

Indirect effects of invasive species affecting the population structure of an ecosystem engineer

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Abstract. Species invasion is of increasing concern as non-native species often have negative impacts on ecosystems that they were introduced to. Invaders negatively affect the abundance of native species due to direct interactions like predation and competition. Additionally, invaders may benefit native biota by imposing indirect effects on resident species interactions. Invaders indirectly affect resident species via both density-mediated indirect interactions (DMIIs) and trait-mediated indirect interactions (TMIIs). Previous studies on these different indirect interactions have largely examined the effects on structuring ecological systems, with paying little attention to the role of body size. Here, we experimentally demonstrate that an invasive habitat modifier of European coastal waters, the Pacific oyster (*Crassostrea gigas*), alters the population structure of native mussels (*Mytilus edulis*) by modifying the size specific predator-prey interaction between the mussels and the shore crab (*Carcinus maenas*). In laboratory split-plot experiments, the presence of Pacific oysters reduced the mortality of unconditioned mussels as well as mussels that were acclimatized in presence of predatory cues, while being exposed to predation by crabs of two different size classes. The reduction in mortality was size-dependent both in terms of the predators and the prey. The presence of oysters notably reduced mussel mortality in presence of small crabs, while the mortality rate in presence of big crabs was less affected. Mussels that benefited the most by the presence of oysters were those of recruitment stages, smaller than 20 mm in shell length. Our results suggest that oysters cause a strong shift in the population structure of *M. edulis*, reducing particularly the mortality of smaller sized mussels.

Key words: *Carcinus maenas*; *Crassostrea gigas*; density-mediated indirect interactions; ecosystem engineer; habitat complexity; indirect effects; invasive species; *Mytilus edulis*; predation; trait-mediated indirect interactions; Wadden Sea.

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INTRODUCTION

The invasion by non-indigenous species is an increasing ecological, conservational and economic problem in ecosystems around the world (Vitousek et al. 1996, Wilcove et al. 1998, Mack et al. 2000, Olden et al. 2004). The introduction of non-indigenous species may affect entire species communities and ecosystems by imposing new

species interactions and altering existing ones (Sax et al. 2005). In the past, most studies on species invasions focused on various negative effects on ecosystems, which all potentially result in a reduction of species diversity. These include: outcompeting of native species, hybridization with native species, increased transmission of pests and diseases and drastic changes in the new habitats and environments (Vitousek et al.

1996, Ruiz et al. 1997, Mack et al. 2000, Crooks 2002, Grosholz 2002). However, the effects of non-native species are not always negative. For example, ecosystems that suffered high (human-based) disturbance in the past, may benefit from the arrival of newcomers that fill vacant ecological niches (Donlan et al. 2006, Griffiths et al. 2010). Moreover, native species may profit from a new partner in trophical or non-trophical species interactions. Thus, invaders may function as additional food source (Bulleri et al. 2005, Carlsson et al. 2009) or may provide protection to native biota (Wonham et al. 2005, Severns and Warren 2008). In addition, there may be more subtle effects caused by indirect interactions between invaders and native species.

Indirect interactions occur when one species influences a second via its interactions with a third species. These interactions can affect ecological communities either by altering densities due to direct consumption or competition (density-mediated indirect interactions (DMIIs)) or by changing behavioral, morphological or physiological traits (trait-mediated indirect interactions (TMIIs)) (Werner and Peacor 2003, Schmitz et al. 2004, Preisser et al. 2005). Research on DMIIs and TMIIs has focused on top-down trophic pathways where interaction cascades are initiated by predators, transmitted by consumers, and received by lower trophic levels, usually primary producers. However, indirect interactions are not limited to top-down trophic pathways. In theory, any organism at any taxonomic level can act as an initiator, a transmitter, or a receiver species. For example, habitat modifying species cause DMIIs by increasing habitat complexity which provides refuge for other species and may influence predator-prey encounter rates (Grabowski 2004, Pearson 2010). Further, habitat modifiers may also impose TMIIs on predator-prey interactions that result in changes of morphological and behavioral traits which may affect predation rates (Griffen and Byers 2006, Byers et al. 2010, Pearson 2010).

Most studies dealing with TMIIs implicitly assumed that all individuals within a population display trait changes of the same order of magnitude. However, a few studies showed that strength of TMIIs within populations varies according to individual behavior (Griffen et al. 2012) and body size (Rudolf 2006, 2008, 2012,

Preisser and Orrock 2012, Krennek and Rudolf 2014). Body size often represents the state of ontogenetic development of individuals (de Roos and Persson 2013) and is affected by changes in resource and habitat use. These changes are referred to as ontogenetic niche shifts (Werner and Gilliam 1984) and may cause alterations of the intensity of species interactions. Hence, TMIIs occurring within size-structured populations may strongly vary with the size of individuals in both predator and habitat modifying species. Ultimately, variations in trait changes between different states of ontogenetic development within a population may result in shifts in population structure. This may also affect the interactions with other species.

STUDY SYSTEM

The Pacific oyster *Crassostrea gigas*, an invasive habitat-modifier, originates from marine waters of Japan and Southeast Asia and nowadays has successfully invaded all temperate coastal ecosystems around the world (Ruesink et al. 2005). In Europe, oysters occupy the same habitats as native blue mussels *Mytilus edulis*. On intertidal soft bottom habitats as the Wadden Sea, *M. edulis* aggregates and forms dense beds, which provide refuge and suitable habitat for an array of associated organisms (e.g., Tsuchiya and Nishihira 1985, 1986). By shaping their environment mussel beds function as ecosystem engineers (Jones et al. 1994, Buschbaum and Saier 2001, Crooks 2002, Gutierrez et al. 2003). They may form very stable and long-lived structures, if losses from factors such as hydrodynamic forces, storm events or predation are balanced by recruitment (Nehls and Thiel 1993, Nehls and Ketzenberg 2002). In the 1990s and the 2000s, natural losses and anthropogenic induced losses (e.g., extensive fishing) could not be balanced by recruitment. Several successive years of poor recruitment resulted in a decline in mussel bed area in many parts of the Wadden Sea (Beukema and Cadée 1996, Nehls et al. 2006). At the same time Pacific oyster bed area increased. However, these trends do not appear to be causally linked but rather both are the effect of global change (Nehls et al. 2006). Field observations indicate that *M. edulis* can coexist alongside *C. gigas* (Troost 2010, and references therein). Moreover,

increasing oyster biomass results in an increased number of *M. edulis* at the expense of individual body condition (Troost 2009). While a decrease in condition indicates direct negative effects on mussels imposed by oysters through food limitation, an increase in mussel numbers might indicate the existence of indirect effects. For example, the presence of oysters may provide shelter from predation and environmental extremes resulting in a reduced mortality of juvenile and adult *M. edulis* within oyster/mussel patches compared to pure mussel patches (Markert et al. 2009). Indirect effects might be crucial for the persistence of mussels especially within areas where recruitment is generally low or during periods of low recruitment. Eschweiler and Christensen (2011) showed that mussels, cohabiting with oysters, experience a trade-off between survival and food supply. This study demonstrated that mussels tend to seek shelter from predation at the costs of growth and condition in presence of the shore crab *Carcinus maenas*, an abundant and widely spread omnivore along European coasts.

The chance of finding shelter for mussels in oyster patches is size dependent. Since the interstices on oyster shells and crevices between small oysters favor mussels of smaller sizes (A. M. Waser, *personal observation*) the order of magnitude of the TMIs induced by the oysters may highly vary with mussel size. When mussels are exposed to predation, oyster initiated TMIs may lower mortality rates in smaller sized mussels. Furthermore, direct encounters of mussels and crabs evoke additional, crab initiated, TMIs that provoke mussels to migrate deeper into the oyster matrix in favor of finding shelter, which may lead to an even stronger decrease in size specific mussel mortality (Fig. 1).

In the present study, we conducted an experiment to examine the indirect effects of oysters, as well as crabs on the mortality of different life stages of *M. edulis*. We hypothesize that the impact of oyster triggered TMIs on mussel mortality is higher in combination with crab triggered TMIs compared to oyster triggered TMIs alone. Therefore, we designed treatments, in which mussels either experienced TMIs initiated by oysters and crabs simultaneously or were unaffected by predator TMIs. These different treatment modifications were executed

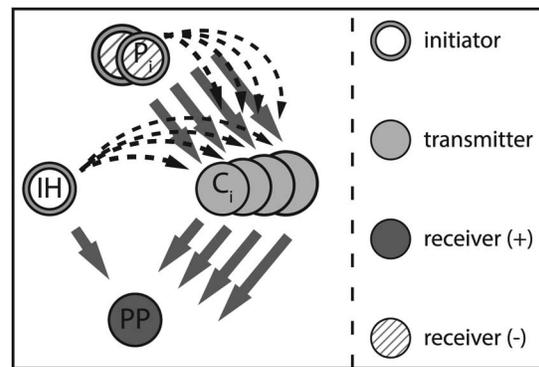


Fig. 1. The indirect interaction pathways within a simplified food web composed of four species: phytoplankton, a primary producer (PP), the blue mussel, a consumer species (C), that feeds on PP, the Pacific oyster, an invasive habitat modifier (IH) and the shore crab, a predator (P), which predate on C but not on IH. Grey solid lines represent trophic interactions and black dashed lines indicate effects on traits of the species to which the arrow is pointing. Different life stages C_i of the structured population C may each transmit the indirect effects that are solely initiated by IH as well as indirect effects arising simultaneously from IH and P with different orders of magnitude.

during the acclimatization phase of the mussels that were either given to experimental units together with or without any oysters. The mussels were exposed to predation by a single individual of *C. maenas*. Prey selection of shore crabs is driven by the maximization of energy intake, as well as by the risk of damaging claws (Elnor and Hughes 1978, Smallegange and Van der Meer 2003), therefore a crab of a certain size will tend to forage on mussel sizes which fit its specific needs best. Consequently, predator size strongly affects the predation pressure of different sized mussels. In order to examine this effect, two different size classes of crabs were used on a range of mussel sizes.

MATERIALS AND METHODS

We experimentally simulated the short-term survival of different sized *M. edulis* in relation to the presence of two sizes of the predatory *C. maenas* depending on either presence or absence of the invasive *C. gigas*. Furthermore, it was tested if predatory cues could stimulate hiding

behavior of mussels, thus enhancing mussel survival. All specimens for this experiment were collected from different places along the westernmost Wadden Sea island, Texel, the Netherlands. Pacific oysters were collected from a wild oyster population on the east coast of Texel. After collection, biofouling was removed from oysters. *M. edulis* were scraped from ballast piers on the west coast of Texel and were cleaned of any attached fouling organisms before the length (ML, maximum length of the shell) of each individual was measured to the nearest 0.01 mm using electronic calipers. Mussels were then assigned to one of four size classes: 6.00–8.99 mm, 12.00–14.99 mm, 18.00–20.99 mm and 24.00–26.99 mm in ML, further on referred to as size class categories 6, 12, 18, and 24. Shore crabs were gathered from the NIOZ harbor by deploying small baited traps (18 L volume). Following their capture, each crab was sized according to carapace width (CW, the maximum distance between the two prominent lateral spines) using electronic calipers and assigned to one of two size classes: small (45.00–49.99 mm CW) and big (60.00–64.99 mm CW). Only undamaged male crabs were used in the experiments in order to reduce variability associated with morphology and sex. Oysters and mussels were kept separately in large basins with continuously running seawater, while crabs were placed individually in plastic aquaria (19 × 12 × 13 cm) that were submerged in a large basin. All basins had a temperature of 15°C at a 12 h light:12 h dark cycle. Mussels and oysters were fed daily with concentrated algal feed (Instant Algae Shellfish Diet 1800, Reed Mariculture, Campbell, CA, USA). Crabs were fed open mussels regularly, but were starved for one week and then fed two days prior to the experiments to standardize their hunger levels. After each experiment crabs were kept in the laboratory for another ten days to make sure they were not in proecdysis. Thereafter, crabs were released.

The experimental design as well as the analysis followed a split plot design approach, where all four mussel size classes were placed together in small aquaria (plots) to which eight different treatments were applied (Fig. 2a), due to the combination of the three different among-plot factors, each with two levels (acclimatization type: control and induced clumping, crab size:

small and big crabs, and oyster presence: presence and absence of oysters). Each of the treatments was replicated 10 times. Due to the complexity and size of the experimental design it was not possible to conduct all trials simultaneously. Consequently, the experiment was divided into four separate experimental periods, each run with 20 plots. Each of the experimental periods, including preparations, took approximately one week. The experiment started in mid-September 2012 and lasted in total six weeks. In the first two periods the trials of the acclimatization control were conducted and trials of the induced clumping treatments were performed in period three and four. At each period the experimental combinations of small crab without oysters, small crab with oysters, big crab without oysters and big crab with oysters were replicated five times. The plots of each of the experimental periods were randomly assigned to a flow through system which provided all of the aquaria with an equal water inflow (about 2–3 L/h) and aeration by membrane pump. Both, the acclimatization of the mussels as well as the experiments were conducted at same conditions as previously described with experiments being carried out in the light period.

Mussels of varying sizes were put together into all experimental plastic aquaria (32.5 × 17.5 × 18.5 cm), with either only a layer of sand and small shell material as substrate or next to sand and shell debris also oysters were offered, in order to allow the mussels to either form mussel patches or to seek shelter in the oyster matrix. A total of 95 mussels, which corresponds to a density of 1670 individuals/m², was introduced per aquarium. The chosen density reflects the abundance of *Mytilus* found in pure mussel beds as well as in mussel-oyster beds in the Wadden Sea ranging between 1000 and 3000 individuals / m² (Buschbaum et al. 2008, Büttger et al. 2008, Markert et al. 2009). In years with high recruitment densities may reach up to 6000 individuals/m² (Büttger et al. 2008). In order to approximately match the total biomass of the different size classes within each aquarium, the amount of mussels given to all aquaria differed between the size classes. The numbers of the different size classes were determined based on ash free dry mass from mussels taken from various mussel beds across the Dutch Wadden Sea in spring and

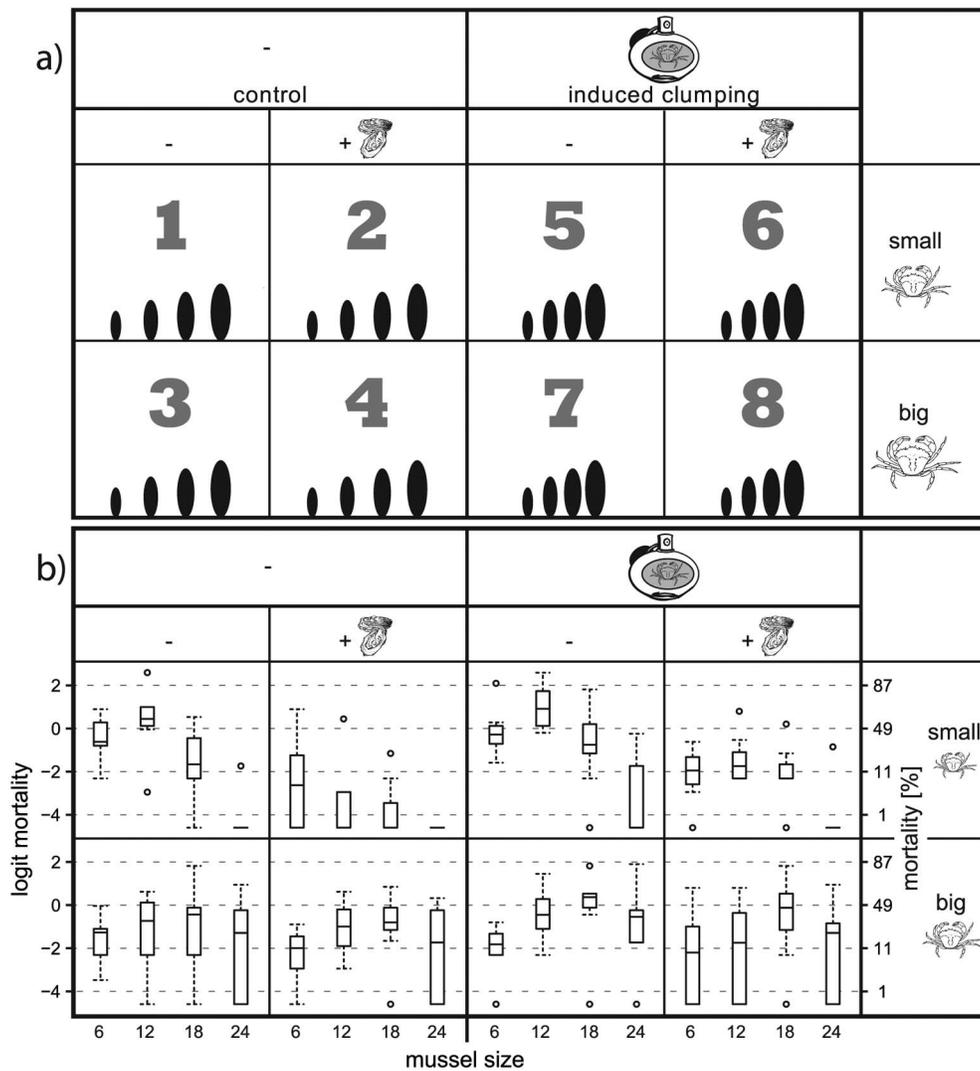


Fig. 2. Scheme of the experimental design (a). Displayed are the separate plots (aquaria) with the different sized mussels (within plot) and different among plot combinations (grey numbering; acclimatization type, crab size and oyster presence). Box plot of the logit mortality of the 4 different mussel size classes under different treatments (b). Box and whisker plots give the median (horizontal line inside the box), interquartile range (box), and outliers (small dots). Grey dashed lines to support orientation.

autumn of the years 2010–2012 (A. M. Waser et al., unpublished data). The size classes 6, 12, 18 and 24 comprised, in descending order, of 50, 25, 13 and 7 individuals of mussels, resulting in densities of 880, 440, 230 and 125 individuals/m². However, equal biomasses were not exactly matched, since the biomass of the smallest size class (6) amounted only about a fourth of the biomass of the other three size classes. Using different numbers of mussel size classes could

potentially lead to disproportionate effects on the percentaged mortality between the different sizes. For example, one consumed mussel of the biggest size class has a much bigger impact on the percentaged mortality than one mussel of the smallest size class. But in order to match energy requirements a crab needs to consume much higher numbers of small mussels compared to bigger ones.

The total volume of oysters in the experimental

Table 1. ANOVA sums of squares Type III under a split plot design for the response variable logit mortality.

Factor	df	SS	MS	F	p
Among plots					
Acclimatization (Ac)	1	25.66	25.66	4.31	0.042
Crab size (C)	1	30.22	30.22	5.08	0.027
Oyster presence (Oy)	1	108.59	108.59	18.25	<0.001
Ac:C	1	8.28	8.28	1.39	0.242
Ac:Oy	1	0.07	0.07	0.01	0.916
C:Oy	1	36.57	36.57	6.14	0.016
Ac:C:Oy	1	8.52	8.52	1.43	0.235
Residual	69	410.60	5.95		
Within plots					
Mussel size (M)	3	149.19	49.73	35.63	<0.001
Ac:M	3	9.70	3.23	2.32	0.077
C:M	3	112.76	37.58	26.93	<0.001
Oy:M	3	19.87	6.62	4.74	0.003
Ac:C:M	3	4.91	1.64	1.17	0.321
Ac:Oy:M	3	1.09	0.36	0.26	0.854
C:Oy:M	3	16.06	5.35	3.84	0.011
Ac:C:Oy:M	3	6.81	2.27	1.63	0.184
Residual	207	288.93	1.40		

aquaria varied between 0.5 and 0.55 L. After oysters were loosely placed in the oyster (+) treatment aquaria, mussels were added to all aquaria and were given 3 days to acclimatize and either hide in the interspaces of the oyster matrix or form aggregates with conspecifics.

Two different treatments of mussel acclimatization were applied, without and with crab and injured conspecifics being present during the acclimatization phase of the mussels. The latter should stimulate clumping behavior of the mussels and therefore create a more comparable setting to field conditions. Crabs that were not involved in the actual feeding trials were placed into rectangular cages (fish net breeder, 16.7 × 12.3 × 13.4 cm) covered with nylon mesh (1 mm), which were mounted on the upper side of the plastic aquaria. This design allowed the scent of predators and damaged conspecifics to reach the mussels at the bottom, but prevented the predators from consuming or damaging the experimental mussels. The crabs in the cages were provided with a continuous amount of fresh mussels. As a result of the feeding process, there were plenty of damaged mussels in these cages. After mussels were acclimatized for three days, crabs were placed into the aquaria and were given a foraging period of six hours, mimicking tidal submersion. Each crab was only used once in the experiment. After the six hours of predation, crabs were removed and aquaria

checked for surviving mussels. The fraction of consumed mussels per size class was logit-transformed to normalize the data using the formula:

$$y = \ln\left(\frac{c + 0.01}{1 - (c + 0.01)}\right),$$

with c as the fraction of consumed mussels per size class.

After experimentation, two crabs were found to be in proecdysis and one died and therefore all trials with these crabs were excluded from analysis. All three crabs originated from the small size class, at which two were supposed to prey in presence of oysters and one in oyster absence, resulting in an unbalanced experimental design. To cope with the unbalance a split plot ANOVA with sums of squares Type III was applied. This type tests for the presence of a main effect after the other main effect and interaction and is therefore valid in the presence of significant interactions. However, the results need to be interpreted with caution (in the presence of interactions, main effects are not easy to interpret). The error structure of the ANOVA is defined in the nested error term, which is the biggest plot size (aquarium) in relation to the within factor (mussel size). Effects were considered to be statistically significant if $p < 0.05$. Statistical analysis was performed using R v3.02 (R Development Core Team 2013) supplemented by the package ez (Lawrence 2013).

RESULTS

Due to the complexity of the experimental design, we will first focus on the among plot variability without regard to within plot variability (i.e., coupled to mussel size) (Table 1). Our analysis indicates that the presence of oysters significantly affected the mortality of mussels, but that the effect varied according to crab size (C:Oy interaction; $F = 6.14$, $p = 0.016$). For all levels of the other two factors (Ac and C), oyster presence reduced the amount of predated individuals (Fig. 3). Yet, the magnitude of reduction in mussel mortality due to oysters was higher in the presence of small crabs. In addition to the impact on the among plot variability, oyster presence also had significant effect on the within

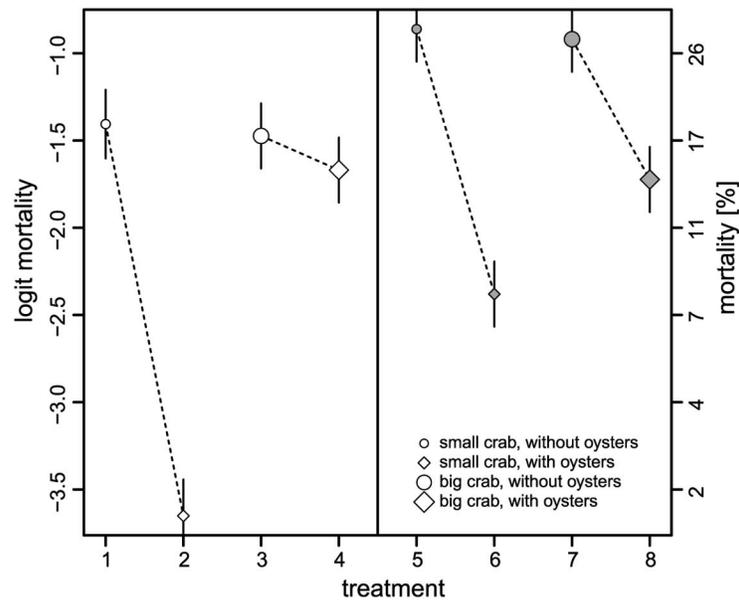


Fig. 3. Mean logit mortality (\pm SE of parameter estimation) of all mussels per individual treatment. White symbols indicate the trials of the acclimatization control and grey symbols the ones for the induced clumping trials.

plot variability. The survival of the different mussel sizes with respect to predator size and oyster presence/absence differed significantly from each other (C:Oy:M interaction; $F = 3.84$, $p = 0.011$). Small crabs predominantly foraged on smaller mussels of category 6 and particularly 12 (Fig. 2b). The biggest size class of mussels (24) was only chosen as prey by a few small crabs resulting in low or no mortality at all in the 4 different treatments (Fig. 2b). Conversely, the presence of oysters reduced mussel mortality in the three smaller mussel size classes (6, 12 and 18) dramatically.

At acclimatization control, mortality of size classes 6 and 12 accounted for 40% and 55% in absence of oysters, respectively, and could be reduced to 6% and 2% in presence of oysters. Mortality in the size class 18 was reduced from 15% in absence of oysters to 1% in the presence of oysters. In trials where clumping was induced, the mussel mortality tended to be higher compared to the mortality in control treatments. However, crabs preferred the same mussel sizes as in the acclimatization control. There was also a dramatic decrease in mortality ranging from 30–70% to 10–15% in mortality of size classes 6, 12 and 18 due to the presence of oysters (Figs. 2b, 4).

Big crabs were capable of foraging on all four mussel sizes offered, but preferably consumed mussels of size classes 12 and 18. The introduction of oysters had a lower effect on the survival of the mussels exposed to predation by big crabs compared to small crabs. In trials with control acclimatization the effect of oysters was minimal, with size classes 12 and 18 being unaffected and only a slight reduction in mortality of size classes 6 and 24 (Fig. 4). The effect of oysters tended to be higher in trials with induced clumping so that consumption rates of size classes 12, 18 and 24, that amounted to 25–50% in absence of oysters, could be reduced to 10–35% when oysters were present. The survival of size class 6 showed little effect.

The chemical cues of crabs and injured mussels during the acclimatization period visually induced a denser clumping of the conspecific mussels. However, the cues did not improve the survival of mussels. Moreover, the consumption of the mussels was slightly higher in the treatments with induced clumping compared to control acclimatization. In addition, there was no significant interaction on the type of acclimatization and the different size classes of the mussels on mussel survival (Table 1).

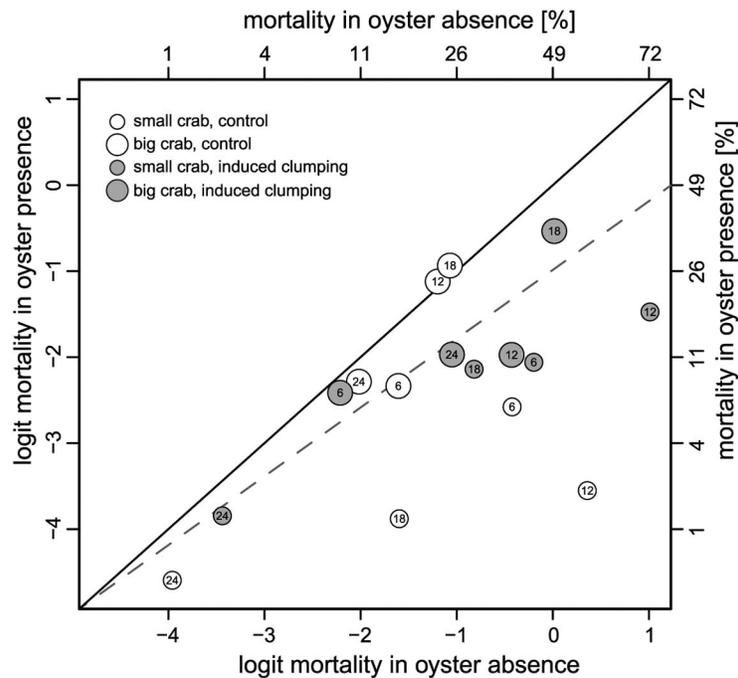


Fig. 4. Mean mortality in presence of oysters in relation to mean mortality in absence of oysters per individual treatment. The numbers within the circles represent the different mussel size classes. Black solid line represents $y = x$ line; circles on or close to the solid line indicate no or minor differences in mortality related to oyster presence. Circles underneath the line point to a higher mortality in the absence of oysters compared to oysters being present. The higher the distance of a circle to the line, the greater the difference in mussel survival between the two levels of oyster presence. The dashed line indicates a drop of the mortality by half of its original value with oysters being absent. All mortality rates below the dashed line could be reduced to 50% or more.

DISCUSSION

Habitat forming species can affect species survival either purely by their physical structure (i.e., reducing predator-prey encounter rates) (DMIIIs) and/or by affecting species behavior (TMIIIs). Here we demonstrate that the Pacific oyster reduces overall mussel mortality by means of crab predation. This result agrees with previous findings, indicating that habitat complexity caused by oysters can reduce bivalve mortality by altering predator-prey interactions (Hughes and Grabowski 2006). Furthermore, studies on other habitat forming species suggest that effects of habitat modifiers on other species may change with ontogeny. For example, seagrass facilitates bivalve recruitment by providing a surface for colonization and/or a refuge from predation (Orth et al. 1984, Williams and Heck 2001), while Gribben and Wright (2014) found no

mediating effect of seagrass structure on predation risk of adult clams. Moreover, seagrass negatively affects adult clam survival since seagrass provokes a shallower burial depths of clams that increases both predation and non-predation mortality (Gribben and Wright 2014). In our study, we found the reduction in mortality of mussel recruitment to be size specific. With the introduction of the Pacific oyster, mussel mortality was particularly reduced in sizes smaller than 20 mm in shell length. These results suggest that, besides the change of general predator-prey encounter rates, also other mechanisms may affect the survival of mussels in presence of oysters. When different sized mussels were placed next to oyster patches in a laboratory setup, mussels were found to migrate towards the oysters and were found to be on average smaller in the interspaces (17.35 ± 4.46 mm) than on the edges of oysters (19.09 ± 4.07 mm) (A. M.

Waser, unpublished data). The size specific differences in hiding behavior are due to the fact that spatial refuges arising from oyster presence are mostly small and provide refuge for smaller individuals of mussels. Furthermore, smaller mussels are more active which would facilitate locating most suitable refuge.

To our knowledge, our study is the first to clearly show a relationship between habitat complexity and size specific mortality. In top-down trophic pathways the importance of body size in the strength of TMIIIs is already well-known (Rudolf 2006, 2008, 2012, Preisser and Orrock 2012, Krenke and Rudolf 2014). Yet, the findings of these studies found mixed support for size specific TMIIIs. While a meta-analysis investigating the role of size range across different species did not find a clear relationship between TMIIIs and prey survival (Preisser and Orrock 2012), a study of an interaction of two predatory hemipteran and one copepod species indicated a clear relationship between size ratio of multiple predators and the strength of TMIIIs (Krenke and Rudolf 2014).

In our study, we only focused on the importance of oyster appearance on the survival of mussels up to 27 mm in shell length. In the Wadden Sea adult *M. edulis* readily reaches lengths up to 65 mm (e.g., Buschbaum et al. 2008). To what extent the oysters affect the survival of the larger individuals of *M. edulis* is unknown. However, we believe that oyster induced habitat complexity has no impact on the survival of the very large mussels in terms of predation by shore crabs, since crabs tend to avoid bigger mussels to either achieve higher net intake rates and to prevent themselves from claw damage (Smallegange and Van der Meer 2003). Even largest size classes of crabs (carapax width of 70–75 mm) prefer relatively small mussels of around 22.5 mm in shell length (Elner and Hughes 1978). Predators that preferably prey on larger mussels are several bird species (oystercatcher, herring gull and common eider). Field observations suggest that oyster presence decreases predation rates of the birds, causing a reduction in mussel mortality (Scheiffarth et al. 2007).

We identified not only differences based on size in the transmitting species, the mussels, but also in the receiving species, the crabs. In our

trials, oysters had a higher impact on the predation efficiency of small crabs compared to big crabs. In presence of oysters, small crabs were less successful in preying on mussels compared to trials where no oysters were present, whilst predation of big crabs was less influenced by oyster presence. These observations contradict previous studies, which found complex substrates to influence predation success of bigger predators more than of small predators, because prey in crevices within complex substrates are still accessible to small sized predators (Clemente et al. 2012, Toscano and Griffen 2013). The contrariety of observations could be based on the experimental setup where oysters were not fixed in the substrate matrix. This allowed, other than under natural conditions, crabs to manipulate the matrix and to move single oysters in order to gain access to hidden mussels. This may explain the lack of effect of oysters on the predation success of big crabs as their increased strength would enable them to move oysters and increase access to more mussels.

We hypothesized that the settling behavior of mussels differs between scenarios where only TMIIIs triggered by oysters were active and scenarios where TMIIIs simultaneously triggered by crabs and by oysters were affecting the behavior of mussels. Simultaneous TMIIIs triggered by crabs and by oysters should cause mussels to migrate away from the outer edges of the oyster matrix towards deep interspaces of the oyster matrix resulting in a lower mortality. Unexpectedly, we found that the addition of crab triggered TMIIIs did not reduce the mortality of mussels. Actually, we observed the opposite trend of higher mortality in mussels where TMIIIs additionally were induced by crabs. On the basis of our experimental design, having all plots of the acclimatization control conducted in the first two blocks and the plots of the induced clumping in the last two, our experiment has limitations about interpreting the survival of mussels in terms of the factor acclimatization treatment. As this factor is confounded with time, we cannot rule out the effect of time related changes, such as the condition of animals, as a reason for differences in mortality. Since we experienced some logistical problems during the experiment (essential material for the induced clumping treatments was not available in the beginning of

the experiment), we were forced to conduct the clumping treatments in different blocks. A factor that might have influenced the survival of mussels is that the mussels used in the experiments were taken from environments where they were constantly exposed to crabs and also other predators. They might have habituated to the presence of predators and may be adapted through alterations in their morphology (significantly thicker shell density and adductor muscle diameter). Adaptive modifications of induced aggregation behavior and attachment in mussels in response to predators can weaken over time in favor of more passive anti-predator response by altering shell density and adductor muscle diameter (Christensen et al. 2011). Also, the cues produced by one crab might have been not strong enough to induce anti-predator behavior. It was found that anti-predator behavior is highly affected by the bodymass of predators, which can be either achieved of one really big individual or by plenty of smaller ones (Hill and Weissburg 2013).

The state ontogenetic development plays a crucial role on the strength of indirect effects. The effects of TMIs therefore vary strongly within size structured populations. This is particularly vital when evaluating the consequences of environmental changes caused by the introduction of new species to ecological systems. So far, effects of invaders on different life stages of the native fauna has received little attention. Sized structured variation in strength of TMIs induced by invaders may ultimately cause shifts in the population structure of native species.

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