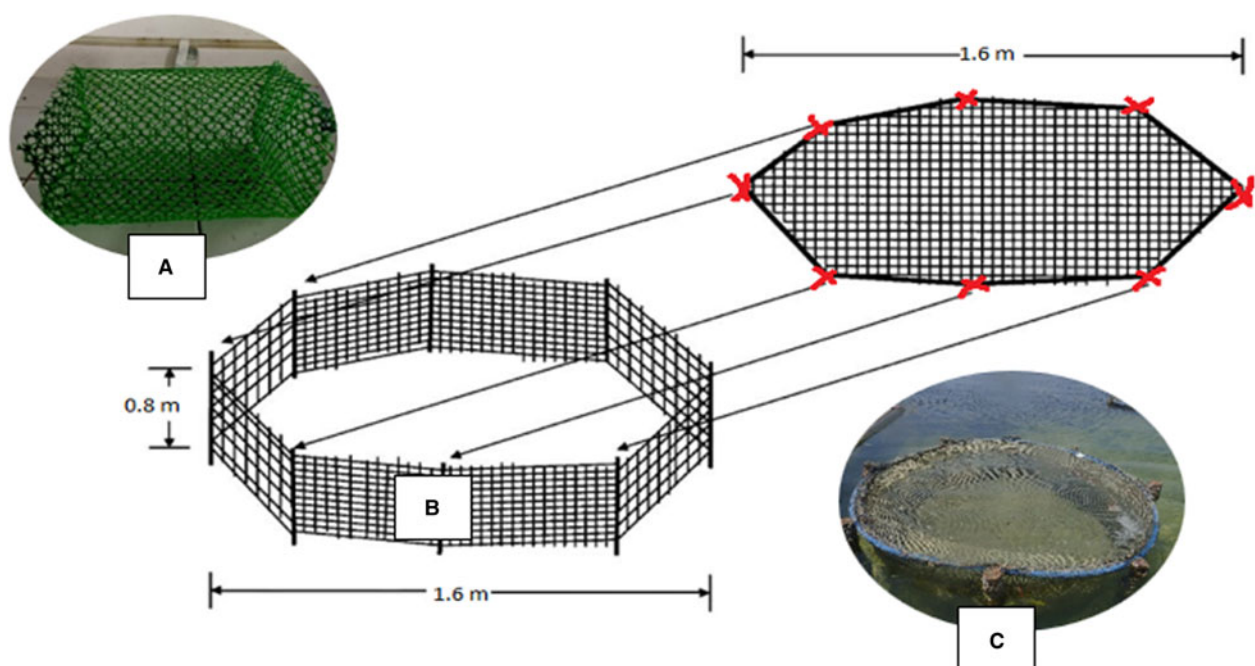


Figure 1. (A) Cages used for crab transport and acclimation in the field. (B) Schematic diagram of pen enclosure design, modified from Brennan *et al.* (2006). The mesh net was tied onto bamboo stakes (red marks) while the entire bottom will be buried approximately 15 cm in the sand. (C) Actual photo of enclosure in the field.

was at $27.4 \pm 0.9^\circ\text{C}$ while mean light level was 2142.5 ± 2036.2 lux, respectively.

Tanks were divided into two unequal portions where both predator and prey were allowed to acclimate. Crabs were acclimated first, confining each individual in an area ($L \times W$: 50×90 cm) directly below the water input using a polyethylene net as a permeable barrier for 24 h. During acclimation, general behaviours of crabs were scored every 6 h for 24 h (total of 4 direct observations) following the ethogram in Table 3. For *Thalamita*, three general behaviours (buried, emerged, and active) were identified and assigned to a corresponding score in the ethogram. This was similarly done for *Dardanus*, however using only behaviours 1 and 2, since the hermit crab is not capable of burying totally. After 24 h, juvenile sandfish were released in tanks to acclimate from 0900–1500 h, corresponding to the diel activity pattern of sandfish when they are mostly at the sediment surface (Mercier et al., 1999). Direct observations of the burying behaviour of juvenile sandfish were then carried out after release by counting emerged individuals in each treatment every 30 min for 2 h, from 0900–1100 h. Crabs were then released from their individual chambers by removing the polyethylene net barrier to freely move in the entirety of the tank.

The experimental design was: 2 crab species \times 2 size classes per crab species \times 8 replicate crabs per size class (+8 control tanks). Fifteen sandfish, five from each of the three size classes, were simultaneously offered to each individual crab size class. There was no crab in the control tanks to determine possible non-predator mortality during the experiment. Juvenile sandfish from each size class had mean weights of 1.43 ± 0.29 g (Small), 3.95 ± 0.36 g (Medium), and 9.55 ± 0.95 g (Large). The study was conducted for 24 h, after which the sediment in each tank was searched thoroughly for 1–2 h to harvest the remaining juvenile sandfish. The proportion of the different sizes of juveniles consumed (number per size group) was then counted per treatment.

Survival and consumption estimates

For both field and laboratory experiments, consumption by crabs was categorized when the entire sandfish was consumed by the crab, with no remnants remaining in the tank. In addition, dead juveniles that were partially consumed (e.g., gut exposure) and those with severe wounds on different portions of the body wall causing evident disintegration of the body wall that will unlikely survive were recorded as sandfish mortality. Non-lethal damage was based on live juveniles that had wounds on their body wall but with no signs of body wall disintegration.

In addition to the number of juveniles consumed per size class, the consumed biomass in each replicate was also analysed per crab size for both species. Initial total biomass was determined as the sum of all juveniles per size class in each replicate. Consumed biomass was estimated by subtracting the pooled weight of the live juveniles and the body remains per size class at the end of the 24 h experiment from the total juvenile biomass at the start of

Table 3. Ethogram of crab behaviour within tanks

Score	Crab behaviour	Description
0	Buried	Full body in sand; only eyes are visible.
1	Emerged	Crab is emerged but not moving.
2	Active	Crab is moving around the tank; possible searching behaviour.

Behaviours were derived from initial observations of crab activities within a 24 h period.

the experiment. Crabs that did not feed on juvenile sandfish were not included in the analyses.

Analyses of data

Data were first tested for normality and heterogeneity using the Shapiro–Wilk test and Levene’s test, respectively; when needed, data were transformed to satisfy assumptions of normality and heteroscedasticity. In cases where normality assumptions were not met, non-parametric tests were used. To achieve datasets large enough for meaningful statistical analysis, juvenile size preferences of each crab size class was determined by pooling the number of juveniles per size class consumed in 24 h from all replicates for both crab species, in field and laboratory trials. χ^2 tests were then used to compare consumption among juvenile sizes within crab size for both species, following Pusack et al. (2018). χ^2 tests were employed to determine whether prey size preferences differed among crab sizes when offered two and three juvenile sizes in the field and the laboratory, respectively. The non-parametric Mann–Whitney U was used to test for differences between crab size classes in the mean number of juveniles consumed, the biomass consumption of juveniles per crab size class and the mean total average biomass consumed. Further, the mortality of juvenile sandfish, all three sandfish size classes combined, was compared between crab species to assess the relative threat of each crab species to juvenile sandfish using a Mann–Whitney U test.

The activity behaviours of crabs scored every 6 h for 24 h (total of 4 direct observations per crab size) during acclimation in laboratory trials were described according to the ethogram presented. Data on juvenile sandfish burying behaviour did not conform with normality assumptions, and therefore juvenile burying behaviour in the three treatments (small, large crab, and control; 4 observations) was analysed using a Kruskal–Wallis test, one analysis for each crab species. All statistical analyses were conducted in Statistica 14.0 (Statsoft, Inc., USA).

Results

Predator confirmatory trials

Both crab species attacked and killed juvenile sandfish. When offered prey of relatively similar sizes for 24 h, *Thalamita* on average attacked 18.8 of the 40 juvenile sandfish (46.9%), and *Dardanus* attacked 36.0 of the 40 juvenile sandfish (90%). In addition, puncture wounds on the lateral sides were common among juveniles that were attacked but were not consumed by *Thalamita*. In contrast, no wounded juveniles were found in the *Dardanus* trials. These trials confirmed that both crab species are predators of sandfish.

Prey size preferences by crabs in the field

Both *Thalamita* and *Dardanus* fed on all juvenile sandfish size classes offered in the enclosures. Total sandfish mortality over a 24 h period ranged from 41.4–43.6% in the *Thalamita* trial, and 53.1–53.2% in the *Dardanus* trial (Table 4a).

Swimming crab (*Thalamita*)

Total mortality of juvenile sandfish (Table 4a) did not differ significantly between *Thalamita* size classes (Mann–Whitney U test, $U = 47.5$, $n = 20$, $P = 0.85$), nor did the crab size classes differ in consumed biomass of large juveniles (Mann–Whitney U test, $U = 35.0$, $n = 20$, $P = 0.28$). Small crabs fed significantly more frequently on small juveniles than on large juveniles (Chi-square

Table 4. (a) Mean total mortality of juvenile sandfish per crab treatment, (b) Mean number of juvenile sandfish that were consumed by two sizes of crabs: *Thalamita* ($n = 20$) and *Dardanus* ($n = 16$), and (c) Total number of juvenile sandfish incurring non-lethal damage per crab in field set-ups after a 24 h period

	<i>Thalamita</i>		<i>Dardanus</i>	
	Small crab ($n = 10$)	Large crab ($n = 10$)	Small crab ($n = 8$)	Large crab ($n = 8$)
(a) Mean total sandfish mortality (%)	41.43 ± 2.78	43.57 ± 7.92	53.06 ± 12.05	53.17 ± 5.20
(b) Mean number sandfish consumed (out of 7 juveniles per size class)				
Small sandfish	3.80 ± 0.39 ^a	2.90 ± 0.60 ^a	4.71 ± 0.81 ^a	5.89 ± 0.35 ^a
Large sandfish	2.00 ± 0.15 ^b	3.20 ± 0.76 ^a	2.71 ± 1.19 ^a	1.56 ± 0.53 ^b
(c) Non-lethal damage				
Small sandfish	1	1	0	2
Large sandfish	4	0	0	1

Values represent mean ± SE. Letters in superscript denote sig. diff. between sandfish size groups consumed per crab size, based on χ^2 tests ($P < 0.05$).

test, $\chi^2 = 15.3$, $df = 4$, $P = 0.005$; Table 4b), but the frequencies of small and large juveniles consumed by large *Thalamita* did not differ significantly (Chi-square test, $\chi^2 = 6.48$, $df = 7$, $P = 0.48$), due to the large variation in the number of sandfish consumed among individual large *Thalamita*. Only one small and four large sandfish had non-lethal wounds after 24 h in the small crab treatment, and a single small juvenile received non-lethal wounds in the large crab treatment (Table 4c). On average, the amount of biomass consumed by large crabs and small crabs did not differ during the 24 h trials (Mann-Whitney U test, $U = 46.0$, $n = 20$, $P = 0.80$, Figure 2A).

Hermit crab (*Dardanus*)

The mortality of juvenile sandfish (Table 4a) did not differ significantly between size classes of *Dardanus* (Mann-Whitney U test, $U = 29.5$, $n = 16$, $P = 0.87$). In addition, small hermit crabs did not show preference for any juvenile sandfish size offered (Chi-square test, $\chi^2 = 7.0$, $df = 6$, $P = 0.32$, Table 4b) while large *Dardanus* fed significantly more often on small juvenile sandfish than on large juveniles (Chi-square test, $\chi^2 = 15.3$, $df = 7$, $P = 0.03$). Only two small and one large sandfish had non-lethal lesions after 24 h in the large *Dardanus* treatment (Table 4c), and no juvenile was wounded in the small *Dardanus* treatment.

The mean number of small and large juvenile sandfish consumed was highly variable among individuals of both size classes of *Dardanus*. As reported for *Thalamita*, there was also no

significant difference between hermit crab sizes in terms of biomass consumed (Mann-Whitney U test, $U = 30.0$, $n = 16$, $P = 0.92$, Figure 2B).

The two crab species did not differ in terms of the total number of juvenile sandfish killed per crab species (large and small crabs combined) (Mann-Whitney U test, $U = 112$, $n = 36$, $P = 0.13$; Figure 3A) or in total biomass consumed per species (Mann-Whitney U test, $U = 151$, $n = 36$, $P = 0.79$; Figure 3B).

Prey size preferences by crabs in the laboratory

Thalamita and *Dardanus* fed on all sizes of juvenile sandfish offered in laboratory trials. Mean total mortality over a 24 h period, all sandfish sizes combined, was 10–32% for *Thalamita* and 34–38% for *Dardanus*. Mean total mortality in the small *Dardanus* treatment was 27.42% higher than in the small *Thalamita* treatment (Mann-Whitney U test, $U = 102.0$, $n = 12$, $P = 0.02$, Table 5a). The absence of mortality and injury among juveniles in the control treatment confirmed that predation was the sole source of mortality.

Swimming crab (*Thalamita*)

Five of the eight replicate crabs in both small and large *Thalamita* trials fed on juvenile sandfish. Mean total mortality of juvenile sandfish (Table 5a) was not quite significantly different between *Thalamita* size classes (Mann-Whitney U test, $U = 3.5$, $n = 10$,

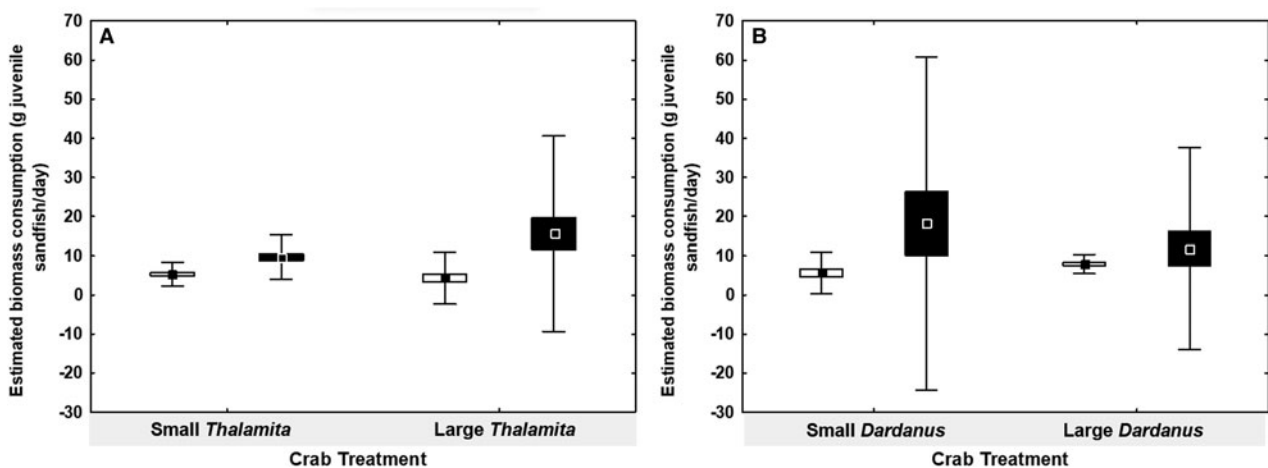


Figure 2. The estimated biomass of small and large sandfish consumed by two size classes of (A) *Thalamita* ($n = 20$) and (B) *Dardanus* ($n = 16$) in field enclosure trials. Boxplots represent small (light) and large (dark) sandfish biomass consumed, respectively. Bars represent standard error.

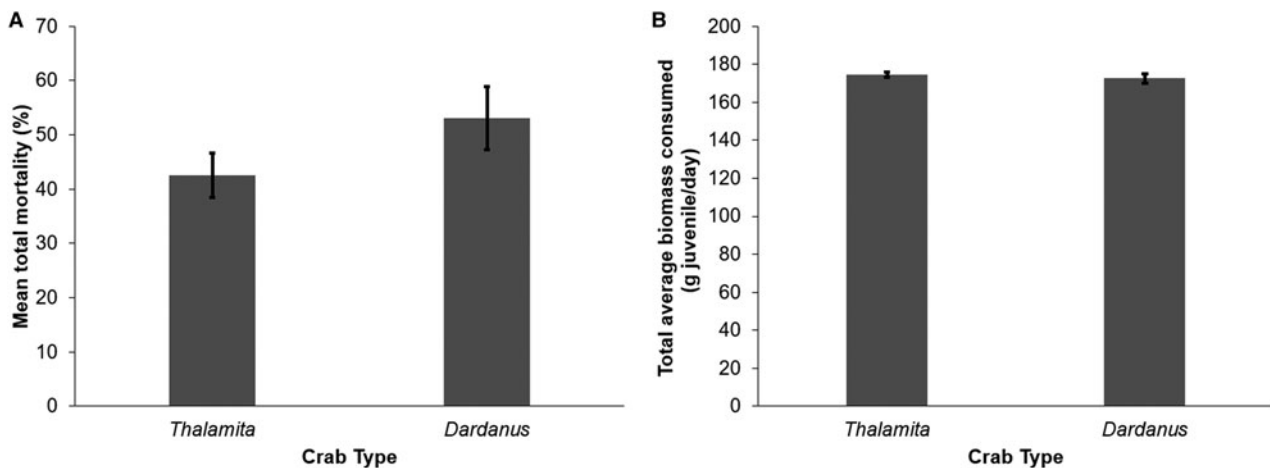


Figure 3. The (A) total mortality, and (B) total biomass of juvenile sandfish consumed by *Thalamita* ($n = 20$) and *Dardanus* ($n = 16$) in field set-ups. Bars represent standard error.

$P = 0.06$). No significant differences in the mean number of juvenile sandfish consumed per size class were observed among small crabs (Chi-square test, $\chi^2 = 3.14$, $df = 8$, $P = 0.53$; Table 5b) or among large crabs (Chi-square test, $\chi^2 = 9.75$, $df = 10$, $P = 0.46$), suggesting no prey size preference. No juvenile sandfish was found with any non-lethal damage in the small crab treatment, while two individuals, one small and one large juvenile sandfish, were wounded in the large crab treatment (Table 5c). Large crabs consumed 61.4% more sandfish biomass than small crabs during the 24 h trials (Mann-Whitney U test, $U = 2.0$, $n = 10$, $P = 0.03$, Figure 4A).

Hermit crab (*Dardanus*)

Juvenile sandfish mortality (Table 5a) did not differ with respect to the size of *Dardanus* (Mann-Whitney U test, $U = 16.5$, $n = 14$, $P = 0.53$). Similar to *Thalamita*, there was no significant difference among juvenile sandfish size classes in the mean number consumed by small (Chi-square test, $\chi^2 = 7.15$, $df = 10$, $P = 0.71$, Table 5b) or by large crabs (Chi-square test, $\chi^2 = 5.4$, $df = 10$, $P = 0.86$) suggesting a lack of size preference by the crabs. Several juvenile sandfish with non-lethal wounds were found after 24 h in the *Dardanus* treatments: 11 individuals in the small crab treatment and 8 individuals in the large crab treatment

(Table 5c). The biomass consumed by both *Dardanus* size classes increased with the size of their sandfish prey (Figure 4B); however, there was no significant difference in estimated consumed biomass between small and large *Dardanus* (Mann-Whitney U test, $U = 18$, $n = 14$, $P = 0.72$).

Pooling the two crab size classes, overall *Dardanus* consumed more juvenile sandfish than *Thalamita* in terms of total average mortality (Mann-Whitney U test, $U = 32.0$, $n = 24$, $P = 0.04$; Figure 5A) and estimated total biomass (Mann-Whitney U test, $U = 28.0$, $n = 24$, $P = 0.02$; Figure 5B).

Non-lethal damage in the field and laboratory

Both crab species inflicted non-lethal damage to juvenile sandfish, in field and laboratory trials. Non-lethal wounds made by *Thalamita* were characterized by punctures on the dorsal and dorso-lateral portion of juvenile sandfish in addition to ventral wounds (Figures 6A, B, 7C). In contrast, wounds inflicted by *Dardanus* appeared as individual craters, mostly found on the dorsal and dorso-lateral portion of juvenile sandfish (Figures 6C, D, 7D). Puncture wounds were found in juvenile sandfish in *Thalamita* trials, whereas crater-like wounds were only present in *Dardanus* trials.

The chelipeds of the two crab species differed in morphology and size. *Thalamita* had equally sized claws, each having pointy

Table 5. (a) Mean total mortality of juvenile sandfish per crab treatment, (b) Mean number of juvenile sandfish that were consumed by two sizes of *Thalamita* and *Dardanus* in a 24 - h period, and (c) Total number of juvenile sandfish incurring non - lethal damage pooled across all crabs in treatment

	<i>Thalamita</i>		<i>Dardanus</i>	
	Small crab ($n = 5$)	Large crab ($n = 5$)	Small crab ($n = 7$)	Large crab ($n = 7$)
(a) Mean total mortality (%)	10.67 ± 2.67*	32.00 ± 6.46	38.09 ± 6.64*	34.44 ± 4.01
(b) Mean number sandfish consumed (out of 5 juveniles per size class)				
Small	0.40 ± 0.08 ^a	2.0 ± 0.84 ^a	2.14 ± 0.40 ^a	2.86 ± 0.76 ^a
Medium	0.80 ± 0.20 ^a	1.80 ± 0.58 ^a	2.43 ± 0.72 ^a	3.71 ± 0.48 ^a
Large	0.40 ± 0.24 ^a	1.00 ± 0.32 ^a	1.14 ± 0.46 ^a	2.29 ± 0.33 ^a
(c) Non - lethal damage				
Small	0	1	2	0
Medium	0	1	5	4
Large	0	0	4	4

Values in (a) and (b) represent mean ± SE. Asterisks denote groups with significant differences among similar size groups between predators, based on Mann-Whitney U tests ($P < 0.05$). Letters in superscript denote sig. diff. between sandfish size groups consumed per crab size, based on χ^2 tests ($P < 0.05$).

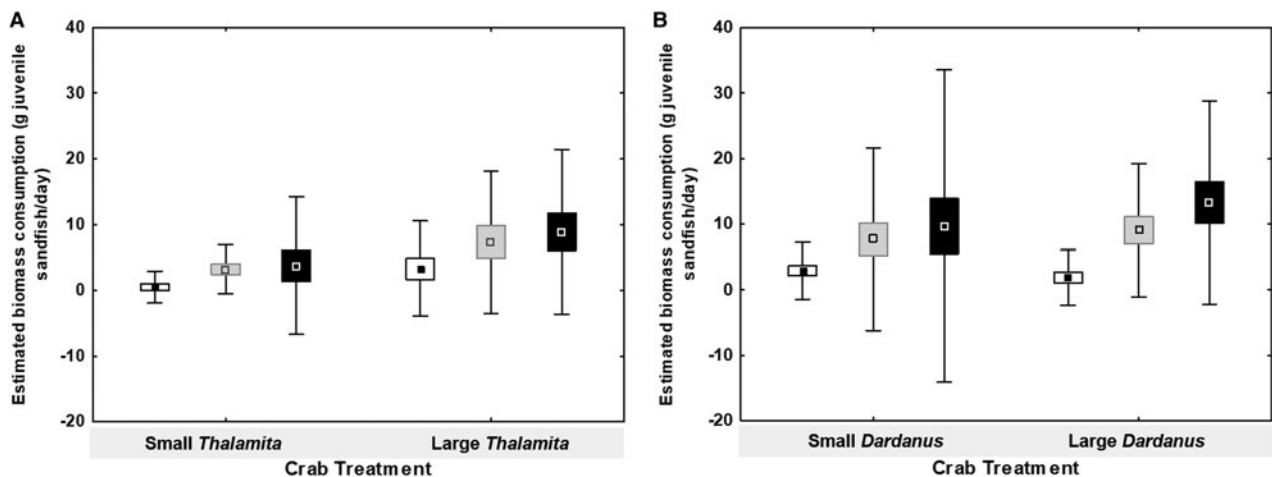


Figure 4. The estimated biomass of juvenile sandfish per size class consumed by two sizes of (A) *Thalamita* ($n = 10$) and (B) *Dardanus* ($n = 14$) in hatchery tank trials. Boxplots represent small (light), medium (gray) and large (dark) juvenile sandfish biomass consumed, respectively. Bars represent standard error.

ends and small tooth-like structures along the bottom dactyl (Figure 7A). In contrast, *Dardanus* had unequally sized claws, with the left cheliped (Figure 7B) approximately twice as large as the right cheliped, both claws being covered with setae and had smooth inner dactyls. Accordingly, the wounds incurred by juvenile sandfish may be attributed to differences in claw design and in prey-handling behaviour.

Predator and prey behaviours

In the laboratory, 27–67% of juvenile sandfish buried themselves in the sediment within 30 min in all treatments of the *Thalamita* trials, including in the controls, while it took approximately 2 h for similar percentages of juveniles to bury in the *Dardanus* trials (Figure 8). In the *Thalamita* trials, the number of buried juvenile sandfish at 0930 h was significantly higher in the small *Thalamita* treatment than in the large *Thalamita* treatment and in the control treatment (Kruskal–Wallis test, $H(2, N = 24) = 16.12$, $P = 0.0004$). At 1000 h, more juveniles were buried in the small *Thalamita* treatment than in the large *Thalamita* treatment (Kruskal–Wallis test, $H(2, N = 24) = 7.77$, $P = 0.03$; Figure 8A) but did not differ from control treatments (Kruskal–Wallis test, $H(2, N = 24) = 0.26$, $P = 1.00$).

In the *Dardanus* trials, the number of buried juvenile sandfish (Figure 8B) did not differ between tanks with small crabs, large

crabs, and the controls at 0930 h (Kruskal–Wallis test, $H(2, N = 24) = 0.91$, $P = 0.63$), 1000 h (Kruskal–Wallis test, $H(2, N = 24) = 3.96$, $P = 0.14$), 1030 h (Kruskal–Wallis test, $H(2, N = 24) = 1.81$, $P = 0.40$), and 1100 h (Kruskal–Wallis test, $H(2, N = 24) = 0.43$, $P = 0.81$). In all treatments of the two predator species, including the controls, 55–80% of juvenile sandfish were already buried within 2 h of placement in tanks.

One of the predator species also buried itself during the trials; 50% of the *Thalamita* buried themselves during daytime monitoring (0600–1200 h). When buried, the entirety of a *Thalamita*'s body was covered by sand, with only its eyes visible on top of the sediment. *Dardanus* did not bury and were always emerged from their shells during the observation periods, but minimal crawling movements were observed regardless of size. No *Thalamita* or *Dardanus* attacked or consumed any juvenile sandfish during the first 2 h after their release in tanks or during subsequent juvenile sandfish behavioural observations.

Discussion

Understanding interactions between predator crabs and juvenile *H. scabra* in seagrass areas provide valuable insights on recruitment success of wild populations. Likewise, the level of predation threat is an important consideration in the release of hatchery cultured juveniles in the wild for restocking and ocean-based culture

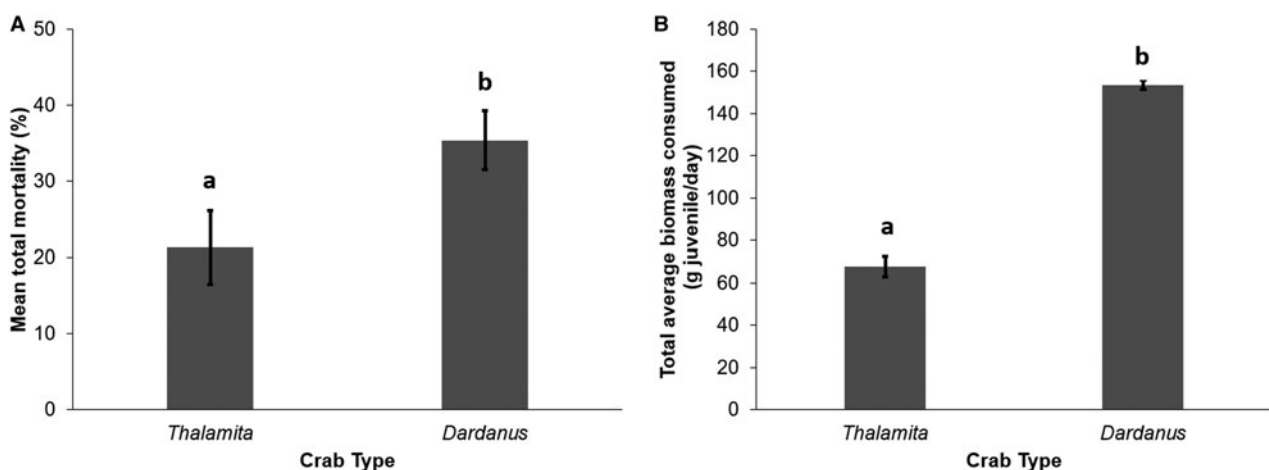


Figure 5. The (A) total average mortality and (B) total average biomass of juvenile sandfish consumed by *Thalamita* ($n = 10$) and *Dardanus* ($n = 14$) in the laboratory. Bars represent standard error. Letters indicate significant differences between crabs (Mann–Whitney U test, $P < 0.05$).

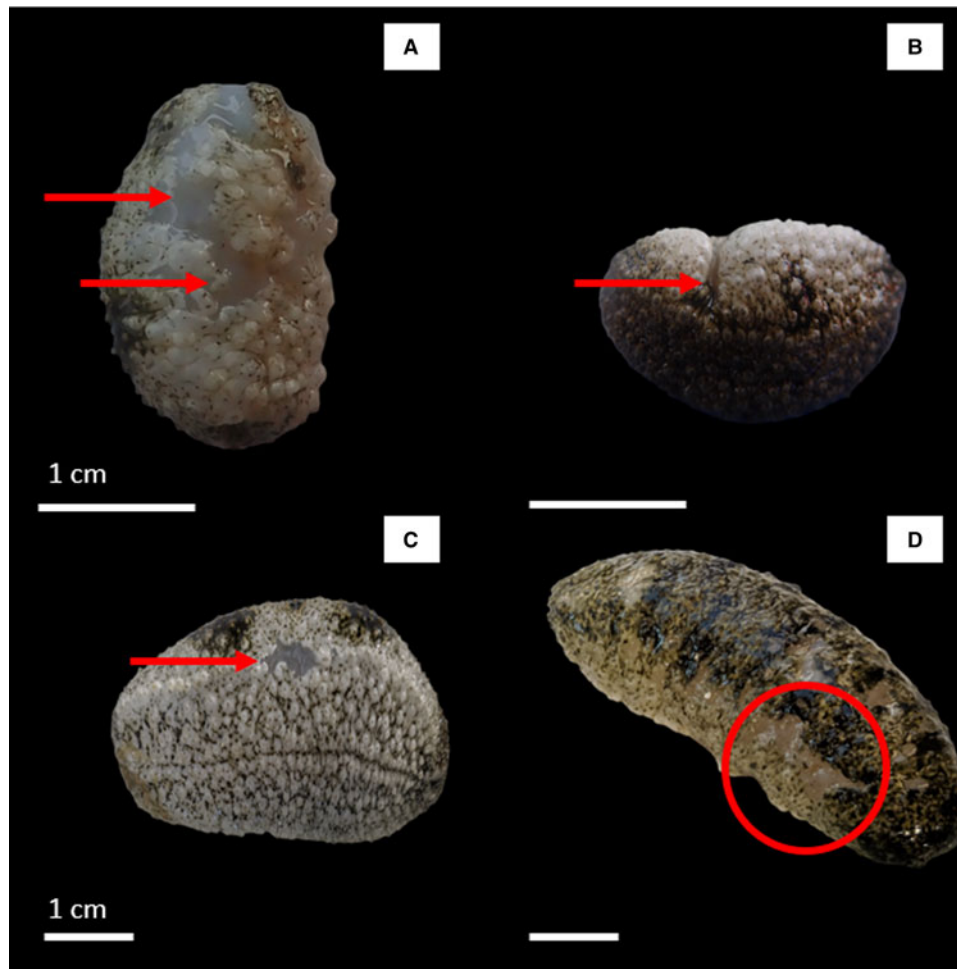


Figure 6. Non-lethal damage among juveniles caused by (A, B) *Thalamita* (C, D) *Dardanus* within enclosures after 24 h. Red marks indicate wounds inflicted by respective predators.

operations. In ocean-based culture operations, predation is often a primary bottleneck (Lavitra *et al.*, 2009; Robinson and Pascal, 2012). Crabs in particular, are often present in pen enclosures and are among the most important consumers of juvenile sandfish (Lavitra *et al.*, 2009, 2015), affecting the growth and survival of juveniles ≥ 3 g (Purcell *et al.*, 2012) and requiring investigation for future mitigation. This study examined the consumption of small and large *T. crenata* and *D. megistos* on juvenile sandfish populations in seagrass areas either through predation or indirect mortality from non-lethal damage (wounds).

Prey mortality and consumption in the field and laboratory

Thalamita crenata and *D. megistos* fed intensively on juvenile sandfish over a relatively wide range (1.0–10.9 g), killing an average of 2.02 and 3.07 juveniles crab⁻¹ day⁻¹, respectively. The size of the experimental units in the laboratory and the field may have limited the crabs' search time and effectively increased encounter rates relative to the natural environment. However, the high consumption rates nevertheless clearly demonstrate that both crab species can cause significant mortality to juvenile sandfish populations.

Juvenile mortality from predation in ocean rearing systems has largely been underestimated by the sandfish aquaculture industry. Predation, specifically by *Thalamita*, can negatively affect sea cucumber farming in areas where crab abundance is high (Lavitra *et al.*, 2015). The present study revealed that sandfish

mortality due to predation by *Thalamita* is likely much higher than previously thought, especially given that crab densities can be as high as 1–4 crabs m⁻² (Cannicci *et al.*, 1996; Eeckhaut *et al.*, 2020). Both trials with either small or large *Thalamita* resulted in high mortality in juvenile sandfish of all sizes offered, where a single small *Thalamita* (4–5 cm CW) can kill an average of 1.7 juveniles and a large one (6–7 cm CW) may kill 2.3 juvenile sandfish in a 24-h period. In addition, estimates of biomass consumption in the laboratory revealed that large *Thalamita* pose a substantial risk to juvenile sandfish upon release. Previous studies reported juvenile sandfish (5–17 g) mortality of up to 95–100% within 5–13 days for *T. crenata* (CW: 5 cm, ~51 g) (Lavitra *et al.*, 2009; Eeckhaut *et al.*, 2020) which is equivalent to about 0.67–0.73 g of juvenile sandfish consumed crab⁻¹ day⁻¹. Our results further highlight that the size of juvenile sandfish at release can greatly affect its survival rate, and that smaller individuals may be more vulnerable to predation by *Thalamita* (4–7 cm CW). Rearing sandfish to larger sizes (≥ 30 g) has been recommended to improve juvenile survival (Lavitra *et al.*, 2009; Eeckhaut *et al.*, 2020). However, the size at which juvenile sandfish becomes considerably less vulnerable to different sizes of *Thalamita* has yet to be determined. The significant loss of juvenile sandfish through predation by *Thalamita* is therefore an important factor to consider when choosing release sites for stock enhancement or restocking, given how quickly these crabs can attack and consume juvenile sandfish.

This study is the first to demonstrate that *D. megistos* is a significant predator of juvenile sandfish. The mortality of juvenile

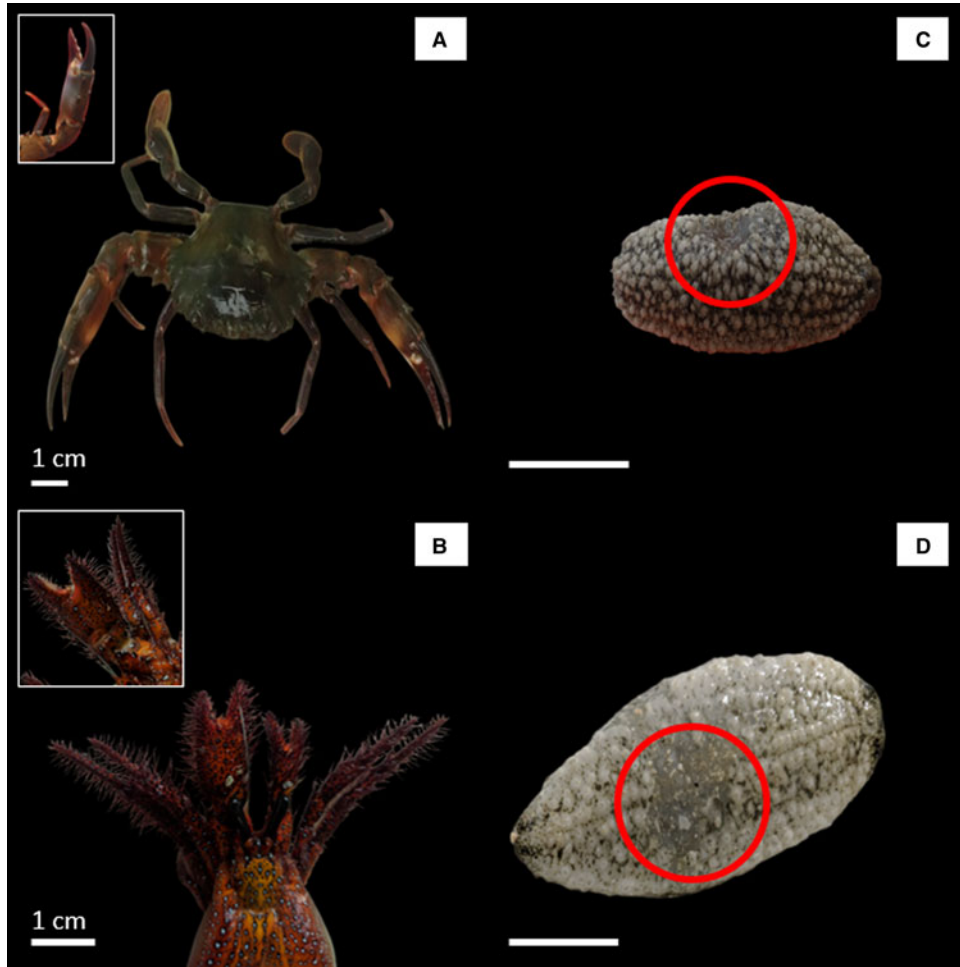


Figure 7. (A) *Thalamita* and (B) *Dardanus* with respective inset photos of chelipeds and their associated wounds (C, D) to juvenile sandfish. Red circles indicate wounds inflicted by respective crabs.

sandfish in both field and laboratory trials was 34–53%, equivalent to an estimate of 2.76 juvenile sandfish consumed crab⁻¹ day⁻¹ corresponding to an estimated biomass of 1.3–50.0 g juvenile sandfish consumed crab⁻¹ day⁻¹ for both trials. These findings show that *Dardanus* is a voracious predator of juvenile sandfish. *Dardanus* consumed more juvenile sandfish in terms of total mean mortality and estimated biomass consumed than *Thalamita* in the laboratory, exceeding initial estimates on

juvenile mortality attributed to crabs. Some hermit crabs are known to be predatory in nature (Gosselin and Chia, 1995), and the consumption of *Dardanus* on juvenile sandfish combined with the frequency of nonlethal wounds among juveniles indicate how aggressive the species is. Moreover, even smaller individuals (SL: 0.90–1.1 cm) were capable of consuming a broad range of juvenile size in field trials. These findings provide new information on the feeding ecology of *Dardanus* and may be useful to

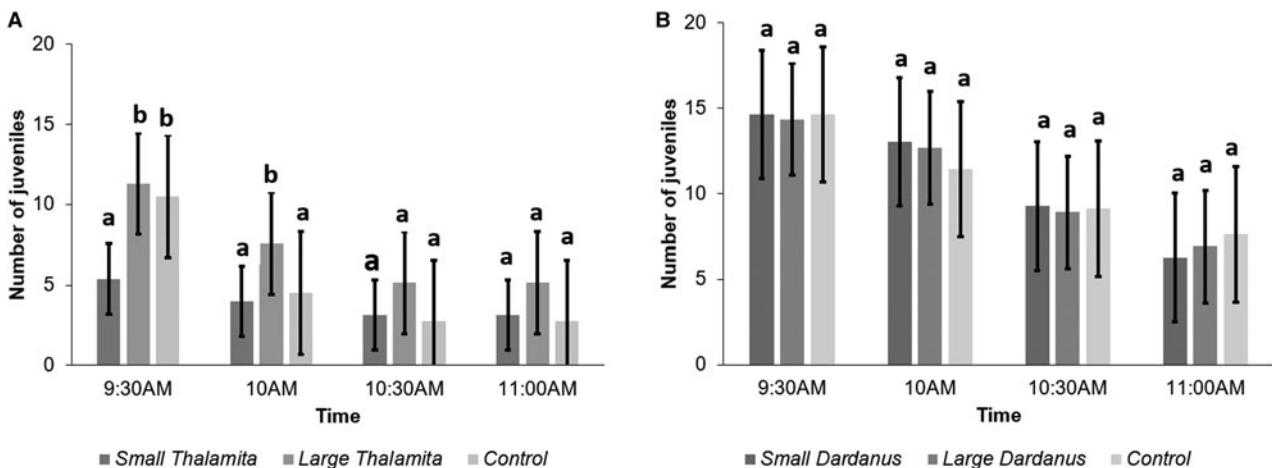


Figure 8. Average number of emerged (not buried) juveniles in small predator, large predator, and control (no predator) treatments. (A) *Thalamita* ($n = 10$) and (B) *Dardanus* ($n = 14$). Bars represent standard error. Letters indicate significant differences (Kruskal–Wallis test, $P < 0.05$).

estimate the predation pressure by this species on juvenile sandfish in seagrass areas where it is also widely distributed (Leite *et al.*, 1998). The results of this study, together with an estimate of the abundance and size distribution of the crabs in a prospective release site (e.g., trapping trials), can be useful in estimating a crab's potential predatory threat.

Prey size preference

Prey size selectivity often dictates the effect of predation in a prey population (Micheli, 1995) with predators subsequently employing mechanisms for identifying prey traits correlated with their potential value (Mascaro and Seed, 2001). Crabs tend to consume individuals below the critical size (Brousseau *et al.*, 2001) foregoing the risk of claw damage (Smallegange and van der Meer, 2003) when feeding on hard-shelled prey. However, claw damage is unlikely when preying on soft-bodied prey such as juvenile sandfish. This may allow crabs to attempt to feed on different sizes of juveniles available, in contrast to prey with shells (Micheli, 1995) or exoskeletons such as shrimps (Mascaro *et al.*, 2003) and amphipods (Blasi and O'Connor, 2016). While *Thalamita* and *Dardanus* fed on all sizes of juveniles, small *Thalamita* and large *Dardanus* in the field showed preference for small juveniles; in addition, small to medium sized prey were consumed more often in the laboratory trials. Overall, in both field and laboratory trials, we observed a trend of higher consumption of smaller juvenile size classes (1–3 g) in all crab sizes for both species. Size limitations on foraging can occur at each stage of the predation process, from the first prey contact up to consumption, typically scaling with body size (Woodward and Warren, 2007) as gape constraints may prevent a predator from feeding on larger prey items (Hart and Hamrin, 1988; Behrens Yamada and Boulding, 1998). Hence, between *Thalamita* and *Dardanus*, physical capture restrictions and handling challenges are probable causes of decreased predation on larger juvenile sizes.

The concept of a size refuge from predators has been well documented in aquatic systems, where prey become less vulnerable to predators as the prey grow larger (Woodward and Warren, 2007). As juvenile sandfish grow, they can be less vulnerable to predators that are gape-limited due to larger individuals having greater body width and thicker body walls (Pitt and Duy, 2004b) which could decrease handling efficiency and subsequently ingestion of larger sandfish. However, feeding on smaller juveniles can also be constrained by swelling of the body, which is a holothurian anti-predatory response (Bourjon and Vasquez, 2016). In this study, large juveniles (1.42–2.43 cm) were almost two-fold wider than the body width of small juveniles, similar to the claw scale of large crabs to small crab counterparts. The difficulty of handling larger prey can lower the chance of a successful predation event (Bromilow and Lipcius, 2017). Our results suggest that the size preferences of *Thalamita* and *Dardanus* were affected by both chela gape limitations and juvenile body width, increasing the probability of survival for larger juveniles. The results of this study lend support to the hypothesis that prey selection and consumption among predators is highly reliant on predator and prey size (Woodward and Warren, 2007), even for soft bodied prey like sea cucumbers that can increase body width. As a result, although a predator's energy reward from prey is expected to increase with larger prey, the energetic cost of handling them may also be higher, conferring a potential advantage of larger (>10 g) juvenile sandfish.

Crab foraging traits

Differences in the types of wounds inflicted by crabs indicate that foraging is linked to both claw morphology and activity patterns.

Claw morphology clearly influenced how both crabs handled sandfish, evident in the varying wounds observed among juveniles. Non-lethal damage caused by *Thalamita* appeared to be puncture wounds occurring on the juvenile's dorso-lateral portions, possibly as a result of its pointed chela tips, described to have cutter claws allowing it to pinch certain prey (Seed and Hughes, 1995) and as effective breakers for hard-shelled prey (Behrens Yamada and Boulding, 1998). In the case of sandfish, its claws may have been used to pin down the juvenile puncturing its side prior to consumption. In contrast, *D. megistos* has unequally sized chelipeds covered with setae, which may trap food material aiding in prey capture and handling similar to other *Dardanus* species (Caine, 1975). Non-lethal damage among juvenile sandfish was more common in *Dardanus* trials than in *Thalamita* trials, with wounds inflicted by *Dardanus* occurring in different portions of the body wall. The frequency of wounds in different parts of the juvenile body wall suggests *Dardanus* may have been able to handle large juvenile sandfish more efficiently than *Thalamita*. Scrapes forming craters were evident on the dorsal and ventral body wall and often resulted into body wall disintegration as well, especially when there were several wounds. The high frequency of non-lethal wounds inflicted by both crab species on juveniles may result in even higher juvenile mortality rates than estimated.

Predation rates are likely affected by the activity pattern of each crab species. In natural conditions, synchrony in the activity of the predator and prey would increase encounter rates. Such rhythmic behaviour could be related to a crab's role as a searcher during foraging periods in the wild, when it would move between a variety of sites in search of prey (Lawton, 1989). Juvenile sandfish are known to bury more frequently than adult counterparts, which was hypothesized to be its main anti-predator behaviour (Mercier *et al.*, 1999). However, cultured juvenile sandfish can be naïve where avoidance patterns such as burying, are lacking and can be a behavioural deficit among individuals (Purcell, 2012). In the present study, burying of juveniles was slow, a pattern that was relatively similar across treatments regardless of whether or not a crab was present, potentially presenting substantial risk for juveniles as they are exposed to crabs. Activity patterns greatly influence predation rates, where predators can feed on prey during periods where both are rhythmically active (Lawton, 1989). *Thalamita* was found to remain buried throughout the day, being active from dusk to dawn (personal observation) which corresponds to the period when juvenile sandfish are also emerged. Thus, the lower mortality of sandfish to *Thalamita* may in part be due to the limited amount of time each day when they are likely to meet, i.e., where both are emerged at night. In addition, shifting tides were also reported to influence the diurnal feeding rhythm of *T. crenata*, its foraging activity mainly occurring at depths of 0.1–0.3 m (Vezzosi *et al.*, 1994; Cannicci *et al.*, 1996). The constant water depth in the tanks may explain the lower consumption rates of *Thalamita* in the laboratory trials compared to the field trials. In contrast, *Dardanus* does not bury and was observed to be emerged from its shell and active throughout the day, unlike a few species of hermit crabs that are known to bury (Rebach, 1974). Moreover, *Dardanus* was capable of digging up buried juvenile sandfish during initial trials (pers. obs.) and may have used this technique to capture and consume buried juvenile sandfish. These findings suggest that *Dardanus* poses a greater threat to juvenile sandfish than *Thalamita*.

Implications for sandfish restocking and ocean-based culture

Predator mitigation measures (i.e., culling, use of pen enclosures) have been suggested to improve juvenile sandfish survival upon

release (Robinson and Pascal, 2012; Lavitra *et al.*, 2015). The high mortality of juveniles (1.0–10.9 g) in both field and laboratory trials in this study emphasize the importance of releasing larger sizes of cultured juveniles. In the sandfish sea ranch, near Bolinao, Philippines where the field study was conducted, juvenile sandfish (>3 g) are reared in several 100 m² enclosures for 1–2 months, to attain larger sizes (>30 g) prior to release within the sea ranch. Despite the additional costs of rearing juveniles in sea enclosures and removal of the crabs in grow-out areas, these may be cost-effective predation mitigating measures, especially in areas where these crabs are abundant. Many aspects of crab predation remain unexplored and warrant further investigation, including the systematic assessment of size refuge from predators. With the growing global interest in sea cucumber culture (Purcell *et al.*, 2018), predation studies are important in optimizing release strategies for cultured sea cucumbers for restocking efforts, ocean-based nurseries, and grow-out systems.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315423000735>

Data. The data that support the findings of this study are available from the corresponding author, OJC, upon reasonable request.

Acknowledgements. This study was funded by Australian Centre for International Agricultural Research (ACIAR) through the project FIS/2016/122 ‘Increasing technical skills supporting community-based sea cucumber production in Vietnam and the Philippines’ and administrative support from the Marine Environment and Resources Foundation (MERF), Inc. We are grateful to the Bolinao Marine Laboratory of the University of the Philippines Marine Science Institute for the use of facilities and equipment. Special thanks to Tirso Catbagan, Garry Bucol, and Tomilyn Jan Garpa for their assistance with field and laboratory work. We also thank JayR Gorospe and Jerwin Baure for comments on the draft versions of the manuscript.

Author contributions. OJC wrote the manuscript along with LAG and MAJM. OJC performed field and laboratory experiments. LAG and MAJM contributed to the conception and design of the study and MAJM was responsible for funding acquisition and project administration. LAG and MAJM revised and edited subsequent drafts of the manuscript. All authors contributed to data interpretation and discussions and have read and approved the final manuscript.

Financial support. This work was supported by the Australian Centre for International Agricultural Research (ACIAR) through the project FIS/2016/122 ‘Increasing technical skills supporting community-based sea cucumber production in Vietnam and the Philippines’.

Competing interest. None.

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