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The effect of an invasive species on predation rates upon intertidal barnacles

Rachel Linaker

Project Advisor: Andy Foggo, School of Marine Science & Engineering, University of Plymouth, Drake Circus, Plymouth, PL4 8AA

Abstract

Non-indigenous species invasions are considered a large threat to native biota however the effects of which have been relatively understudied with respect to intertidal systems. Current literature surrounds the movement of species, however relatively little attempt has been made to quantify the effect. Using the invasive oyster drill *Ocenebra erinacea* and the native dogwhelk *Nucella lapillus*, this study aimed to investigate the effect of an invasive species' on predation rates over a one-week period feeding on the intertidal barnacle *Chthamalus montagui*. This was conducted by testing for the effects of increased conspecific density (abundance increase) and biodiversity (species number/identity) against the background predation rates established in single whelk trials at two different temperatures. As expected due to metabolic demand, there was a positive effect of temperature on predation rate. The results also revealed a significant occurrence of underyielding, whereby the whelks predated less efficiently in both density and biodiversity tests. Despite plant or algal studies expecting a degree of increased ecosystem function to occur with an increase in species richness and functional diversity, it was assumed that due to both species having a similar distribution and trophic niche, interspecific competition for resource acquisition would have occurred. Warming air and oceanic temperature trends are expected to alter the distribution and abundance of both native and invasive species, and the effects of which are effectively predicted using this study. However, both create problematic scenarios that need to be addressed promptly.

Introduction

Biological invasions and the constant spread of invasive species are considered to be some of the most serious global environmental threats alongside climate change (Stachowicz et al. 2002). There is a lot of debate surrounding the definition of an 'invasive species' however for this study, it refers to one that is non-indigenous to that area (Carlton 1989). Invasive species occur outside of their natural range as a consequence of two processes; either natural range expansions or by anthropogenic introductions into new environments (Carlton 1987; Troost 2010). An increase in human activity around coastal areas has resulted in them being among the most heavily impacted systems, particularly in terms of biological invasions (Kylafis & Loreau 2008). These biological invasions may also have disastrous consequences to the economy, such as the effect of the invasive marine gastropod *Ocinebrellus inornatus* on French oyster aquaculture (Goulletquer et al. 2002; Martel et al. 2004). Despite this, marine and coastal invasions are still relatively understudied.

Human-mediate biological invasions have occurred historically since the utilisation of ships for travel in the 1700s. Here, the hulls were often encrusted with fouling organisms or contained within the dry ballast. When scrubbed clean at each port, the now non-indigenous species were expelled into the new area (Bax 2003). Recent examples may include the introduction of larval organisms for aquaculture or the transportation of organisms for the aquarium industry (Matlock 2004). An opening or 'invasive window' (Johnstone 1986) must be created by proper combinations of ecological and biotic factors (Carlton 1996) which effectively remove a barrier to an invasion, thus allowing the invasion to occur (Shea & Chesson 2002). Successful establishment generally occurs if the conditions at the destination match those of the invader's tolerance range (Hoegh-Guldberg & Bruno 2010). Invasive window size is effectively increasing with climate change, particularly in high-latitude environments. In these areas, the chance of a low-latitude species becoming established is increasing (Stachowicz et al. 2002; Hoegh-Guldberg & Bruno 2010)

Anthropogenic climate change and the subsequent alteration in thermal regime have been documented within every ocean, on every continent and in major taxonomic groups (Parmesan 2006). Due to temperature absorption within the oceans, a 0.5°C average increase has been reported within the last few decades (McCarty 2001; Walther et al. 2002; IPCC 2007; Hoegh-Guldberg & Bruno 2010). Some of the most rapid changes have occurred in the north-east Atlantic (IPCC 2007; Hawkins et al. 2008), with an increase of 1°C already detected in the western English Channel off Plymouth since 1990 (Mieszkowska et al. 2006). Climatic variability can also induce a more natural invasion of non-indigenous species due to alterations in geographic distribution surrounding thermal limits (Stillman & Somero 2000) and the importance of this has been implied in many studies (Walther et al. 2002; Heikkinen et al. 2006; Sanford & Swezey 2008). Thermoregulation has been regarded as a highly important factor for determining an organism's ecological niche or 'thermal limit' (Porter & Kearney 2009). Temperature has both a direct and indirect effect upon the physiology of an organism and so variations in thermal regimes are important (Muñoz et al. 2005), potentially leading to lethal temperatures which can induce a shift in geographic range (Dahlhoff, Buckley, & Menge 2001).

Intertidal organisms are already assumed to be close to their thermal tolerance limits (Stillman & Somero 1996; Stillman & Somero 2000; Helmuth et al. 2002). Localised

extinctions may occur should air and water temperatures continue to rise, resulting in population fragmentation (Zippay & Hofmann 2009) and the opening up of subsequent windows of opportunity for invasive species to colonise. With warming trends, geographic ranges and distribution limits are expected to shift towards the poles as long as dispersal and resource availability allow it (Mieszkowska et al. 2006; Hawkins et al. 2008). This expectation assists the movement of invasive species and allows those introduced via human methods to become well established in the new environment (Carlton 2000). The combination of erratic changes in temperature (air and water) and the addition of invasive species can have disastrous consequences on the overall ecosystem functioning as well as having direct consequences on individual resident species.

Existing studies surrounding the influence on species diversity and composition and ecosystem function as a whole are relatively numerous with a majority of studies surrounding either plant or algal assemblages (Tilman et al. 1997; Fridley 2001; Schmid et al. 2008; Griffin et al. 2009). Due to inconsistency across studies, the influence of species diversity on ecosystem functioning is a controversial topic (Fridley 2001). Whilst only two species are studied in this instance, it is deemed appropriate to gauge the effect of an invasive species, assuming that predation rate (essentially resource processing) will contribute to the overall ecosystem function. Very few publications have dealt with the effects of invasive species on native biota, however Krisp & Maier (2005) concluded that invasive gammarid species cause a steep decline in native macroinvertebrate populations. The invasive *Dikerogammarus villosus* had a much higher feeding rate on a broader range of prey than either another invasive species of the same family (*Echinogammarus ischnus*) or native gammarids. Whilst their results did not prove that predation by these invaders is a major cause for the decline observed, it was suggested that invasive species could interfere with native species through competition or altering interspecific interactions. With respect to the actual effect that invasive species may have on resident species, there have been very few publications supporting this study despite the expectation that non-indigenous species that achieve high densities in recipient areas will have negative effects on native competitors (Brenneis, Sih, & De Rivera 2010)

As supported by the Optimal Foraging Theory (MacArthur & Pianka 1966), foraging behaviour and organismal fitness are assumed to be causally related (Burrows & Hughes 1990). It is therefore ideal to study the effects of resource processing (through predation rates) to assess the potential impacts on both fitness levels and ecosystem functioning. The oyster drill, *Ocenebra erinacea* (Linnaeus 1758) is originally a resident of France (Goulletquer et al. 2002; Martel et al. 2004) and other warm-water European coasts (Garcia-Meunier 2002). It has been an established on west and south-west British and some Irish coasts since introduction around the 1800s (JDD Bishop, pers. comm.) and overlaps in distribution and trophic niche with the boreal-Lusitanian dogwhelk *Nucella lapillus* (Linneus 1758). As both species feed on barnacles, the warm-water Montagu's stellate barnacle *Chthamalus montagui* (Southward 1976) was chosen for the prey item.

The predation rate of both species in isolation will first be established at two different temperatures. Secondly, by increasing conspecific density the study will effectively mimic group feeding to observe the potential impacts of increasing species

abundances. Thirdly, the effect of biodiversity will be studied by varying species identity and composition as both factors present within a system determine the traits influencing ecosystem process, thus species diversity has functional consequences that need to be addressed (Chapin et al. 2000). If the predation rate in the multiple whelk trails is greater than expected based on the weighted average of the monoculture yields of the component species, then non-transgressive overyielding has occurred whereby ecosystem function increases (Loreau 1998; Hector et al. 2002; Schmid et al. 2008). Conversely, should the net yield result in a negative value, then ecosystem function has decreased and underyielding has occurred (Woodward 2010). Based on the premise that the species inhabit similar niches and predate on similar prey items, it is predicted that the two species would be in direct competition for the food source and subsequently foraging rates should decline. The magnitude of change however, depends on how the species react in isolation.

Materials and methods

Specimen collection and collection site

100 *Nucella lapillus* and 100 *Ocenebra erinacea* individuals were collected from the site of distribution overlap on the eastern side of Batten Bay, Mount Batten (OS: SX 488 529), during September 2010. Shards of rock covered in barnacles were also collected using a hammer and chisel. The rock chips were approximately equal in size, dominated by *Chthamalus* spp. and were collected regularly throughout the duration of the experiments.

Collected whelks and barnacles were kept in oxygenated aquaria within a stock-holding room and maintained at a constant temperature (15°C). Water was changed and barnacle chips were added regularly until whelks were required for experimentation. Any dead barnacles were removed.

Size: dry mass ratio

The relation between size and dry mass was established for both *species* so that the external dimensions of the whelks used in trials could be used to determine dry mass of the predators. 30 individuals of varying sizes from each were cleaned of epibiota. Shell length (apex of shell to tip of siphonal canal) and shell width (the widest point across the operculum) was measured to the nearest 0.1mm using digital vernier callipers for each individually labelled whelk. Wet masses (to the nearest 0.0001g) were measured using a Fisherbrand PS-200 balance. Whelks were dried in an oven set at 45°C. All individuals were measured using this method, and the balance was recalibrated after each reading. Shell length evidently provided a better relationship to dry mass than shell width, and so in subsequent experiments only shell length was measured.

Single whelk trials

40 individuals from each species were selected, half for the 15°C C.T. room and half for the 20°C C.T. room. 23 x 500ml aquaria containing 250ml of seawater in each were set up in each room (46 total). Whelks were placed in 40 of the tanks, aerated and covered – the three additional aquaria in each room acted as control tanks, present to measure background barnacle mortality. Whelks were starved for 72 hours, allowing hunger levels to be standardised as well as allowing them to acclimatise to the ambient temperature.

On the day of the experiment, 86 rock chips with a barnacle density of approximately 50 individuals were selected out of the holding tank. Dead barnacles were removed from each chip. Barnacles other than the dominating species were also removed. Barnacle chips were then added to each of the labelled test tanks, with three of the chips used in the control tanks. This marked the start of the experiment at zero hours.

48 hours after barnacle addition, barnacles were removed from their allocated tanks and placed under a microscope for dimensions to be taken. Barnacles were probed with forceps to see whether they were dead or alive. Dead barnacles were measured using an eyepiece graticule (0.1mm divisions) and removed to prevent recounting. Chips were returned back to their allocated tanks. This process was repeated after a period of 96 and 168 hours had passed.

Multiple whelk trials

An additional 60 individuals were collected (30 *O.erinacea* and 30 *N.lapillus),* eradicating the risk of altered behaviour due to captivity. 20 x 1.5litre aquaria with 750ml seawater in each were set up in the 15°C room. Each tank was given an I.D. number (1-20) and whelks were added as follows: Aquaria 1-5 contained 3x *N.lapillus* individuals; aquaria 6-10 contained 3x *O.erinacea* individuals; aquaria 11-20 contained a mixture of both, 2x *N.lapillus* and 1x *O.erinacea* (11-15), and 1x *N.lapillus* and 2x *O.erinacea* (16-20). As with the single whelk trials, both seawater and whelks (without food) had to be left in the temperature controlled room for 72 hours before trials started in order to standardise seawater temperature, hunger levels, and allow the whelks to acclimatise to the new environment.

20 larger rock chips bearing a minimum 150 barnacles were chosen for this experiment. As with the previous trials, they were prepared prior to the experiment starting – checking for dead barnacles and other species. Once experimentation was underway, the same protocol implemented for the single whelk trials was used here, with barnacles being checked at 48, 96 and 168 hours.

Calculating the net effect of diversity and species richness and identity.

The mean results generated from the single whelk trials for both species were applied in order to calculate the net effect of (a) diversity and (b) species richness and composition. This was achieved by evaluating the deviation from the expected ('null') rate of predation based on species' rates in isolation. This would result in the effect of biodiversity on ecosystem functioning, as suggested by Emmerson & Raffaelli (2000), using predation or resource utilization as a factor. For calculating the net density effect, the expected predation rate was calculated by multiplying the mean predation rate (per unit of barnacle per unit of whelk dry mass per 24 hours) for that time slot (48, 96, 168 HRS) by the dry mass of the whelk tested. The observed rate (the actual predation rate experienced) was then divided by this rate. For calculating the net composition effect (using two combinations of species composition, 2N1O and 1N2O) a very similar approach was applied. In this case, a substitutive design was utilized when calculating the expected (E) value whereby (E) is obtained from a weighted average of the species used at the same total density of the species mixture. This is based on the equation supplied by (Loreau 1998)

Statistical analyses

All statistical analyses were conducted using SPSS version 18.0. Repeated-measures analysis of variance (ANOVAs) was used to determine the effect of the variables on whelk predation rate, using time (48, 96, 168 hrs) as the within-subjects variable. In order to determine the difference between the base foraging rates of both species at two different temperatures, a repeated–measures analysis of variance (ANOVA) was performed with temperature (15°C and 20°) and species used (N = *N.lapillus*, O = *O.erinacea*) as the two between-factor variables and time (48, 96, 168 hrs) as the within-subjects variable. To determine whether there was a significant difference between whelk predation rates at an increase conspecific density, another repeated-measures ANOVA was conducted using species (N, O) as the between-subjects variable and time as the within-subjects variable. A repeated-measures ANOVA was used to test for significant differences between two mixed-species polycultures (2N1O, 2O1N) using species composition used as the between-factor variable, and time as the within-factor variable. Similarly, and relating to the same set of trials, the final test analysed the effects of species composition on predation rate across time. This used the four possible composition combinations (3N, 3O, 2N1O, 2O1N) nested within the appropriate level of species richness (1 for single species, 2 for mixed species) and time was used as the within-subjects variable. All data was tested for deviations from sphericity using Mauchly's Test (A Foggo, pers. comm.) and deviations from sphericity were corrected by modification of degrees of freedom (A Foggo, pers. comm.)

Results

Table 1: A summary of the mean predation rates across time for each treatment (temperature: 20°C/15°C; density trials; mixed trials), explicitly stating which species were used (O/N for temperature trials; 3O/3N for density trials; 2N1O/2O1N for mixed trials). For density and mixed trials, these were the actual mean values obtained and thus *not* the difference between observed and expected values. *n* = replicates per trial.

Treatment	Species	Hours			Mean	*n*
		48	96	168		
20°C	**O**	787.86	771.03	742.20	767.03	20
	N	1335.31	1121.58	879.14	1112.01	20
15°C	**O**	265.72	260.19	312.36	279.42	20
	N	607.86	800.14	827.27	745.09	20
Density (3 individuals)	**O**	168.19	285.58	273.19	242.32	5
	N	321.59	552.93	607.71	494.08	5
Mixed (3 individuals)	**2N1O**	568.27	546.49	470.26	528.34	5
	2O1N	444.03	462.33	367.98	424.78	5

Predation rates of species in monoculture at different temperatures

N.lapillus and *O.erinacea* predation rates in the 15°C room were consistently lower than in the 20°C. Predation rates in *N.lapillus* increased over time at 15°C, with a relatively stable rate of predation exhibited at 96 and 168hrs, but decreased in the 20°C room (Figure 1). *O.erinacea* on the other hand exhibited a relatively stable predation rate across time in both treatments. Disregarding the effect of temperature, *N.lapillus* had an average predation rate 1.8 times greater than *O.erinacea* (Table 1), this difference however was not significant (ANOVA $F_{2,152}$=1.156 P>0.05; Figure 1). Three separate two-way ANOVAs verified this. The effect of temperature on predation rate (over time) and the interaction between temperature, species and time were significantly different however (ANOVA $F_{2,152}$=9.032 P<0.001 and $F_{2,152}$=5.415 P=0.005 respectively; Figure 1).

Predation rates of whelks at an increased conspecific density

Increasing conspecific density resulted in a decrease in predation rate of both species, however the greatest extent was shown in *N.lapillus,* implying a greater effect of density at approximately 1.2 times that of *O.erinacea* (figure 2). Despite this, the average predation rate of *N.lapillus* was still greater than that of *O.erinacea* (table 1.) In this, a significant difference was found between the mean predation rates across time, as well as the predation rates respective of species and time (ANOVA $F_{2,16}$=237.109 P<0.001 and $F_{2,16}$=204.553 P<0.001 respectively; figure 2), thus supporting the observations made.

Whelks in polyculture; the effect of biodiversity

The difference between the mean values of each species combination across time was significant (ANOVA $F_{1.28,\ 10.239}$=4.778 P<0.05; figure 3), with the least difference (thus greater predation rate) being exhibited at the start of the time period. The differences in the mean predation rate between either single species (3N, 3O; species richness = 1) or multispecies (2N10, 2O1N; species richness = 2) tests over time was significantly different (ANOVA $F_{1.44,\ 23.039}$=45.564 P<0.001) as was the effect of species composition embedded within species richness (ANOVA $F_{2.88,\ 23.039}$=53.846 P<0.001), illustrating that it isn't just the number of species which cause an effect, but the composition of species within.

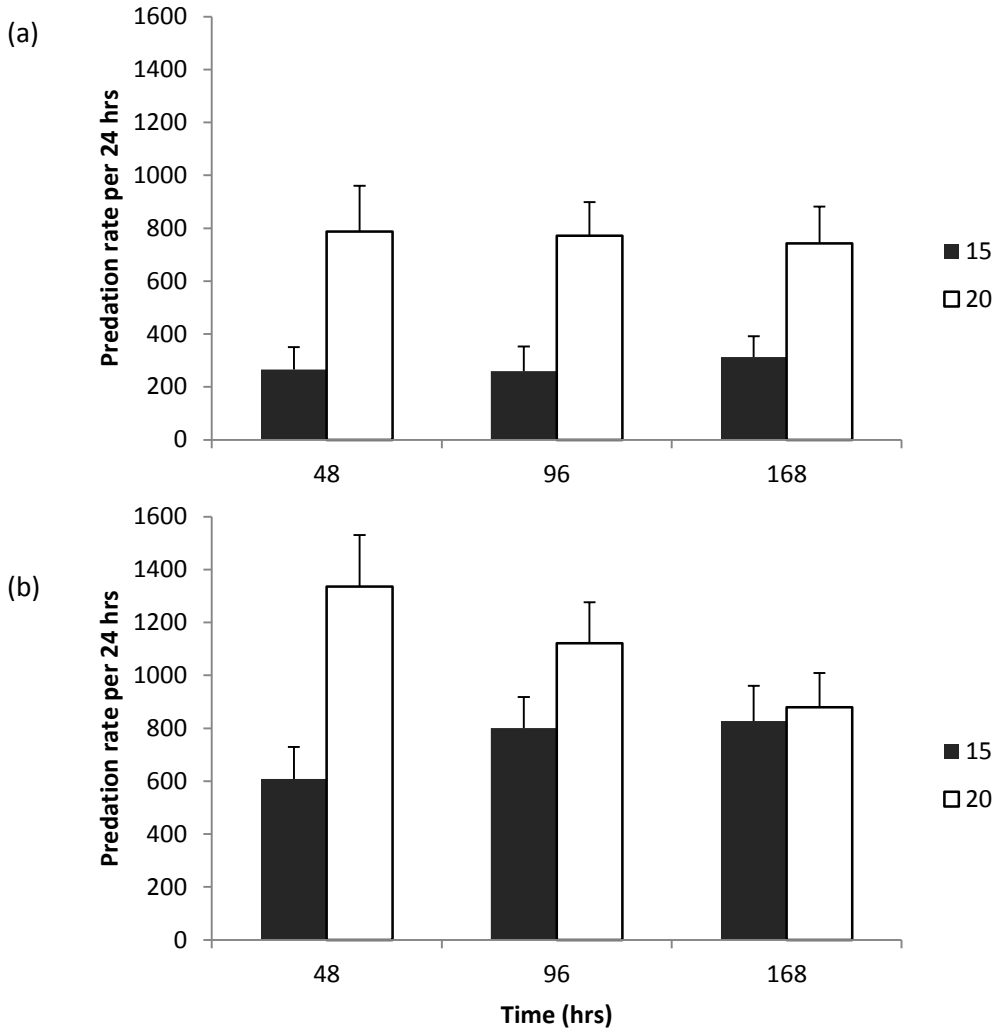

Figure 1: Whelk predation on intertidal barnacles during timed laboratory trials. Two whelk species (*Ocenebra erinacea,* top panel (a); *Nucella lapillus*, bottom panel (b)) were tested in monoculture at two different temperatures (15°C/20°C) across three time intervals. Bars depict the predation rates measured as unit of barnacle consumed per unit of dry whelk (mg) per 24 hours. Error bars show +SE; N = 20 replicates for each species and each temperature.

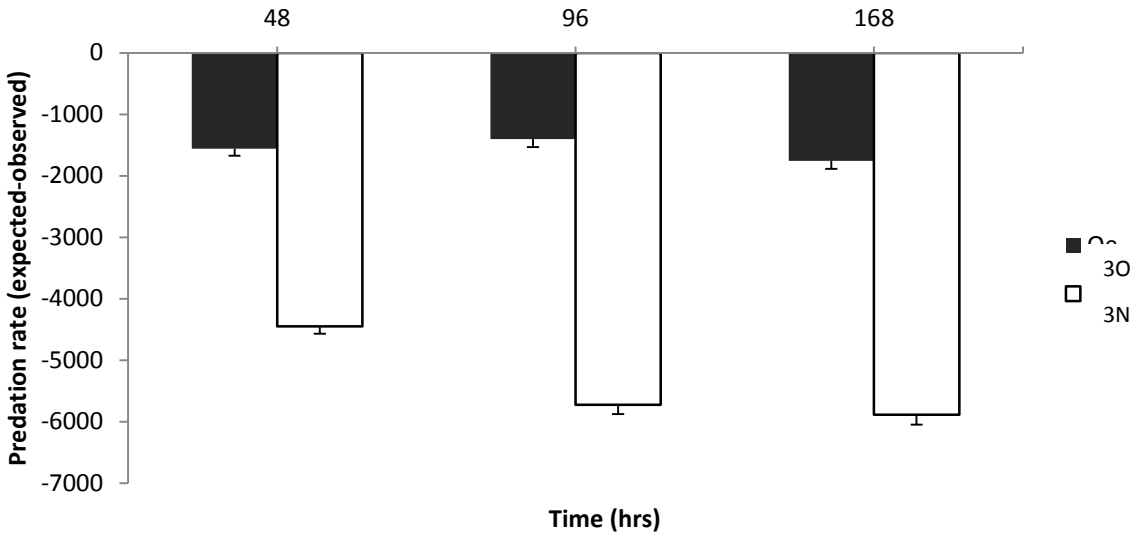

Figure 2: The difference between the observed and expected mean values for whelk predation rates, using *O.erinacea* (3O) and *N.lapillus* (3N) when tested at an increased density of a single species mix. Bars illustrate the extent of the difference (o-e). Error bars show -SE; N = 5 replicates for each treatment (3N or 3O)

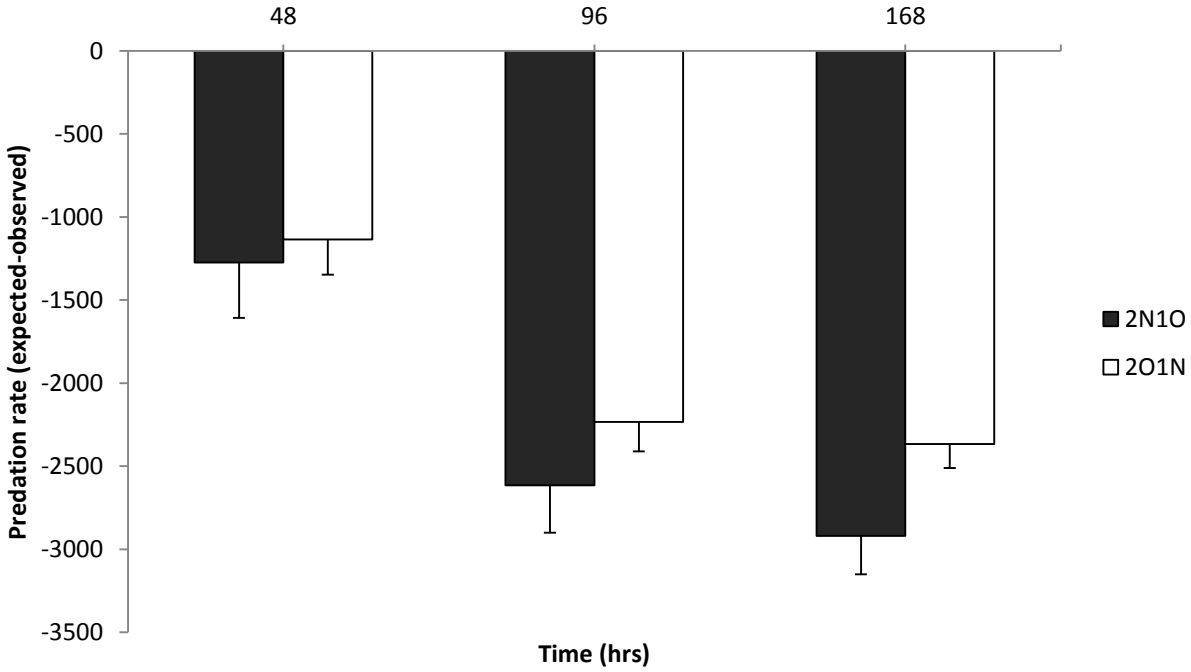

Figure 3: The net effect of species composition on predation rate generated from the expected-observed values, using either a composition compiling of two *N.lapillus* and one *O.erinacea* (2N1O) or two *O.erinacea* and one *N.lapillus* (2O1N) in polyculture. Bars illustrate the extent of the difference (o-e). Error bars show -SE; N = 5 replicates for each composition.

Discussion

The predatory rates of both *Ocenebra erinacea* and *Nucella lapillus* were quite different under laboratory conditions, with distinct trends depending on the treatment that the whelks were subjected to. The natural cycle of foraging in marine gastropods is closely associated with changing weather conditions such as temperature (Burrows & Hughes 1989; Sanford 2002b); this is demonstrated in this study depicted by the differing predation rates exhibited at both temperatures. Both whelk species responded in a positive manner, with a significantly greater predation rate exhibited at the warmer temperature. For *N.lapillus,* the increase in temperature elicited a 1.5 times increase in predation rate, consistent with Largen's (1967) study. A decrease in foraging behaviour at cooler temperatures is likely to be due to a decrease in metabolic demand (Rilov, Gasith, & Benayahu 2005) and a subsequent reduction in consumption level (Sanford 2002a; Sanford 2002b). Whilst 20°C is not a temperature that exceeds either species' thermal limits, it is important to consider that exceeding the individual limit could also result in a torpor response as well (Rilov, Gasith, & Benayahu 2005). Different species have different thermal limits which are reflected in their distributional limits. Generally, the thermal range limit of *N.lapillus* is found to be between 3°C (where feeding activity begins) and 27-28°C (where heat comas may be induced). Feeding is found to be optimal between 20-22°C (Largen 1967), and Gardestrom et al. (2007) found that at 30°C, there was a 50% rate of thermal induced mortality. *O.erinacea* has relatively little information surrounding its thermal limit; Hancock (1960), however, observed that 100% mortality occurred in this species exposed to temperatures below 1.5°C. Whilst not strictly related to the trials, this information could support the difference observed in predation rates as *N.lapillus* are more adapted to cooler waters.

A relatively negative interaction was found between an increase in conspecific density and predation rates. Both species' rates were found to be lower than the expected values thus underyielding occurred. The effect of an increased conspecific density elicited a relatively consistent pattern with time although predation rates were slightly higher at the start of the experiment, possibly because energy requirements overrode any competition between individuals. Although relating to an alternative biotic interaction, the need for energy has overridden the threat of predation risk

Another observation made was that the extent of the effect of density on both species was significantly different with *Ocenebra erinacea* predation rates being affected less than *Nucella lapillus*. Despite *N.lapillus* being prevalent within the intertidal zone, their distribution range is large compared to *O.erinacea.* In the trials, species were restricted to one barnacle chip in a relatively small tank and so intraspecific competition may have contributed to the end result especially with *N.lapillus* predation rates being exceedingly higher than *O.erinacea* in the first place. Group foraging in gastropods is relatively unstudied, however due to the size of the prey item it is not considered adaptive within this group (Brown & Alexander 1994). In *Stramonita haemastoma*, group feeding does occur in the field however does not occur in laboratory conditions – *N.lapillus* is not thought to feed in groups in the field, however. Group feeding was predicted to only occur for the consumption of large prey items (Packer & Ruttan 1988).

As expected from the pattern that emerged with conspecific density, a similar negative response was elicited from the effects of species identity within mixed trials.

As *Nucella lapillus* exhibited a greater effect of increase conspecific density, it could be assumed that both intra- and interspecific competition played a role in explaining why the composition comprising two *N.lapillus* and one *Ocenebra erinacea* showed the greatest difference between the observed and expected values. Drawing conclusions from both sets of results for these tests, it could be assumed that as the energy requirement of *O.erinacea* appears to be less than that of *N.lapillus*, there is no major competition for resources as these are numerous and abundant. Of course, without any direct observation of which species contributed to most of the barnacle-consumption, this is merely a speculation of what could have occurred.

Competition between invasive and native species has been documented in species which have had a particular detrimental effect on native populations. The Argentine ant *Linepithema humile* provides an excellent example of this following its worldwide invasion. This invasive species has successfully displaced many native species due to it having a competitive advantage as a result of heightened aggressive behaviour (Human & Gordon 1999; Buczkowski & Bennett 2008). Another equally renowned invasive species is the North American crayfish *Pacifastacus leniusculus* which often replaces native crayfish species (Vorburger & Ribi 1999). In this example, dominance was largely size-dependent which favoured the invasive species as it is a larger and faster-growing species. In a less well-known example, Corbin & D'Antonio (2004) observed that exotic annual grasses significantly reduced native perennial grass productivity yet the invasive species remained unaffected, signifying which species was competitively dominant. Although at this time *Ocenebra erinacea* seems highly unlikely to displace *Nucella lapillus* due to lack of evidence supporting the competitive capabilities of *O.erinacea*, there is still an effect of a reduction in prey processing exhibited in *N.lapillus.*

Invasive species aside, species diversity as a whole may increase the eventual productivity in a number of ways as outlined by Fridley (2001): either via complementarity or facilitation between species or sampling effect. However as suggested earlier, many of the examples supporting these are in fact plant based, such as facilitation by “nurse plants” (Fowler 1986). As suggested by Jonsson & Malmqvist (2000), facilitation between species could also account for the results their study demonstrated whereby leaf-eating aquatic insect species richness resulted in an increase in ecosystem process rate. Whilst this study does not portray any evidence of facilitation between *N.lapillus* and *O.erinacea*, intra- and interspecific interactions (including competition) as suggested are important.

Like all ectotherms, intertidal invertebrate body temperatures are regulated by external factors including solar radiation, relative humidity and air/sea temperatures (Helmuth et al. 2002; Helmuth et al. 2006). Considering this, the upper zonation limit of intertidal organisms is thought to be established by aspects of these (Connell 1972; Helmuth et al. 2006), including the influence that temperature can have on rock temperature (Gilman, Wethey, & Helmuth 2006). Climate change can influence temperature variability experienced within this system which can have an impact on the local distribution of organisms. *Ocenebra erinacea* is a predominantly sublittoral species yet emerges onto the sheltered intertidal zones during the summer months (Skewes 2005). As sea temperatures increase with the climate change, it could be predicted that this species will follow suit and also increase its range up the shore. Simultaneously, an increase in temperature also leads to an increase in desiccation,

both of which are factors which cause the zonation patterns seen within the intertidal zone (Stillman & Somero 1996). The upper thermal limit of *Nucella lapillus* may be shifted vertically towards the lower-shore due to this temperature/desiccation increase. Should this occur, the zone of distribution overlap and subsequent shared niche zone will increase between the two species and the effects revealed in the mixed-species trials may become evident in the field. An improvement in conditions may also result in an increase in abundance of *O.erinacea* and so effects could be greater. Whilst at present the niches may not overlap substantially in both species, this study could help map the effects should climate change drive both species together.

Extremes in temperature and weather conditions could effectively kill off many invasive species not used to the variability within the extremes of summer and winter temperatures. Following several occurrences of cold weather, *Ocenebra erinacea* nearly reached a point of extinction. On the east coast, population numbers declined substantially following the 1928/9 and 1939-41 cold winters (Orton & Lewis 1931) and did not reappear until 25 years later (Mistakidis & Hancock 1955). In 1962-63, the species suffered the same fate even in the South-West after another severe winter (Crisp 1964), indicating its intolerance to cold weather. Should another cold winter event recur, there may be a high probability that *O.erinacea* may be affected again, thus reducing the population, and potentially reducing the effects of mixed-species habitats.

Without empirical evidence supporting the wider-scale impacts of invasive whelk species on their native counterpart, it is difficult to propose any confident predictions on what will or may happen to other species within the ecosystem. Future studies must therefore be undertaken in order to expand our knowledge on the relationship between intertidal organisms and the introduction or expansion of an invasive species. Ideally, this would involve testing both species in such a way that the individual effects can be disentangled allowing us to conclude which species is affected more. From the results of this study, it can be assumed that the amount of prey processing is greatly reduced due to interspecific competition. Also, how an invasive species can induce trophic level effects is relatively understudied. Both species are intertidal carnivores and as predation has been found to be a key factor controlling community structure and processes within the intertidal (Menge 1978) it is a crucial area for investigation. As previously discussed, when both species were combined to mimic an increased species richness there was a significant decline in predation rate, so what implication does this have on the prey item abundance? If both species are present at relatively high abundances, prey availability may be reduced subsequently increasing interspecific competition. Similarly, the effects at higher trophic levels are not understood. Resident predators of *Nucella lapillus* may not react the same way to *Ocenebra erinacea* due to it being a relatively novel prey item. This occurred in the case of the Sanford & Swezey (2008) study on the range expansion of the volcano barnacle *Tetraclita rubescens* and the response by two native northern-species dogwhelks.

Although the investigations into the effect of *Ocenebra erinacea* on *Nucella lapillus* predation rates has been successful and that highly relevant data has been produced, there is still a requirement for more information surrounding both direct and indirect effects. Nevertheless, it creates a starting point for future research into

the effect that invasive organisms have on native biota. This, coupled with increasing air and sea temperatures as a result of climatic warming, creates a problematic scenario that must be addressed.

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