Blue mussel (*Mytilus edulis* L.) association with conspecifics affects mussel size selection by the common seastar (*Asterias rubens* L.)

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ABSTRACT

Prey selection by predators is of interest to community ecologists. By choosing some prey over others, predators affect prey population dynamics and the strength of food webs. According to Optimal Diet Theory (ODT), as prey density increases predators will select more profitable prey. Thereby, prey population dynamics can also affect predator behaviour. Prey profitability involves the prey energetic value, energetic costs associated to predation (time spent searching, capturing and handling prey) and certain characteristics such as body size, abundance and behaviour. We examined the effect of the blue mussel (*Mytilus edulis*) association with conspecifics at different densities on prey selection and behaviour by the seastar *Asterias rubens*. Contrary to ODT prediction, when mussels were tightly clumped in high densities, the size range of the mussels consumed by *A. rubens* did not differ of the size range of the mussel population. Mussel association at high density caused seastars to feed locally, reducing their exposition to risks. Moreover, preying without selecting for a specific mussel size did not result in a decrease of net profit, rather it was increased. We concluded that under certain circumstances, not selecting prey results in an increase of net profit at prey size.

We discuss our results in the context of the mussel industry where the effect of prey selection on the prey population dynamics is of importance. Mussel size selection by seastars, as described in previous works, will impact the size distribution of mussels within cultured populations affecting growth of the population and reproductive output among others, thus increasing the impact of seastar predation beyond that of just removing mussels from the population. However, this study shows that seastars prey upon availability at high densities, typically encountered in cultivated populations, and therefore their effect on mussel population is restricted to removal of mussels without affecting the size distribution of the population.

1. Introduction

Active selection of prey by predators is a fundamental mechanism in ecosystem functioning and community interactions mediating the strength of food web interactions (Kéfi et al., 2012). Preference for certain prey individuals affects prey population structure and is a potential source of density dependency in predator prey interactions (Smallegange and Van Der Meer, 2003). Due to this relevance, ecological theory has long been trying to describe and understand the mechanisms that drive predators to choose their prey. Optimal diet theory (ODT) (Macarthur and Pianka, 1966; Pyke, 1984) states that prey selection is driven by net profit: prey are selected to maximise net energy intake per unit of time. Nowadays, it is widely acknowledged that net gain is not the only or even the main driver behind prey selection (Gilliam, 1990; Smallegange and Van Der Meer, 2003). Prey selection is

involved in a trade-off between net profit and other factors such as predator's predation risk (Gilliam, 1990) or avoiding being damaged by prey (Hummel et al., 2011; Smallegange and Van Der Meer, 2003). These factors can drive predator behaviour to select prey items that would be suboptimal when only considering prey profitability (net profit per prey item).

Predators will prey more often or discard other items in favour to the preferred prey items as prey density, and therefore the abundance of preferred prey, increases (Charnov, 1976; Pulliam, 1974; Sih and Christensen, 2001; Smallegange, 2007). This implies that prey population dynamics influence prey selection. However, highly dense populations of prey can protect individuals by various means (van de Koppel et al., 2008; van der Heide et al., 2014). Density-dependent or associational defence mechanisms can have an effect on how predators approach prey, how much time is spent handling prey, and ultimately
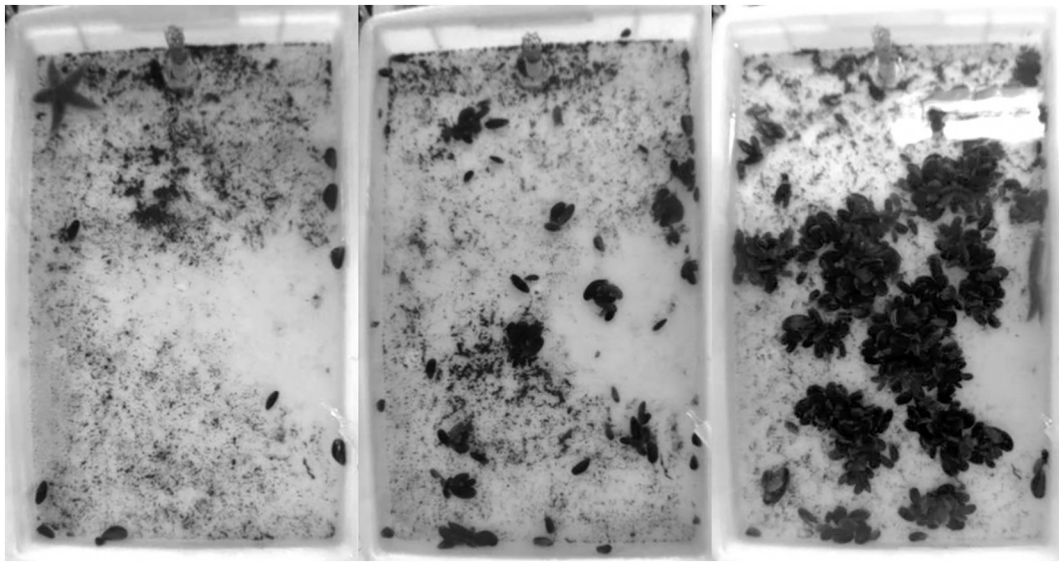

Fig. 1. Experimental trays showing the different mussel association complexity for the three different density treatments. From left to right: 0.1, 0.5 and 3 kg m^{-2} of *Mytilus edulis*.

on risk assessment by the predator. As such, while an increase of prey density should make it easier for the predator to find the preferred prey item (Charnov, 1976; Pulliam, 1974; Sih and Christensen, 2001), associational defences (which make predation more difficult) can affect handling time (Hossie and Murray, 2010; Kishida et al., 2010) and thus prey profitability as well as predator behavioural responses. These effects may lead to a change in preferred prey size that maintain both maximum possible net profit and avoid prolonged exposition to risks for the predator. While there exists a vast literature on prey selection to assess ODT and the role of risk to predators (Charnov, 1976; Pulliam, 1974; Sih and Christensen, 2001), few studies have focused on the changes in net profit driven by prey behaviour or defence mechanisms, and to our knowledge none has explored the role of prey density as a defence mechanism on prey profitability and predator behaviour when approaching prey.

The well-known combination of seastars and mussels as a predator-prey system (Agüera et al., 2015; Navarrete and Menge, 1996; Paine, 1966) is suitable to study the influence of prey density and associational defences in a predator specialised on bivalve prey. When present in large numbers mussels form dense matrices where individuals are closely associated (Buschbaum et al., 2008). The association of mussels forming clumps or beds is thought to serve as a defence mechanism against predators and harsh environmental conditions (Dolmer, 1998; Robles et al., 2009; van de Koppel et al., 2008). As mussel density increases so does the complexity of their association with conspecifics. By forming dense matrices, mussels reduce the probability of predators finding an isolated individual (van de Koppel et al., 2008). The common seastar (*Asterias rubens* L.) has a high preference for blue mussels *(Mytilus edulis* L.) (Gaymer et al., 2001a) and is able to control distribution and abundance of mussels in sublittoral habitats (Sloan, 1980; Witman et al., 2003). Seastar populations can cause large economic losses to the mussel aquaculture industry (Agüera et al., 2012; Smaal, 2002). The availability of mussel prey, understood as the prey physically present that can be consumed by the seastar (Menge, 1972), is mainly constrained by the size of the prey that can be handled and successfully consumed by the seastars' own size (Gaymer et al., 2004; O'Neill et al., 1983). Further, some studies have suggested that seastars select the largest available prey within the size range they can consume (Hummel et al., 2011; O'Neill et al., 1983).

Knowledge on how mussel association affects selective predation is important to determine the predator impact on prey populations (Hughes and Seed, 1995), yet it has never been addressed. Many studies

have investigated prey selection by mussel predators (Hummel et al., 2011; O'Neill et al., 1983; Smallegange and Van Der Meer, 2003), but mostly focused on predator behaviour and the profit of the prey in standardised lab systems were mussels are offered in isolation or in groups of homogeneous size range. As such, they fail to describe the effect of mussel associative behaviour on both the net profit of prey and the behaviour of predators when approaching mussels at different levels of association.

Selective predation by seastars can affect mussel population structure and production and thereby affect the way these predators impact cultivated and natural mussel resources. The present study aims to test the hypothesis that prey net profit at size changes with different levels of prey association, and hence prey selection and behaviour of predators changes accordingly. We use behavioural observations to examine underlying mechanisms related to the interaction between seastars and mussel association at different mussel densities.

2. Material and methods

2.1. Animal collection

Seastars (ranging between 41.3 and 55.2 mm arm length: measured from the mouth to the tip of one arm) were collected in the Oosterschelde estuary (the Netherlands) during April 2013, from the subtidal using a small dredge. After 24 h in a flow-through system, 45 intact seastars were randomly selected and transported to the lab, where they were kept in a 600 l tank and fed mussels. Mussels (ranging between 5.6 and 33 mm shell length: maximum antero-posterior axis) were collected from the subtidal (collision buoys) at the NIOZ Harbour at Texel, the Netherlands. Mussels used in the experiments were kept in a 130 l aquarium.

2.2. Experimental design

The experimental set-up consisted of three closed circulation systems, each composed of a buffer tank (130*l*), a biofilter and three experimental trays (50x30x6.5 cm). This system was set inside a climate-controlled room, kept at a constant temperature of 13 °C and 12:12 h photoperiod. Each tray was monitored 24 h from above using a digital IR capable video camera (one camera per tray). Three mussel density treatments (0.1, 0.5 and 3 kg wet weight per m^2) were added to the trays, with all the trays within a recirculation system sharing the same

Table 1

Definitions of behaviour terminology used for seastars (*Asterias rubens*) offered mussel (*Mytilus edulis*) prey.

| Terminology		Definition
Activities	Foraging	When the seastar was either searching for prey or handling prey. For simplification, foraging time included any time the seastar was not quiescent.
	Searching	When the seastar was exploring its surroundings, including contacting prey or moving over them.
	Prey Handling	When the seastar was manipulating and consuming prey, beyond just contacting them or moving over it, often taking a humped posture over the prey.
	Quiescent	When the seastar stayed still without handling a prey.
Events	Attack	An attack was counted when a searching seastar switched to handling a prey (i.e. started manipulating a prey), after searching, handling a previous prey or being quiescent.
	Consumption	When a prey being handled was completely consumed and the empty shell was abandoned.
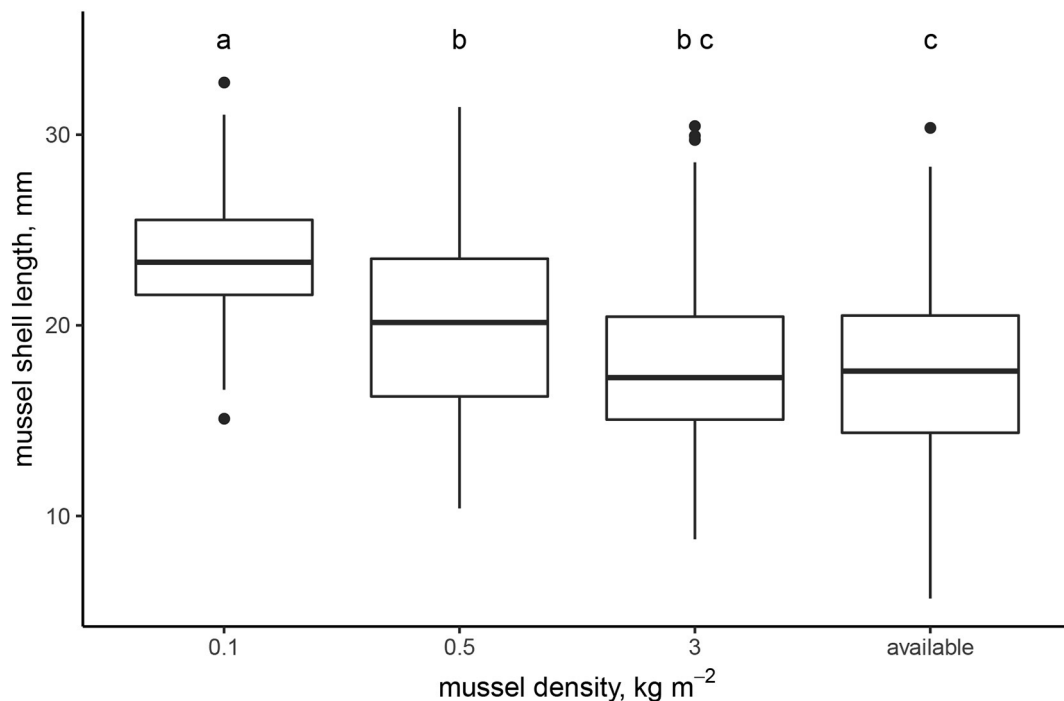
Fig. 2. Shell length of mussels (*Mytilus edulis*) consumed by seastar (*Asterias rubens*) per treatment level compared among them and with the size range of offered mussels. Different letters indicate significantly different treatments levels (n = 750, p < .01) as determined by post-hoc group mean comparisons. Tukey boxplots.

Table 2

Summary of fixed effects output from the linear mixed effects (lmer) model testing the difference of the size range of mussels (*Mytilus edulis*) preyed upon by the seastar (*Asterias rubens*) under different treatments levels and the size range of mussel offered.

	Estimate	S.E.	t	p
Intercept	23.445	0.456	51.385	< .001
0.5 kg m^{-2}	−3.332	0.567	−5.878	< .001
3 kg m^{-2}	−5.191	0.693	−7.486	< .001
offered	−5.816	0.504	−11.532	< .001

mussel density (pseudoreplication). These densities resulted in three levels of association between mussels: loose mussels (0.1 kg m^{-2}), loose + small groups (0.5 kg m^{-2}) and mid to large clumps (3 kg m^{-2}) (Fig. 1).

Mussels were taken randomly from their storing aquaria and manually detached from each other. Then, they were placed in the trays 48 h prior to the addition of a seastar to allow for self-organization and attachment among themselves or to the substrate (tray). Afterwards, one seastar, of known arm length and weight was added to each tray. The seastar and mussels were left in the trays over 4 d and their behaviour recorded by video camera. Each day, the shell of consumed mussels were removed from the trays and measured to the 0.1 mm using digital callipers. To keep the length distribution and mussel

density constant, eaten mussels were replaced by live ones of the same size in the treatments levels 0.5 and 0.1 kg m^{-2}. We assumed that replacing eaten mussels was not necessary in the treatment level 3 kg m^{-2}, as mussel density was very high and predation did not cause any significant change in the length distribution of available prey or in the density over 4 d. The experimental trial was replicated 3 times with different mussels and seastars, and changing the arrangement of the density treatments used in each recirculation system. We thus had observations of predation behaviour of 27 seastars, feeding at three different prey densities (9 replicates per treatment).

A random sample of mussels, of about 100 individuals, was taken each week from the experimental stock before each trial. These mussels were measured to the 0.1 mm to obtain the shell length distribution of the mussels used in the experiment. About 30, selected to cover the whole shell length distribution, were opened, their flesh content weighed to 0.001 g and processed for ash free dry weight (AFDW) following the procedure by Kamermans et al. (2009). These data were used to obtain the relationships between mussel shell length, wet weight and AFDW, to later transform mussel shell length to flesh content and AFDW. Seastar feeding rate was measured as total number of mussels eaten during each trial (~4 days).

2.3. Video analysis

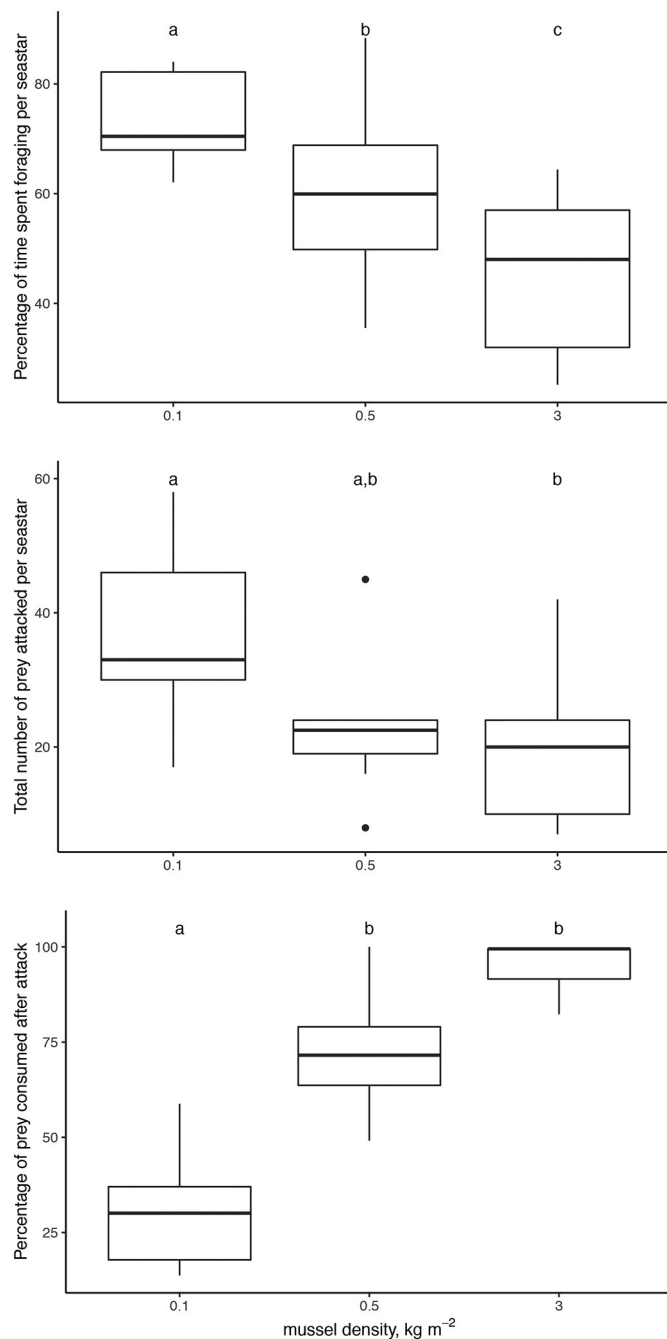All video footage available (~96 h per seastar, a total of 2592 h) was

Fig. 3. Foraging behaviour of seastar (*Asterias rubens*). Top: time spent foraging. Middle: total number of mussels (*Mytilus edulis*) recorded. Bottom: percentage of attacks that ended with a consumed prey. Different letters indicate significantly different treatments levels (n = 9 per level, p < .01) as determined by post-hoc group mean comparisons. Tukey boxplots.

analysed at fast playback using VLC media player v.3.0.7 (www.videolan.org). Video recordings were used to analyse individual seastar behaviour, classified in a series of different activities and foraging-related events (Table 1) (Gaymer et al., 2001b; Nadeau et al., 2009). As such, the proportion of time searching, handling prey and being quiescent were recorded. Attack and consumption events were counted.

2.4. Data analysis

General linear mixed models (glmer) and linear mixed models

Table 3
Summary of fixed effects results from the general linear mixed effects models (*glmer*) testing seastars (*Asterias rubens*) foraging behaviour while preying at different mussel (*Mytilus edulis*) treatment levels.

	Percentage of time spent foraging per seastar			
	Estimate	*S.E.*	*z*	*p*
Intercept	1.015	0.125	8.114	< .001
0.5 kg m^{-2}	−0.456	0.158	−2.887	.004
3 kg m^{-2}	−1.213	0.158	−7.693	< .001
	Total number of prey attacked per seastar			
Intercept	3.5966	0.1297	27.722	< .001
0.5 kg m^{-2}	−0.4623	0.1899	−2.435	.015
3 kg m^{-2}	−0.5762	0.1896	−3.039	.003
	Percentage of prey consumed after attack			
Intercept	−0.8999	0.2759	−3.262	.001
0.5 kg m^{-2}	2.1146	0.4591	4.606	< .001
3 kg m^{-2}	3.7719	0.6772	5.570	< .001

(lmer) were used to analyse the various dependent variables, namely size of consumed and offered mussels, consumption rates, behaviours and prey profitability. Video data and consumption rate data were combined to calculate two different prey profitability indices: prey handling time and consumed AFDW per hour spend handling the prey. The density treatment was a fixed factor. The interaction of trial (replicate) and recirculation system (pseudo-replicate) was used as random variable to account for the possible dependencies created by the experimental design. This approach does not fully account for the dependencies created by the experimental set-up and the error term may still be underestimated, which may mean an increase in Type I error. To reduce the implications of the increase of Type I error on the interpretation of the results we used a significance level of 0.01. The assumed distribution of a dependent variable was selected based on the type of data: binomial for probabilities (percentages), Poisson for count data, and Gaussian for the rest. Post-hoc pairwise group mean comparisons were performed among the different levels of density treatment using Welch-Satterwaite method and adjusting the *p*-values for multiple comparison using the Tukey method (Lenth, 2016). Models performances were assessed by examination of residuals plots (Supplement Information, SI1).

All analyses were performed using R v3.5.2. (R Core Team, 2018). Functions lmer and glmer from package lme4 (Bates et al., 2016) and function lsmeans from package lsmeans (Lenth, 2016). Details on the models, complete summary of results and validation plots are provided in the Supplement Information, SI1.

3. Results

3.1. Seastar foraging behaviour at different mussel densities

According to the lmer model the size of mussels consumed by seastars under the treatment 0.1 kg m^{-2} were significantly larger than those consumed at 0.5 and 3 kg m^{-2}, as well as the size distribution of the offered mussels. The mussels consumed at 0.5 kg m^{-2} were also significantly larger than those offered. However, the size of consumed mussels at 3 kg m^{-2} were not significantly different from that of mussels offered (Fig. 2, Table 2).

Foraging activity of seastars was lower at higher mussel densities (Fig. 3 top, Table 3). This increase in foraging activity was accompanied by a significant increase in the attack rate at the lower mussel density (Fig. 3 middle, Table 3). However, with the increase in the number of attacks, seastars started to reject prey and the percentage of prey consumed after being handled became significantly lower at lower prey densities (Fig. 3 bottom, Table 3).
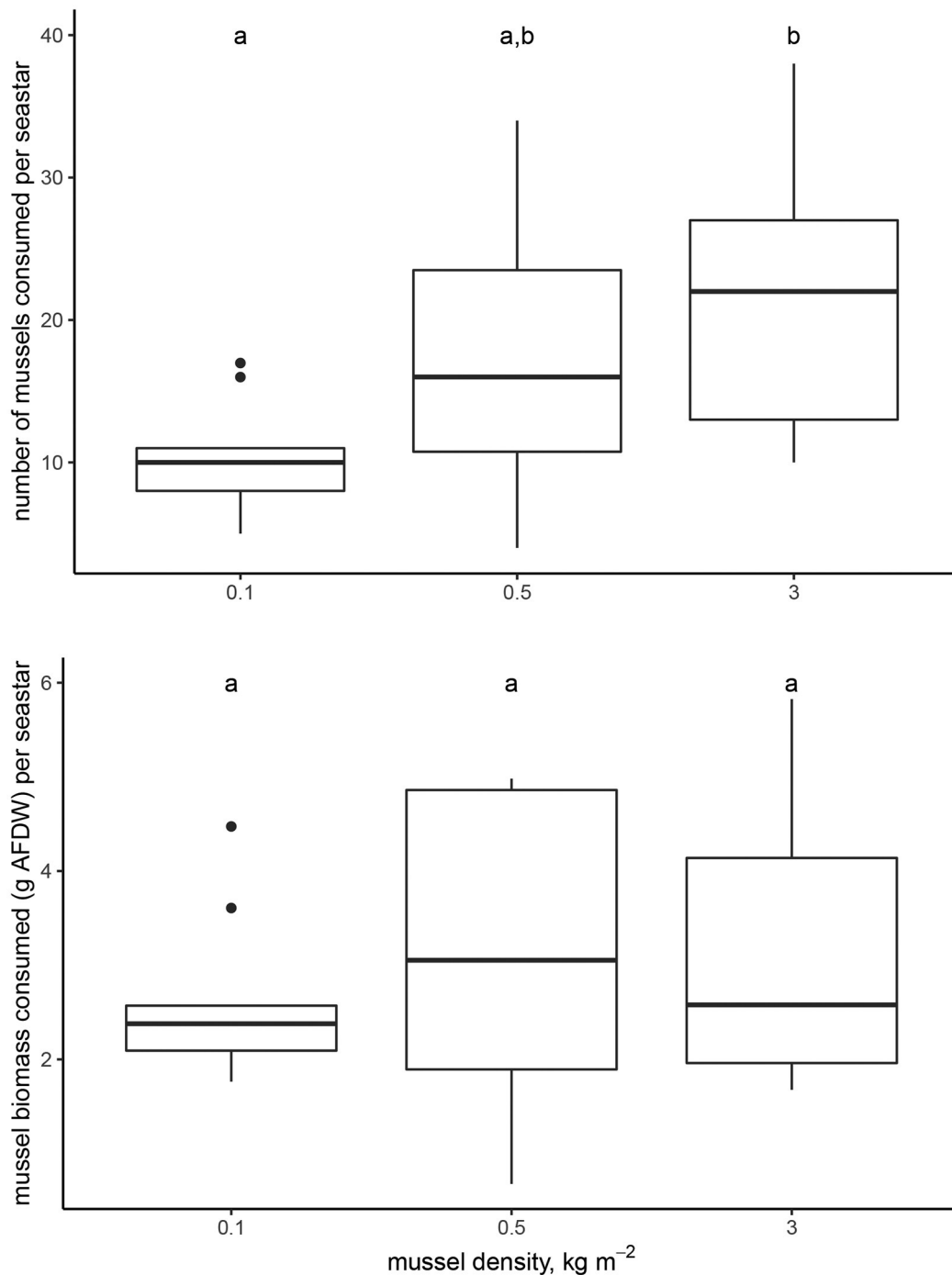
Fig. 4. Seastar (*Asterias rubens*) consumption rates as total number of consumed mussels (*Mytilus edulis*) during a trial of 4 days (top) and of consumed mussel AFDW (bottom). Different letters indicate significantly different treatments levels (n = 9 per level, p < .01) as determined by post-hoc group mean comparisons. Tukey boxplots.

3.2. Seastars consumption rate and prey profitability at different mussel densities

The different behaviour of seastars at different mussel densities resulted in different patterns when considering feeding rate as number of mussels consumed or as biomass (as AFDW) of mussels consumed (Fig. 4, Table 4). For number of mussels consumed per predator, consumption increased with mussel density (Fig. 4 top, Table 4). However, the decrease of consumed mussel size at higher densities resulted in no significant differences for consumed mussel AFDW among treatment

levels (Fig. 4 bottom, Table 4).

Time spend handling each mussel consumed significantly decreased at higher densities (Fig. 5 top, Table 5), as was expected when handling smaller prey. However, prey profitability, defined as AFDW consumed divided by time handling prey was significantly higher at higher densities where no active selection was taking place (Fig. 5 bottom, Table 5).

Table 4
Summary of fixed effects results from the general linear mixed effects models (*glmer*) testing for seastars (*Asterias rubens*) consumption of mussels (*Mytilus edulis*) at different mussel densities.

	Number of mussels consumed per seastar per trial			
	Estimate	S.E.	z	p
Intercept	10.306	2.052	5.023	< .001
0.5 kg m^{-2}	7.513	3.087	2.434	.015
3 kg m^{-2}	11.056	3.106	3.560	< .001
	Biomass of consumed mussels per seastar per trial			
Intercept	7.8637	0.1560	50.393	< .001
0.5 kg m^{-2}	0.1573	0.2207	0.713	.476
3 kg m^{-2}	0.1582	0.2207	0.717	.473

4. Discussion

Contrary to our expectations the present study showed that a predator does not necessarily increase the consumption of an a priori-determined most profitable prey when prey are available at higher densities. Net profit is a complex property that results from the trade-off between energy intake from prey (prey energy content) and the energetic costs associated with predation (energy necessary to handle prey). However, as density of mussels increases, so does the complexity of their association with conspecifics (Agüera et al., 2015; Buschbaum et al., 2008). This association makes prey harder to dislodge and consume, leading to longer handling time and hence a higher energetic cost of predation. Our results seemingly contradicted the expectation, based on ODT, that selection of larger, more profitable prey should occur when prey density is high. Instead we found that seastars optimize predation by minimizing the amount of energy spent collecting a fixed amount of prey. They do that by preying locally on smaller prey, diminishing their overall foraging time, specifically their handling time per prey. However, they still consume the same amount of flesh per unit of time than when prey were at lower densities. In that manner, our results conform to the underlying principle of ODT, that predators select prey items to optimize net energetic gain, with the added complexity that the association of mussels at higher densities changed the relationship between prey size, handling time and prey profitability. This cascaded into a change in the predator behaviour.

Prey typically exhibit behaviours or adaptations aimed at making predation more difficult (Hossie and Murray, 2010; Kishida et al., 2010). In organisms like mussels, association with conspecifics forming clumps is known to have an effect on how predators approach them (Dolmer, 1998), with clumping thought to serve as a protection against predation and environmental conditions (van de Koppel et al., 2008). Our study showed that when seastars preyed on clumps of mussels, they did not select for size; however, by doing so they were still optimising net profit. Seastars reduced their foraging activity while reducing their prey locally by feeding consistently on the same clump. This change of tactics, compared to that exhibited when preying on low-density mussel plots, resulted in an increase in the net profit of smaller mussels (Fig. 5b). The absence of both size selection and increased profitability in the high-density treatment level may be explained by destabilization of the mussel clump caused by the predator itself. Mussels in clumps attach to each other and, as the predator removes individuals, the attachment strength of subsequent prey in that clump is decreased (Aveni-Deforge, 2007). Therefore, it may be more efficient, and result in a higher net profit, to attack a smaller mussel in an unstable clump than a larger mussel in a stable clump or strongly attached to substrate. Mussel association leads to net profit improvement for the predator, making handling of prey easier when considering subsequent predation in the same spot/clump.

Preying locally within a clump may also be a behaviour response not necessarily linked to maximisation of net profit. By preying on the same clump, seastars avoid displacements over the mussels and stay protected by the mussels themselves. Predation risk is one of the main drivers for prey selection (Charnov, 1976; Smallegange and Van Der Meer, 2003), and prey selection is often a trade-off between prey profitability and the risk of the predator being preyed itself. By preying locally seastars keep a reasonable net profit and at the same time reduce the risk associated to exposing themselves on top of the mussels where they may be subject to predation (Nehls, 1989) or currents (Agüera et al., 2015).

Changing from selective to non-selective predation may have important consequences on mussel population dynamics and mussel bed-functioning. Mussels are thought to attain size refuge under certain circumstances (Agüera et al., 2012; O'Neill et al., 1983): a predator that consistently selects the bigger prey within its predation size-window actively reduces the probability or proportion of prey individuals that will overgrow that maximum size-window and attain size refuge. In contrast, non-selective predation may lead to a higher number of individuals attaining size refuge or reaching maturity, improving the reproduction output (De Roos et al., 2008).

Mussels are cultivated for human consumption in many parts of the world, and the effect of prey selection on the prey population dynamics is important for the culture industry. Previous studies suggested that seastars always selected bigger prey (Gaymer et al., 2001b; O'Neill et al., 1983). By doing so seastars can reduce the mean individual size of the mussel population, and therefore they hamper the ability of the population to grow to commercial valuable size. However, this is not the case at high densities, typically encountered in cultivated populations. By feeding in accordance to prey size available, seastars do not affect the average individual size of the mussel population, and predation does not affect the growth of the population into commercial size, though it will still cause losses in production. Moreover, moderate predation serves to reduce intraspecific competition within the mussel matrix which can result in enhanced population productivity (Angelini et al., 2011; Menge, 1995).

In this study offered mussels were within the size range that the used seastars can prey upon (Hummel et al., 2011; O'Neill et al., 1983). Therefore all mussels offered were deemed as available (Menge, 1972). It was not in the scope of this study to assess the effect of mussel association on the size range available for seastars. Such effect relates to how the mussels organise themselves when clumping. However, a difference between the size range of consumed mussels and those offered shall be expected if mussel clumping resulted in changes on the size of prey available.

There are several trade-offs that have an effect on predator behaviour and prey selection. We showed that prey net profit changes when mussels are associated with conspecifics, a density-dependent trait. This variation in prey net profit allows the predator to at least maintain net energetic gain without actively selecting prey. A selective process may still happen as seastars may choose prey that are already detached or loosely attached to the clump while just staying within the mussel matrix to avoid risks. We conclude that size selection does not always lead to an improvement of net profit.

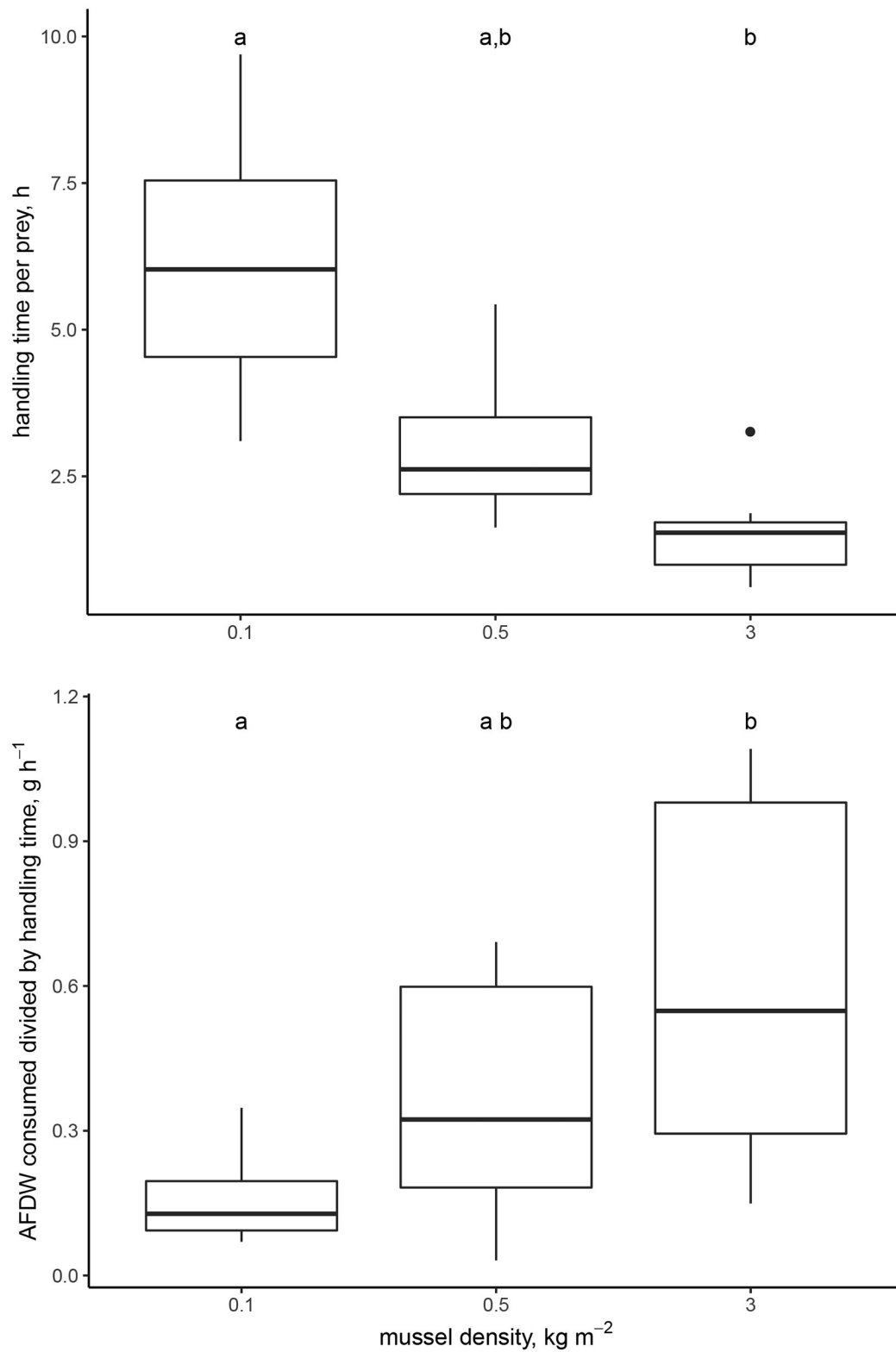**Declaration of Competing Interest**

Acknowledgements

Fig. 5. Profitability of mussels (*Mytilus edulis*) preyed upon by the seastar (*Asterias rubens*). Top: handling time per prey. Bottom: mussel AFDW consumed per hour spent handling prey. Different letters indicate significantly different treatments levels (n = 9 per level, p < .01) as determined by post-hoc group mean comparisons. Tukey boxplots.

Table 5

Summary of fixed effects results from the linear mixed effects models (*lmer*) testing the profitability of mussels (*Mytilus edulis*) preyed upon by the seastar (*Asterias rubens*) at different treatment levels.

	Handling time per prey			
	Estimate	*S.E.*	*t*	*p*
Intercept	6.128	0.583	10.513	< .001
$0.5\,\mathrm{kg\,m^{-2}}$	−3.072	0.844	−3.638	.01
$3\,\mathrm{kg\,m^{-2}}$	−4.620	0.824	−5.605	.002
	Biomass consumed by handling time			
Intercept	0.164	0.085	1.930	.066
$0.5\,\mathrm{kg\,m^{-2}}$	0.203	0.124	1.636	.115
$3\,\mathrm{kg\,m^{-2}}$	0.466	0.120	3.872	< .001

Appendix A. Supplemetary data

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