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The world is their oyster: Differences in epibiota on sympatric populations of native *Ostrea edulis* and non-native *Crassostrea gigas* (*Magallana gigas*) oysters.

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Running title: Epibiota of Native and non-native oysters

Abstract

In this study we aimed to assess the relative effects of native *Ostrea edulis* and non-native *Crassostrea gigas* and their associated epibiotic biodiversity. We recorded epibiont location on the shell as well as the upper or lower valve. Epibiont species richness was significantly lower on *C. gigas*. The epibiota communities differed significantly between the two oyster species. The continued spread of *C. gigas* may potentially impact the epibiont biodiversity associated with oyster species in Strangford Lough. Management strategies should prevent sustained population expansion and associated changes in colonisation habitat.

Key words: Invasive species, epibiota, biodiversity, *Crassostrea gigas*, *Ostrea edulis*.

1. Introduction

Oysters have long been recognised as ecologically important within both the intertidal and subtidal environments (Korringa, 1951; Yonge, 1960). They are not only an economically important fishery resource but also provide a suite of ecosystem services that benefit the health and wellbeing of their surrounding environments (Cranfield et al., 2003). Oysters are renowned for their ecosystem services such as; water column filtration, sediment stabilisation and benthic pelagic coupling and as such can be considered ecosystem engineers (Rodney and Paynter, 2006; Thurstan et al., 2013; Smyth et al. 2018). Their intrinsic value to the marine environment was highlighted during a Cost Benefit Analysis (CBA) into the feasibility of a proposed European oyster restoration initiative. The CBA revealed that the non-marketable consequential environmental improvements of *O. edulis* restoration (e.g. biodiversity, environmental services) would provide habitat managers with significantly greater monetary value than that of a commercial fishery (Laing et al., 2006).

A key aspect of the environmental contribution of the oyster is via the shell through the provision of a rich calcium carbonate substrate (Gosling, 2003). The shell

provides a favourable hard surface for the settlement of numerous bentho-pelagic larvae such as algae, barnacles and tube-building polychaetes (Wells, 1961; Gutiérrez et al., 2003; Smyth and Roberts, 2010). The gregarious nature of oyster settlement also has the potential to increase habitat heterogeneity, particularly when reefs are formed, many of which have been shown to support substantial commercial fisheries (Summerhayes et al., 2009; Grandcourt, 2012). However the effects of over-exploitation and pollution have led to the decimation of many wild oyster stocks (Thurstan et al., 2013; Smyth et al., 2016). Consequently oyster aquaculture has increased considerably over the last 50 years in order to meet consumer demand (Laing et al., 2006; Sawusdee et al., 2015). The European oyster *O. edulis* can still command a high market price although, low brood stock numbers and its susceptibility to disease have meant alternative species have been used to meet industry demands (Laing et al., 2006).

The Pacific oyster *Magallana gigas* formerly *Crassostrea gigas* was initially considered an ideal replacement for many struggling native oyster fisheries due to its fast growth rates and resilience to disease (Kerckhof et al., 2007). Its success as a culture species led to its translocation to over 60 countries outside of its native range and at one point it accounted for > 80% of global oyster culture (Ayers, 1991; Kong et al., 2015). When *C. gigas* was initially introduced into northwest Europe in the late 1960s, it was believed that the species would not reproduce successfully under the environmental conditions (Steele and Mulcahy, 1999). However, as a result of climatic changes and the environmental conditioning of aquaculture stock, the species spread from culture sites (Cognie et al., 2006; Cardoso et al., 2007; Troost, 2010; Wrange et al., 2010).

The spread of non-native species in this way can greatly alter the function and structure of native communities and ecosystems (Occhipinti-Ambrogi and Savini, 2003; Walles et al., 2015). As assemblages of non-native species become established they can lead to changes in the physical habitat and resource availability. These can have wide reaching effects particularly as interactions will be experienced throughout the associated trophic chain leading to numerous individual and group biotic interspecies interactions (Thomas et al., 2016).

In conjunction with being an excellent aquaculture species *C. gigas* is also a successful marine invader (Troost, 2010). It is highly fecund, fast growing and relatively disease resistant equipped with these traits it's an adept competitor with many indigenous species for space and food (Dankers et al., 2006). Its spread in coastal regions of the Northeast Atlantic represents a particular cause for concern as it is in direct competition for resources in the mid-intertidal with *Mytilus edulis* which is of significant commercial value to countries in the region (Gollasch and Nehring 2006; Brandt et al., 2008; Eschweiler and Christensen, 2011). It is currently competing with tentative recovering assemblages of *O. edulis* on the lower-intertidal zone of Strangford Lough Northern Ireland (Guy and Roberts, 2010). A similar scenario is also taking place along the Pacific coast of North America where *Ostrea lurida* assemblages have been settled on by *C. gigas.* As a result the North American native oysters have experienced depressed survival rates of >45% and reductions in growth of >20% (Trimble et al., 2009). In the Oosterschelde estuary in the Wadden Sea *C. gigas* has been forming large assemblages which have transformed intertidal mudflats important to bird life into oyster reefs (Wolf and Reise, 2002; Stelios et al., 2014). Dramatic changes in habitat of this type can herald shifts in nutrient cycling, food web dynamics and biodiversity (Jackson et al., 2001; Reise et al., 2017). In the Wadden Sea shifts from mussel beds to *C. gigas* reefs have been extensive and rapid resulting in extensive changes to benthic epifaunal communities (Kochmann et al., 2008; Stelios et al., 2014).

At Strangford Lough Northern Ireland, records of commercial harvesting of the native oyster *O. edulis* date back to the 17th Century (Kennedy and Roberts, 1999; Smyth et al., 2009). However, as a result of overfishing *O. edulis* populations collapsed in the 1900s, after which the species was no longer commercially viable. The feasibility of reinstating a commercial oyster fishery within Strangford Lough was examined by Parsons (1974) and Briggs (1978) through a series of growth trials using *C. gigas.* As a result of their success, several intertidal commercial *C. gigas* farms were established (Kennedy and Roberts, 1999). Approximately twenty years after the first *C.gigas* sites had been established the oyster was recorded outside of its licensed sites (Smyth et al. 2009). Subsequent surveys have identified feral populations

throughout the northern basin of the lough (Smyth et al., 2018). However, settlement density and growth appears to be slow as the Allee effect may be limiting population expansion and the temperature regime of the region is not optimal (Guy and Roberts, 2010). Nevertheless the discovery of *C. gigas* is of particular concern as the region is a designated Special Area of Conservation (SAC) under the 2009/147/EC Habitats Directive on the conservation of wild birds (Smyth et al., 2018). The mudflats in the northern basin are of particular importance as they accommodate the over-wintering of > 50% of the international population of Brent geese (*Branta bernicla hrota*) (Mathers et al., 2000). Any habitat change to these mudflats could affect the feeding behaviour of the Lough's internationally important wintering birds (Tinkler et al., 2009). Furthermore, *C. gigas* has the potential to negatively impact the recovery of *O. edulis* within the Lough. A species which has received considerable interest lately from NGO's, habitat managers and commercial fisheries and has been recognised within both the UK Biodiversity Action Plan and the OSPAR convention as a species which warrants conservation and expansion (Kennedy and Roberts, 1999; Smyth et al. 2018).

Investigations into the effects of invasive species often occur after the non-native has become established and little can be done to prevent its further colonisation or mitigate its impacts (Giraldes et al., 2015). In this classic "closing the gate after the horse has bolted" scenario the emphasis is on reporting the changes which have occurred as a result of the invasive, rather than predicting what changes may occur should the species become well established. The high water retention which typifies the northern basin of Strangford and influences the ecosystems (Kregting et al., 2016) in the region has meant that both oyster species co-occur at similar heights along the intertidal (Zwerschke et al., 2016). Consequently, native and non-native oyster populations are expanding sympatrically providing a unique opportunity to compare epibiota associated with each species before *C. gigas* has established reefs. As a result of this it was possible to assess if non-native oysters attracted more epibionts than natives. This comparison establishes a baseline from which potential changes in biodiversity resulting from rapid expansion of *C. gigas* populations in Strangford Lough and elsewhere may be assessed and or predicted.

2. Material and methods

2.1 Study Area

Strangford Lough is located on the northeast coast of Ireland and lies between 54° 35′ N and 54° 20′ N and between 5° 41′ W and 5° 34′ W enclosing an area of 150 km^2 (Figure 1). The depth of the lough ranges from 14-60 m**,** with substrate varying from bedrock to fine sediments determined by the gradient of tidal water movement. The lough can be divided into a mud flat soft sediment environment in the north and mixed sediment / bedrock habitats in the south (Kregting and Elsäßer, 2014).

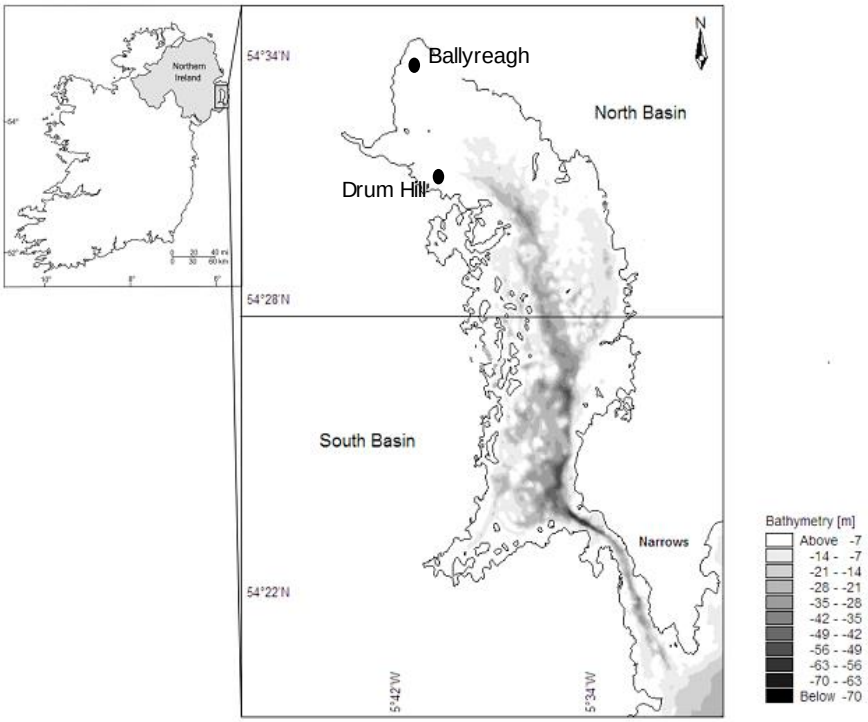

Figure 1. Strangford Lough Northern Ireland with associated bathymetry and relevant oyster sites.

2.2 Survey site and sample collection

The survey was undertaken at Drum Hill (54˚31´11˝N 5˚39´59˝W) (Figure 1) located on the northwest shore in close proximity to decommissioned *C. gigas* aquaculture trestles. Physical parameters at the site were measured by a governmental monitoring buoy which recorded: temperature 2–17.6°C, salinity 33ppt, mean nutrient concentrations (µmol l^{-1}) of 2.8 ammonium, nitrate 13.5, phosphorus 2, and silicate 4.3 with a mean nutrient load (ton year^{-1}) of 1,202 nitrogen and 126

phosphorus during 2009 (www.afbini.gov.uk/costal). Site selection was on the basis that the first wild settlements of *C. gigas* amongst intertidal *O. edulis* were recorded from this location (Kennedy and Roberts, 1999; Smyth et al., 2009).

Oysters were collected, during June 2009 on a spring tide < 0.5m below chart datum. A random belt transect and timed search methodology was employed with sampling taking place parallel to the low water mark as per Smyth et al., (2009). In order to minimize environmental impact and loss to a recovering assemblage of *O. edulis* sample size was limited to 17 individuals of > 50 mm in length from both *O.edulis* and *C. gigas*. Oysters were individually bagged with care being taken not to dislodge any epibiota.

2.3 Processing of Samples

Oysters were examined individually with shell length recorded from the umbo to shell lip and wet weight taken prior to shucking. All samples were fixed in formalin and preserved in industrial methylated spirits. Shell surfaces and rinse water were examined using a Nikon© SMZ400 stereomicroscope with epibionts counted and identified to the highest level. Colonial species were recorded in terms of the number of individual colonies present. Species associated with colonies attached to the shell were also considered as associated flora and fauna. The position of epibiota on the shell was recorded as upper / lower valve or detached.

Shell surface area was determined by wrapping the external surface of the upper and lower valves in aluminium foil ensuring no overlapping. The foil was removed and weighed and a calibration plot constructed plotting foil weight and surface area. All shell samples were aged using the umbonal acetone etching methodology as per Richardson et al., (1993).

2.4 Data Analysis

The relationship between epibiont richness, age and surface area for the oysters was examined using Analysis of Covariance (ANCOVA). A one-way ANOVA tested for differences between the epibiont richness on the shells and a variation of the Burnham and Anderson, (2004) model evaluated using a small sample corrected version of the Akaike information criterion AIC_c and an adjusted r^2. The lowest value of AIC_c defined the model with the best fit for the lowest level of complexity. The 'oyster species only' model was compared to a model including age, surface area and species abundance. The significance of the model, was calculated by adding the sum of squares together, divided by the number of degrees of freedom (3) to give a mean square which was divided by the residual mean square to give an F value.

Ranked matrices of similarities, based on presence/absence data, were generated using a Bray-Curtis similarity matrix in PRIMERvr6©. Ordination was by non-metric multidimensional scaling (MDS). Statistical analysis of differences between samples was carried out using the analysis of similarity (ANOSIM) test. To identify characteristic epibionts associated with *C. gigas* and *O. edulis,* a similarity percentage (SIMPER) analysis was employed.

3 Results

3.1 Univariate Comparisons

The ANCOVA revealed a significant difference between epibiont species richness and oysters for both age $F_{1,31}$=1.15, p>0.05 and surface area $F_{1,31}$=0.11, p>0.05.
C. gigas examined during the investigation were found to range from 2 to 5 years with a mean of 3.6 years. *O. edulis* ranged from 3 to 7 years with a mean of 4.4.
A similar number of epibionts were recorded during the study for both oysters; 51 species on *C. gigas* (30 exclusive) and 48 species on *O. edulis* (27 exclusive) (Table 1). The cirriped *Semibalanus balanoides* and the polychaete *Scolelepis* sp were most commonly associated with *C. gigas* and the rohodophytes *Laurencia pinnatifida* and *Lithothamnium calcareum* with *O. edulis*. The most frequent to both was *Elminius modestus* and *M. edulis.*

Table 1. Sample of the mean number of taxon on *C. gigas* and *O. edulis* collected at Drum Hill, Strangford Lough.

Phylum	Scientific Name	*C. gigas*	*O. edulis*
Annelida	*Oligochaete sp*	0.82	0
	Tubificoides pseudogaster	0.29	0
	Capitella capitata	0.12	0
	Eulalia viridis	0.06	0
	Phylodocid sp	0	0.24
	Gattyana cirrosa	0	0.12
	Harmothoe imbricata	0.06	0
	Harmothoe impar	0.41	1.12
	Harmothoe lunulata	0	0.06
	Hesionidae sp	0.06	0
	Kefersteinia cirrata	0	0.18
	Lagisca extenuata	0.06	0
	Nereis diversicolor	0	0.41
	Nereis pelagica	0	0.12
	Phyllodoce laminosa	0	0.06
	Phyllodocidae	0.06	0
	Pomatoceros triqueter	0.53	17.59
	Scolelepis foliosa	0.24	0
	Scolelepis squamata	0.41	0
	Spirobis spirobis	0.12	0
	Syllidae	0	1.06
	Syllis gracilis	1.41	0.12
Arthropoda	*Ampithoe gammaroides*	0	0.06
	Carcinus maenus	0.12	0.12
	Chaetogammarus marinus	0.12	0.06
	Chaetogammarus sp	0.06	0
	Semibalanus balanoides	6	0
	Balanus balanus	0.12	0
	Chaetogammarus stoerensis	0.06	0
	Eliminus modestus	224.29	706.29
	Chthamalus montagui	0.12	0
	Cressa dubia	0.06	0
	Cyrtolaelapidae	0.18	1.29
	Cyrtolaelapidae hydrogamasus	1.41	0.06
	Eulimnogammarus obtusatus	0.47	0
	Gammarus	0	0.06
	Halacaridae	0.06	0
	Harpacticoda sp	0	0.18
	Harpacticus	0.29	0
	Hydrogamasus	0	0.24
	Isotoma maritima	0.29	0

	Jaera sp	0.41	0.12
Phylum	**Scientific Name**	***C. gigas***	***O. edulis***
	Melita palmata	0.06	0
	Orchomene sp	0	0.12
	Sunamphitoe pelagica	0.43	0
Chordata	*Aplidium proliferum*	0	0.58
	Botryllus schlosseri	0.06	0
	Didemnid sp	0.06	0.24
Cnidaria	*Edwardsiella carnea*	0	0.12
	Actinia equina	0	0.12
Echinodermata	*Ophiura albida*	0.24	0
Mollusca	*Anomia ephippium*	0	.24
	Mytilus edulis	5.59	34.47
	Venerupis saxatilis	0.24	0
	Buccinum undatum	0	0.18
	Clathrus clathrus	0	0.06
	Gibbula cineraria	0.06	0
	Gibbula umbilicalis	2.06	0.88
	Littorina littorea	0.12	0.29
	Littorina mariae	2.18	1
	Lunatia catena	0.06	0
	Nucella lapillus	0.12	0
	Patella vulgata	0.29	0
	Tectura tessulata	0	0.12
	Acanthochitona crinitus	0	0.18
	Lepidochitona cinereus	0	0.29
	Leptochiton asellus	0.06	0
Nemertina	*Nemertopsis flavida*	0	0.06
Ochrophyta	*Fucus spiralis*	0.18	0
	Leathesia difformis	0.12	0.29
Porifera	*Halichondria panicea*	0.29	0.18
Rhodophytae	*Ahnfeltia plicata*	0	0.06
	Ceramium spp	0	0.88
	Chondria dasyphylla	0	0.12
	Chondrus crispus	0.06	0.65
	Corallina officinalis	0	0.06
	Hildenbrandia rubra	0.41	8.24
	Osmundea pinnatifida	0	3.12
	Lithothamnium calcareum	0	3.18
	Membranoptera alata	0.06	0
	Palmaria palmata	0	0.18
	Polysiphonia lanosa	0	0.06
Ascomycota	*Caloplaca marina*	0	0.12
Chlorophyta	*Cladophora rupestris*	0.06	0
	Enteromorpha compressa	0	0.06

Phylum	Scientific Name	*C. gigas*	*O. edulis*
	Elachista fucicola	0.06	0
	Scytosiphon lomentaria	0.06	0

O. edulis ranged from 3 to 7 years (mean 4.4 ± 0.2) and were significantly older than *C. gigas* which ranged between 2 and 5 (mean 3.5 ± 0.2) (ANOVA, MS = 5.765, df =1, F =5.723, $p < 0.02$). In relation to surface area, *O. edulis* samples ranged from 83.1 to 225.4 cm^2 (mean 139.3 ± 9.4) and were significantly smaller than *C. gigas* which ranged from 127.8 to 342.2 cm^2 (mean 221.9 ± 15.9) (ANOVA, MS = 58016.3, d.f = 1, F = 20.276, $p < 0.001$).

C. gigas had significantly fewer epibiotic species, (8.4 ±0.97) per individual than *O. edulis*, (12.6±0.78). Epibiont species richness was shown to be significantly different between the oysters (Table 2), with the model having an AIC_c of 209.56 and an adjusted r^2 of 25.02%.

Table 2. ANOVA showing difference between the species richness found present on the two oyster species *C. gigas* and *O. edulis*

Species richness	df	Sum of Squares	Mean Square	F	*P* <
Oyster Species	1	156.7	156.7	12.01	0.005
Error	32	417.6	13.1		
Total	33	574.4			

The models, (Table 3a and b), had adjusted r^2 values of 25.23% (AIC_c = 212.27; $F_{3,30}$=4.71; p <0.01) and 23.49% (AIC_c = 213.05; $F_{3,30}$=4.38; p <0.05) respectively. The difference in the AIC_c values between the models was < 4 and non-significant. Based on the adjusted r^2 however, we can conclude that the three variable predictor models which included age were marginally better than the 'oyster species only' model. The model predicts increasing epibiont species richness for older, fouled *O. edulis* shells than that of *C. gigas*.

Table 3. ANOVA showing the difference between a) surface area and b) age of the two oyster species, *C. gigas* and *O. edulis*.

a) **Surface area**	Sum of Squares	df	Mean Square	F	*p* <
Between Groups	58016.260	1	58016.260	20.276	0.001
Within Groups	91562.993	32	2861.344		
Total	149579.253	33			

b) **Age**	Sum of Squares	df	Mean Square	F	*p* <
Between Groups	5.765	1	5.765	5.723	0.05
Within Groups	32.235	32	1.007		
Total	38.000	33			

3.2 Multivariate Comparisons

3.2.1 Comparison of assemblages associated with O. edulis and C. gigas

Assemblages on the shells of the two types of oyster species were found to be significantly different (ANOSIM, R = 0.284, $p < 0.001$).

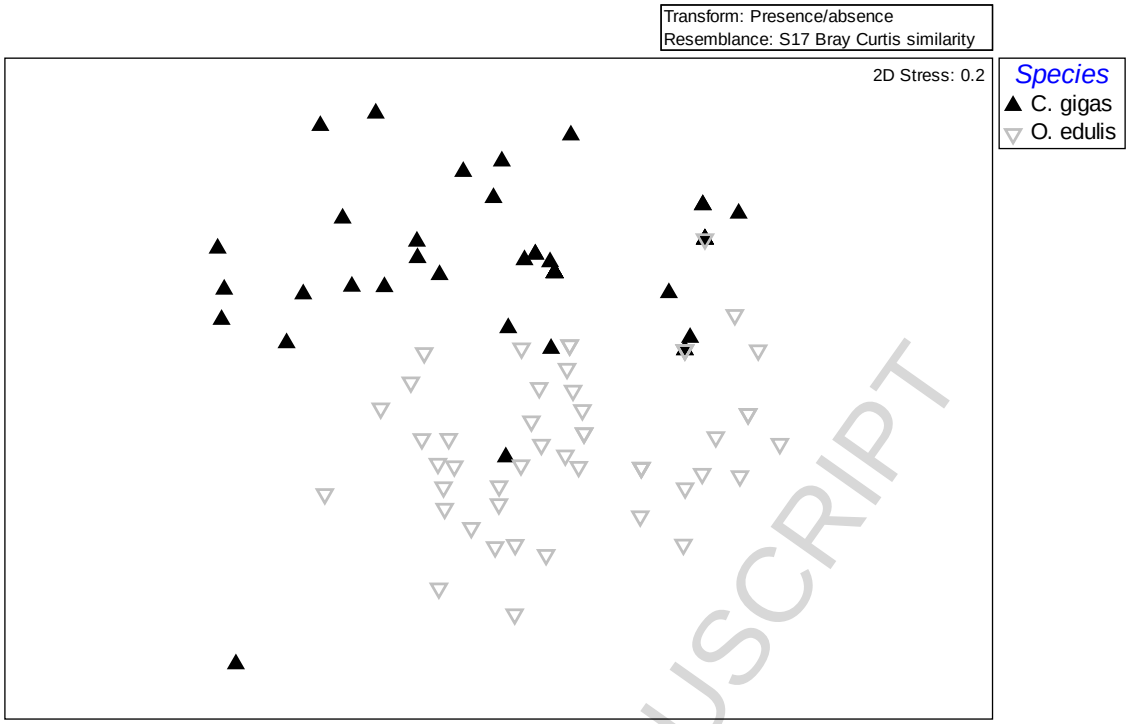

Figure 2. MDS plot showing the separation between *C. gigas* (shaded) and *O. edulis* (open).

SIMPER analysis revealed that *C. gigas* assemblages had an average similarity of 41%. *Elminius modestus*, *Mytilus edulis* and *Littorina mariae* contributed 93.32% of the conspecific similarity in *C. gigas* epibiota. The average similarity of assemblages on *O. edulis* was 47% with; *Elminius modestus*; *Mytilus edulis*; *Pomatoceros triqueter*; *Hildenbrandia rubra*; *Lithothamnium calcareum* and *Laurencia pinnatifida* contributing 92.89%. Average dissimilarity between the oysters was found to be 65.39%. The majority of this was accounted for by *Lithothamnium calcareum* (5.73%) and *Spirobranchus triqueter* (9.7%) both found exclusively on *O. edulis*.

3.2.2 Comparison of assemblages on upper and lower valves associated with O. edulis and C. gigas

Epibiotic communities attached to the upper and lower valves of each oyster showed considerable overlap within species (Fig. 3). However, despite some outliers, there was obvious separation between *O. edulis* and *C. gigas* (Fig. 3).

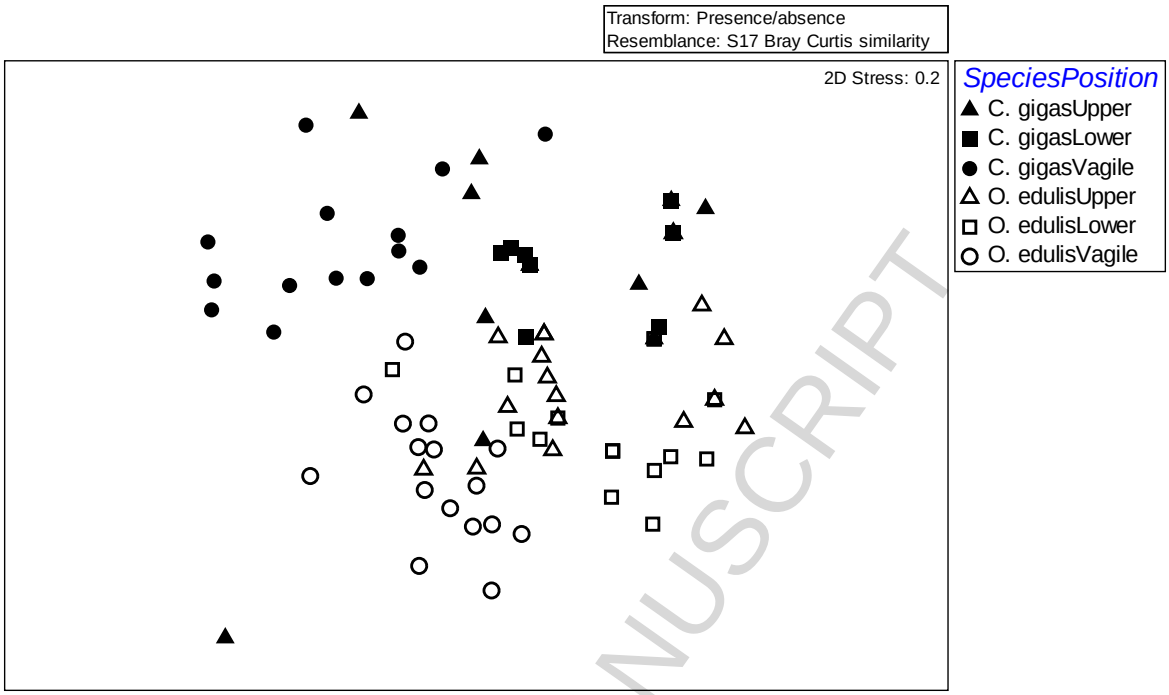

Figure 3. MDS plot showing shell position (upper, lower and vagile) of epibiota: *C. gigas* (shaded) and *O. edulis* (open).

The MDS stress = 0.2 indicated a good fit to the data. However, an ANOSIM comparing the assemblages on the upper and lower valves of the oysters produced a $p < 0.001$ and an R value of $0.226 < 0.25$ and therefore not significantly different.

3.2.3 Comparison of sessile and vagile communities associated with O. edulis and C. gigas

Sessile and vagile communities were assessed separately to investigate differences between associated epibiota and shell surface settlement. MDS plots of species list categorised into vagile and sessile showed some separation in communities with a stress value = 0.15 (Fig. 4). Vagile species associated with the two species were found to overlap although some degree of separation was shown for sessile

communities. An ANOSIM revealed no significant R = 0.075, p >0.05 and likewise for the sessile communities R = 0.092, p >0.05.

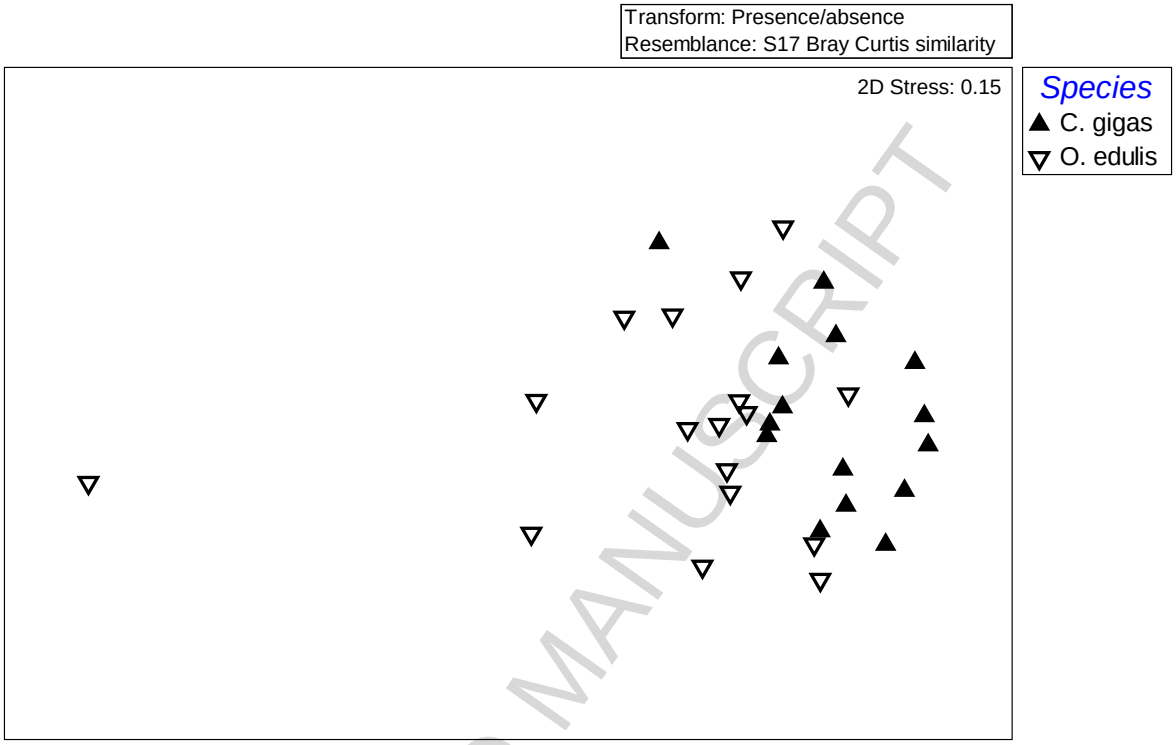

Figure 4. MDS plot showing variation in the assemblages of vagile epibionts associated with *C. gigas* (shaded) and *O. edulis* (open) with a stress value of 0.15.

4. Discussion

During this study a total of 78 species were identified, 51 on *C. gigas* and 48 on *O. edulis*. The overall epibiotic species richness associated with the two oysters appeared to be relatively similar. However, the ANOVA and model comparison revealed significant differences p < 0.01 in species richness present on individual specimens from the two species. The native oyster *O. edulis* was shown to have significantly higher species richness in comparison to *C. gigas*. It is possible that this observation may be linked to differences in shell rugosity between the oysters. *O. edulis* unlike *C. gigas* has an obvious line of consecutive scaling on the lower valve surface (Gosling, 2003; Smyth and Roberts, 2010). It is probable that the increased

3-D structure created a greater habitat complexity which is suitable for specific niche epibiota. The amplitude of the shell surface may therefore account for the disparity of epibiont colonisation. The influence of rugosity on species richness has been described on a grander scale in relation to biogenic reef complexities. Newman et al., (2015) showed that the more complex a reef surface the greater the associated richness. Egerton et al., (2018) concurred, with results from hydroacoustic surveys of reef structures in the Arabian Gulf which revealed that the less complex a reef matrix the lower the richness. This current research also highlighted a linkage between species richness and associated surface complexity in relation to the two oyster species, albeit on a micro scale. It would be insightful to make an assessment of shell rugosity for both *C. gigas* and *O. edulis* using laser techniques during future research in order to further investigate the drivers behind these variations.

A SIMPER dissimilarity of 68% highlighted differences in the specific species commonly associated with the oysters suggesting that *O. edulis* provided a preferential habitat to a niche suite. The SIMPER identified four *O.edulis* epibionts; *Spirobranchus triqueter*, *Hildenbrandia rubra*, *Lithothamnion lithothamnium* and *Osmundea pinnatifida* which contributed 47% of the differences between the oysters. Three of these were Rhodophyta indicating that the sampled *O. edulis* were settled lower on the shore. However, this was not the case as both oysters were sampled from the same shore height. However, the four species significant to *O. edulis* do possess a mutual characteristic in that they are all considered intolerant of smothering by sediment (Hiscock, 1983; Dethier, 1994).

An explanation as to why these species were not abundant on *C. gigas* may be due to the influence of low resolution hydrodynamics in the direct vicinity of the individual oyster. Hydrodynamics play an important role in the settlement process of colonising larvae (Gross et al. 1992). The *O. edulis* individuals were found predominantly orientated in an almost vertical position and therefore exposed to a greater amount of micro-scale turbulence allowing for less sedimentation on the surface of the shell. The cleaner vertical shell surface of *O. edulis* would offer a more favourable settlement substrate to propagules of *S. triqueter*, *H. rubra*, *L. lithothamnium* and *O.*

pinnatifida than the horizontally positioned *C. gigas*. Fine-scale spatial and temporal variations in hydrodynamics can have defining influences on larval settlements and consequently intertidal community structure (Porri et al., 2008; Whitman and Reidenbach, 2012).

The Pacific oyster *C. gigas* has now become environmentally conditioned throughout much of its introduced range leading to declines in many of its indigenous counterparts (Stelios et al., 2014). Habitat managers and NGO'S are concerned by the trend which follows its establishment. The expectations being that it's functional similarity with indigenous species will increase the intensity of competition and result in detrimental consequences for the surrounding associated environment (Melo et al., 2010). Indeed, these predictions have materialised throughout numerous countries were *C. gigas* has been introduced. In the Wadden Sea populations of the native mussel *M. edulis* have been impacted due to the range expansion of *C. gigas* (Diederich, 2006; Troost, 2010; Stelios et al., 2014; Riese et al., 2017). In New South Wales (NSW) Australia the faster feeding and rapid growth rate of *C. gigas* has impacted the wild standing stock densities of *Saccostrea glomerata* and altered associated biodiversity (Wilkie et al. 2012).

In Strangford Lough *C. gigas* and *O. edulis* overlap in their habitual niche on the lower intertidal zone (Smyth and Roberts, 2010; Zwerschke et al. 2016). It would therefore be reasonable to suggest that *C. gigas* would have to leave lag phase population growth before it would impact native oyster populations in terms of outcompeting and impacting biodiversity. This study revealed an average *O. edulis* growth rate of 18 mm per annum, with 94 mm oysters found to be six years old. The large amount of variation observed in the growth data of *C. gigas* could be accounted for by differences with initial settlement substratum. The species tends to adopt the shape of the chosen settlement material and therefore the shape and size of the individual is dependent on the amount of space available for growth. Despite the variation observed in the age / length study, the data was found to be comparable with other growth rates cited for the species where *C. gigas* of 130 mm in length were aged at five years (Hewitt et al., 2002).

The research showed as an individual oyster grows and the available shell surface area increases, there is annual recruitment of epibiotic species already present rather than novel taxa settling and colonising. A scenario also described by Wilkie et al. (2010) in relation to the *C. gigas* in NSW. Reasons for this phenomenon could be in part due to chemical cues (either conspecific or prey) which have been shown to act as settlement triggers for many invertebrates (Morse and Morse 1984; Maki et al., 1990; Bryan et al., 1997). The juveniles are attracted to cues released by adults and so settle close to conspecifics as it denotes an area where their species can thrive. This is particularly important for sessile species as their reproductive success is hindered by the Allee effect, however inter and intra specific competition may occur for finite resources (Bryan et al., 1997). As *C. gigas* grows faster than *O. edulis*, the shell space of *C. gigas* would be available for a comparatively shorter period of time than that of *O. edulis*. While the rough, fluted surface of *C. gigas* may appear to provide a larger surface area for colonisation it is possible that the thinner, flaky texture is more prone to breakage and less suitable for attachment than the more robust periostracum of the native oyster (Elston et al., 1982).

Analysis examining epibiont valve preference showed a high degree of overlap with species found on the upper and lower valves. In the case of *O. edulis* this is perhaps not surprising as they appear to settle preferentially on small fragments of substrate therefore, orientation can vary due to water movement. *O. edulis* settlement of this type allows both shell surfaces to be exposed to larval attachments (Yonge, 1966) with epibiotic species having equal access to both valves resulting in similar assemblages on both. The lower valve of *C. gigas* are commonly found entirely or partially adhered to a substrate. Despite the lower valve apparently not having the same potential exposure to planktonic larvae due to its orientation it appears to support similar assemblages as that of the upper valve. However, when *C. gigas* is cultured in suspended trays with both valves exposed the oyster can support a complex invertebrate community, with a greater abundance and richness of species (Switzer, 2010). The model constructed during this research predicted increasing epibiont species richness for older, more fouled shells with more species on *O.*

edulis than *C. gigas*. The final orientation of the oyster after settlement and amount of available settlement area may be an influencing factor in this prediction.

There was a large degree of overlap between the vagile species associated with the two oyster species. The sessile epibiota however were less evenly distributed and variations in the sessile communities of both species were observed not significant. Vagile species are able to move when necessary to find food, shelter and mates. There was no significant difference between vagile communities associated with the two oysters suggesting that recorded differences between the entire shell communities were being driven by sedentary species.

5. Conclusion

In conclusion, the two species revealed significantly different indices of epibiotic species richness. It is possible that the spread of *C. gigas* may impact the biodiversity of oyster epibionts in Strangford Lough if competition for settlement space becomes an issue. Conversely, as the native oyster populations are found in such low densities (Guy and Roberts, 2010) it is unlikely that major shifts in oyster epibiota biodiversity will occur. As *C. gigas* is a more fecund species with a faster growth rate, it is possible that the low intertidal areas where *O. edulis* is more commonly found could become overrun if environmental conditions continue to be favourable in the future. With a continued trend in rising global sea temperatures it is likely that the species will be able to spawn more frequently with a subsequent higher post settlement survival rate. It would therefore be prudent to take steps to arrest the spread of this highly adaptable species while it is in lag phase population growth as it has been seen to produce broad scale environmental change in other non-native areas (Wolff and Reise, 2002). As Strangford Lough is designated as an SAC and MPZ a pilot cull scheme should be trailed to cover all sites where *C. gigas* is presently found in an attempt to fragment the broodstock sites and impede future spawning events.

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Tables

Table 1. Mean pooled numbers of each taxon on shells of *C. gigas* and *O. edulis* collected in June 2009 at Drum Hill, Strangford Lough.

Phylum	Scientific Name	*C. gigas*	*O. edulis*
Annelida	*Oligochaete sp*	0.82	0
	Tubificoides pseudogaster	0.29	0
	Capitella capitata	0.12	0
	Eulalia viridis	0.06	0
	Phylodocid sp	0	0.24
	Gattyana cirrosa	0	0.12
	Harmothoe imbricata	0.06	0
	Harmothoe impar	0.41	1.12
	Harmothoe lunulata	0	0.06
	Hesionidae sp	0.06	0
	Kefersteinia cirrata	0	0.18
	Lagisca extenuata	0.06	0
	Nereis diversicolor	0	0.41
	Nereis pelagica	0	0.12
	Phyllodoce laminosa	0	0.06
	Phyllodocidae	0.06	0
	Pomatoceros triqueter	0.53	17.59
	Scolelepis foliosa	0.24	0
	Scolelepis squamata	0.41	0
	Spirobis spirobis	0.12	0
	Syllidae	0	1.06
	Syllis gracilis	1.41	0.12
Arthropoda	*Ampithoe gammaroides*	0	0.06
	Carcinus maenus	0.12	0.12
	Chaetogammarus marinus	0.12	0.06
	Chaetogammarus sp	0.06	0
	Semibalanus balanoides	6	0
	Balanus balanus	0.12	0
	Chaetogammarus stoerensis	0.06	0
	Eliminus modestus	224.29	706.29
	Chthamalus montagui	0.12	0
	Cressa dubia	0.06	0
	Cyrtolaelapidae	0.18	1.29
	Cyrtolaelapidae hydrogamasus	1.41	0.06
	Eulimnogammarus obtusatus	0.47	0
	Gammarus	0	0.06
	Halacaridae	0.06	0
	Harpacticoda sp	0	0.18
	Harpacticus	0.29	0

	Hydrogamasus	0	0.24
	Isotoma maritima	0.29	0
	Jaera sp	0.41	0.12
Phylum	**Scientific Name**	**C. gigas**	**O. edulis**
	Melita palmata	0.06	0
	Orchomene sp	0	0.12
	Sunamphitoe pelagica	0.43	0
Chordata	*Aplidium proliferum*	0	0.58
	Botryllus schlosseri	0.06	0
	Didemnid sp	0.06	0.24
Cnidaria	*Edwardsiella carnea*	0	0.12
	Actinia equina	0	0.12
Echinodermata	*Ophiura albida*	0.24	0
Mollusca	*Anomia ephippium*	0	.24
	Mytilus edulis	5.59	34.47
	Venerupis saxatilis	0.24	0
	Buccinum undatum	0	0.18
	Clathrus clathrus	0	0.06
	Gibbula cineraria	0.06	0
	Gibbula umbilicalis	2.06	0.88
	Littorina littorea	0.12	0.29
	Littorina mariae	2.18	1
	Lunatia catena	0.06	0
	Nucella lapillus	0.12	0
	Patella vulgata	0.29	0
	Tectura tessulata	0	0.12
	Acanthochitona crinitus	0	0.18
	Lepidochitona cinereus	0	0.29
	Leptochiton asellus	0.06	0
Nemertina	*Nemertopsis flavida*	0	0.06
Ochrophyta	*Fucus spiralis*	0.18	0
	Leathesia difformis	0.12	0.29
Porifera	*Halichondria panicea*	0.29	0.18
Rhodophytae	*Ahnfeltia plicata*	0	0.06
	Ceramium spp	0	0.88
	Chondria dasyphylla	0	0.12
	Chondrus crispus	0.06	0.65
	Corallina officinalis	0	0.06
	Hildenbrandia rubra	0.41	8.24
	Osmundea pinnatifida	0	3.12
	Lithothamnium calcareum	0	3.18
	Membranoptera alata	0.06	0
	Palmaria palmata	0	0.18
	Polysiphonia lanosa	0	0.06
Ascomycota	*Caloplaca marina*	0	0.12

Chlorophyta	*Cladophora rupestris*	0.06	0
	Enteromorpha compressa	0	0.06
Phylum	**Scientific Name**	**C. gigas**	**O. edulis**
	Elachista fucicola	0.06	0
	Scytosiphon lomentaria	0.06	0

Table 2. ANOVA showing difference between the species richness found present on the two oyster species *C. gigas* and *O. edulis*

Species richness	df	Sum of Squares	Mean Square	F	*P* <
Oyster Species	1	156.7	156.7	12.01	0.005
Error	32	417.6	13.1		
Total	33	574.4			

Table 3. ANOVA showing the difference between a) surface area and b) age of the two oyster species, *C. gigas* and *O. edulis*.

a) **Surface area**

	Sum of Squares	df	Mean Square	F	*p* <
Between Groups	58016.260	1	58016.260	20.276	0.001
Within Groups	91562.993	32	2861.344		
Total	149579.253	33			

b) **Age**

	Sum of Squares	df	Mean Square	F	*p* <
Between Groups	5.765	1	5.765	5.723	0.05
Within Groups	32.235	32	1.007		
Total	38.000	33			

Highlights

- Epibiont richness was significantly lower on *C. gigas*
- Significant differences in species present on native and non-native oysters
- *C. gigas* may impact biodiversity

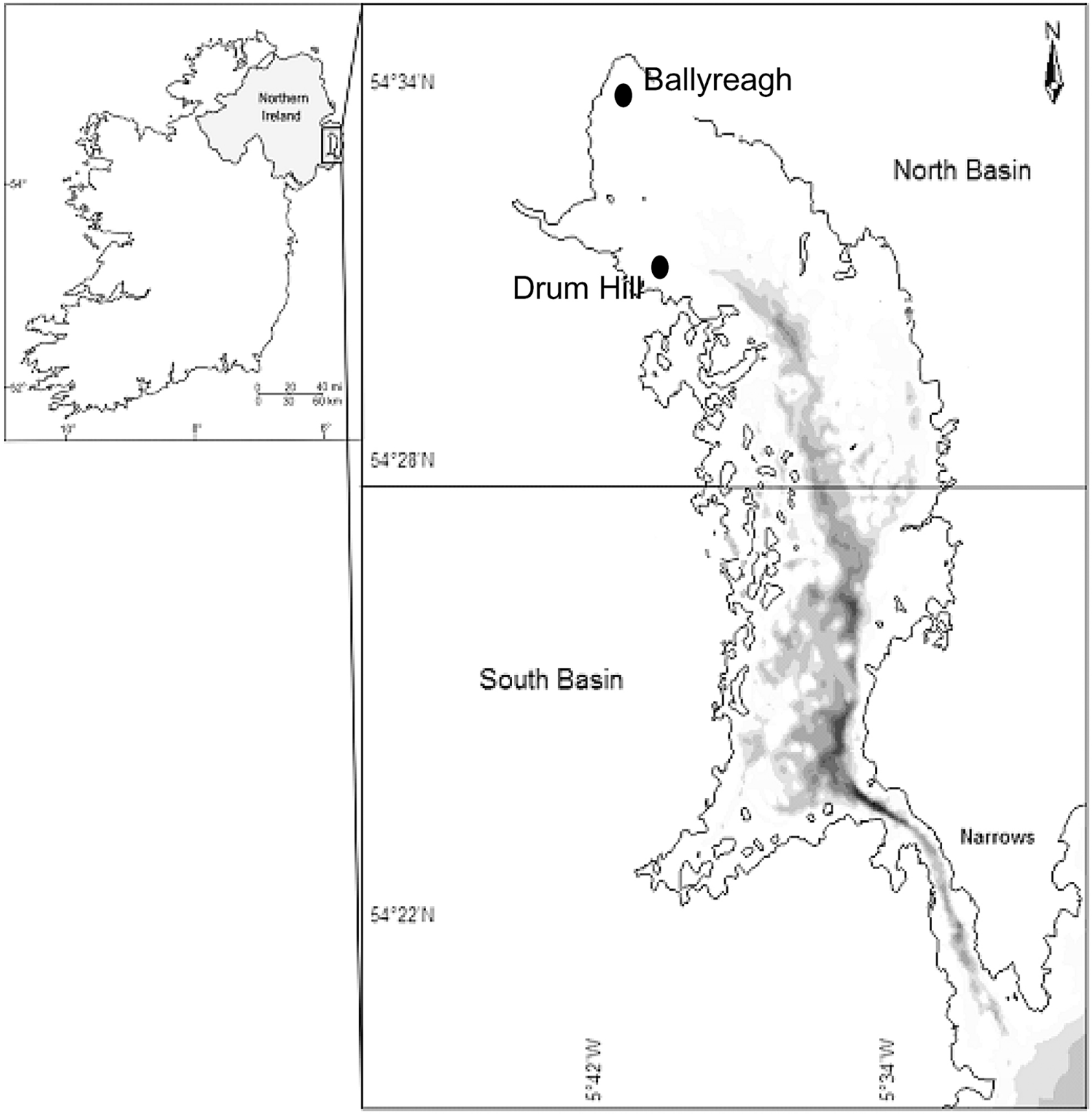
Northern Ireland
Ballyreagh
Drum Hill
North Basin
South Basin
Narrows
54°34'N
54°28'N
54°22'N
5°42'W
5°34'W
N
Bathymetry [m]
Above -7
-14 - -7
-21 - -14
-28 - -21
-35 - -28
-42 - -35
-49 - -42
-56 - -49
-63 - -56
-70 - -63
Below -70

Figure 1

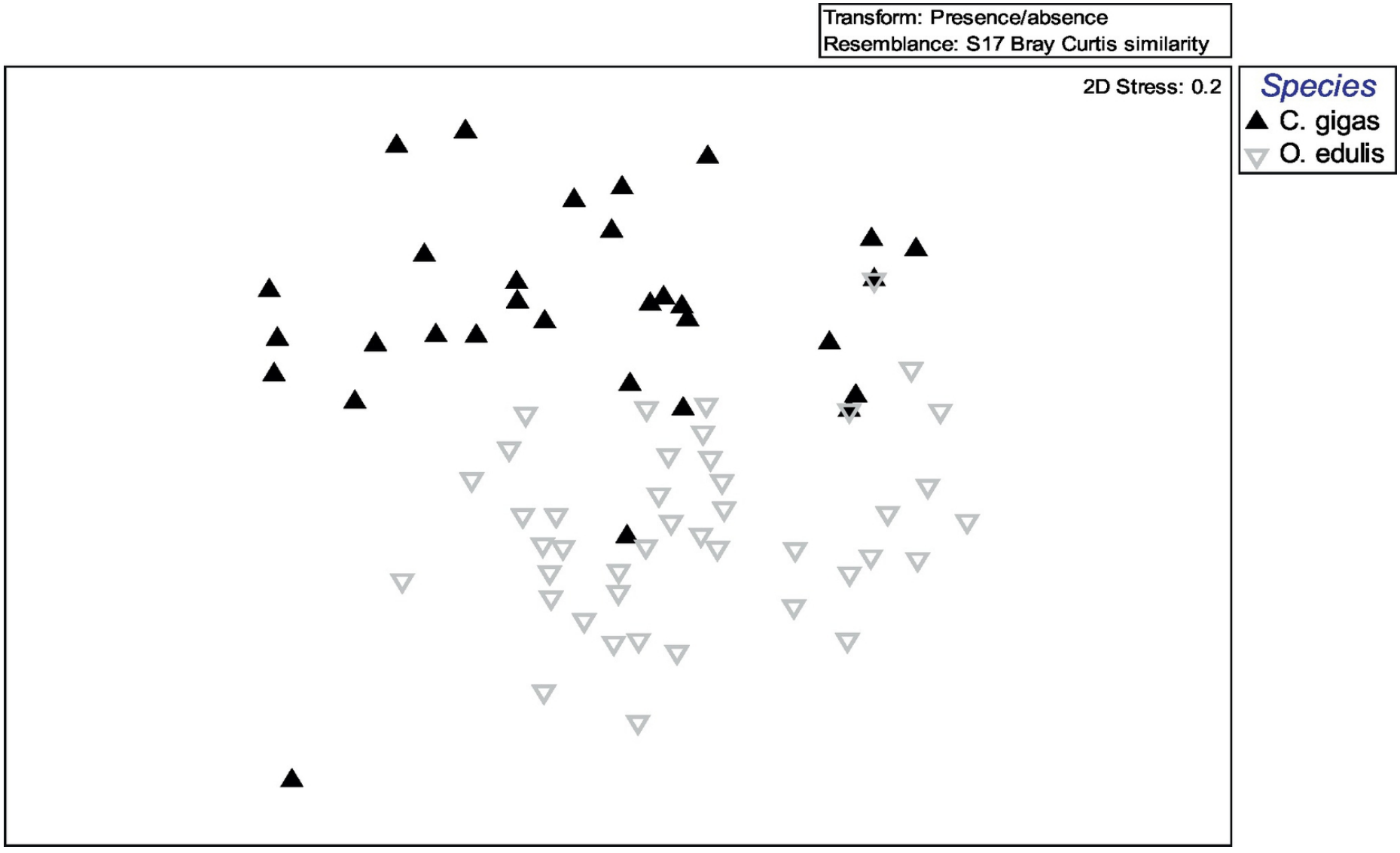
Transform: Presence/absence
Resemblance: S17 Bray Curtis similarity
2D Stress: 0.2
Species
C. gigas
O. edulis

Figure 2

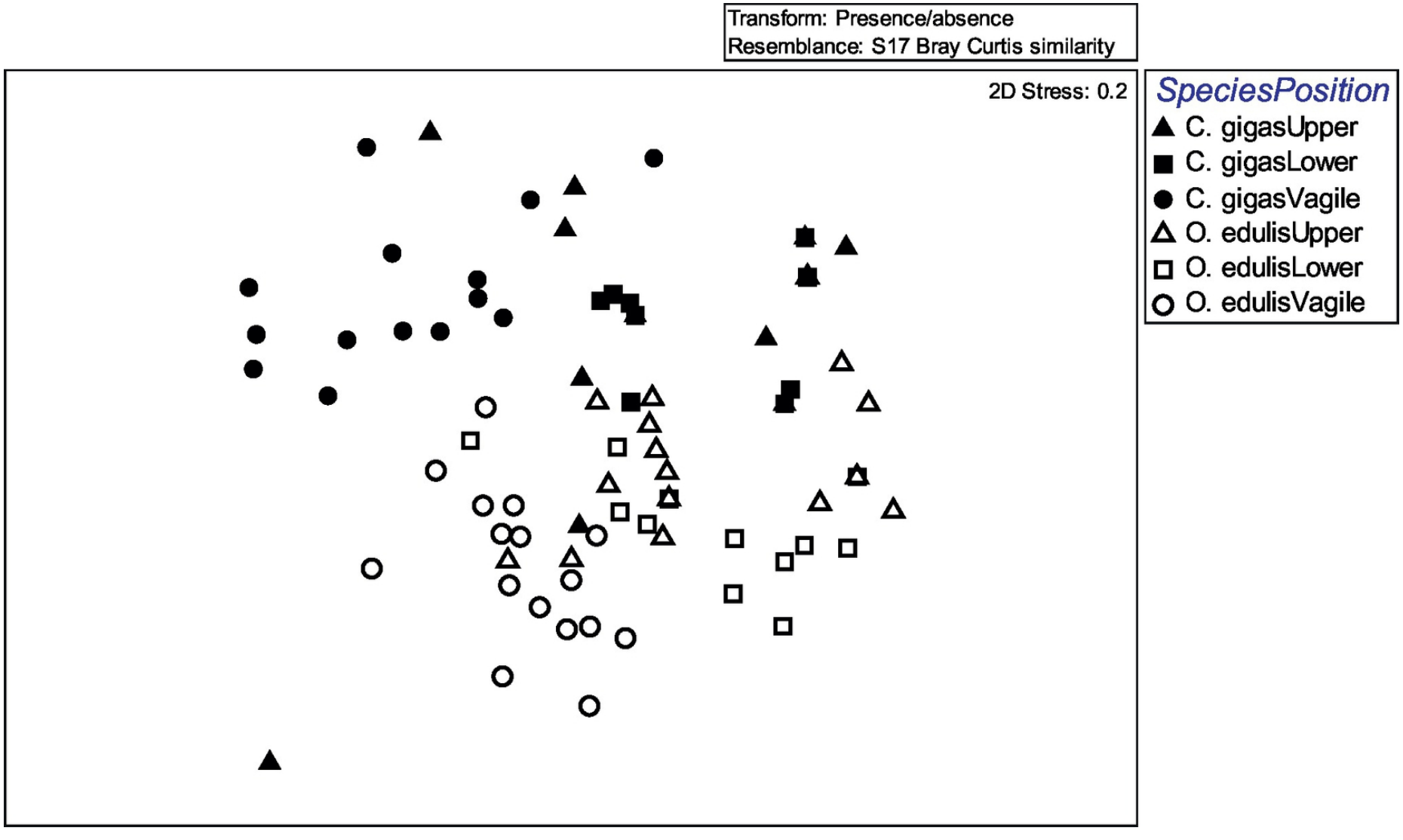
Transform: Presence/absence
Resemblance: S17 Bray Curtis similarity
2D Stress: 0.2
SpeciesPosition
C. gigasUpper
C. gigasLower
C. gigasVagile
O. edulisUpper
O. edulisLower
O. edulisVagile

Figure 3

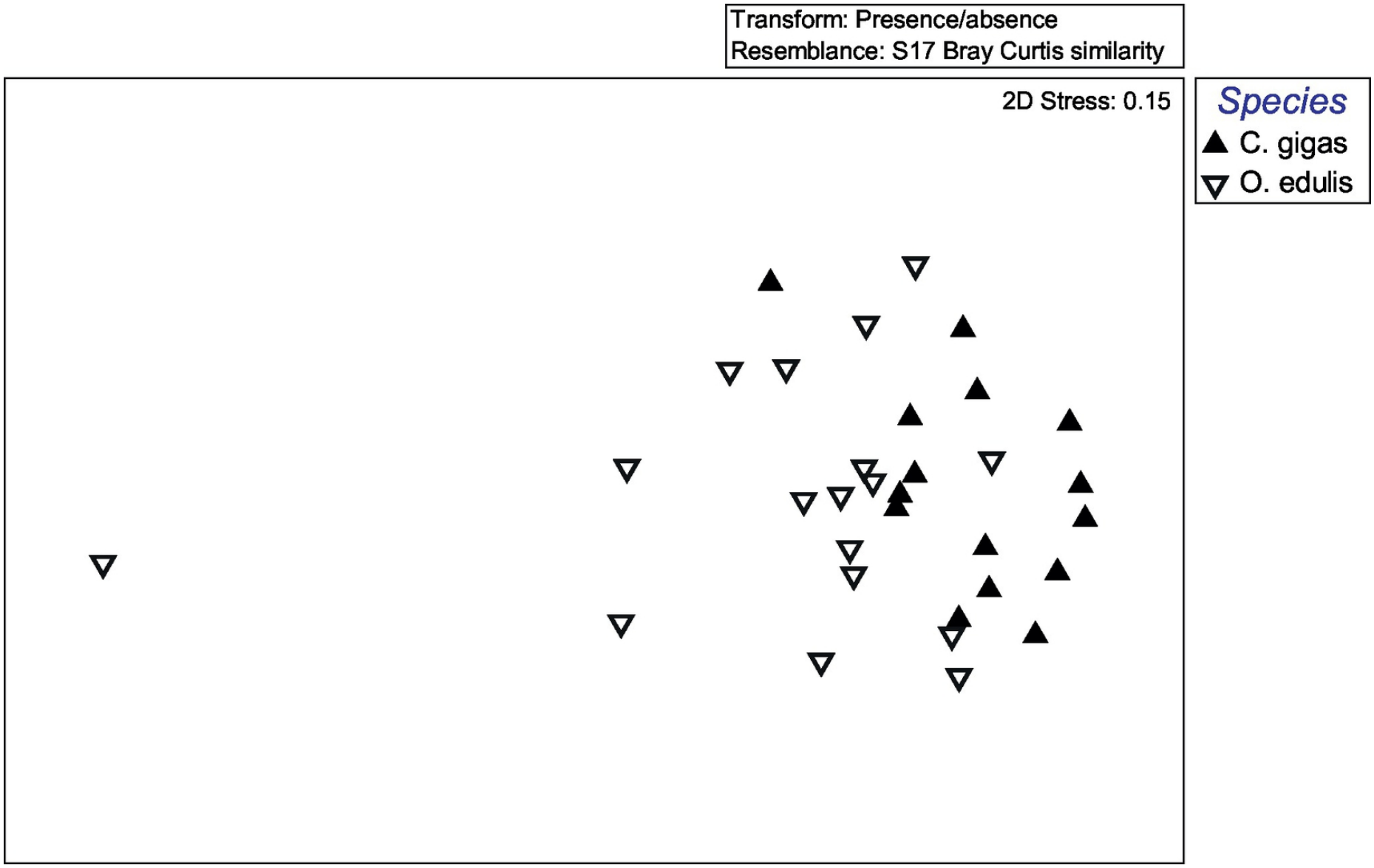
Transform: Presence/absence
Resemblance: S17 Bray Curtis similarity
2D Stress: 0.15
Species
C. gigas
O. edulis

Figure 4