Predicting the response of nekton assemblages to seagrass transplantations in the Venice lagoon: an approach to assess ecological restoration

Scapin L.*, Zucchetta M., Sfriso A., and Franzoi P.

Dipartimento di Scienze Ambientali, Informatica e Statistica (DAIS), Università Ca' Foscari Venezia

*luca.scapin@unive.it

Abstract

1. One of the major challenges to ensure effective restoration of estuarine habitats is to establish success criteria to determine whether the goals of restoration are met.
2. The aim of this work is to propose and test an approach to identify reference conditions and assess the recovery of nekton (fish, decapods and cephalopods) assemblages at seagrass restoration sites.
3. Nekton sampling took place from 2014 to 2017 in the northern Venice lagoon (northern Adriatic Sea, Italy) during spring at eight sites subjected to seagrass (*Zostera marina* and *Z. noltei*) transplantation. In spring 2016, five natural seagrass sites in the same area were additionally sampled, and physico-chemical water parameters and habitat structure were also recorded.
4. A multivariate GLM approach was adopted in order to disentangle the relative effect of water quality and seagrass habitat structure on nekton assemblages of natural habitats. Models were subsequently employed to predict species composition of nekton fauna at each transplantation site, to identify the reference assemblage expected under site-specific abiotic and habitat characteristics.
5. The average distance of the observed assemblage from reference conditions was used to track temporal trajectories of nekton colonization at transplantation sites, and to ultimately evaluate the recovery rate towards restoration goals.
6. This study highlights how a predictive approach could serve management purposes in ecological restoration, providing a concise tool to assess the functionality of restored habitats for associated fauna.

Keywords: biodiversity, dredging, fish, invertebrates, lagoon, nutrient enrichment, recolonization

Published: Aquatic Conserv: Mar Freshw Ecosyst. 2019;1–16.
DOI: 10.1002/aqc.3071

1. Introduction

Restoration of ecosystems is considered to be a strategic tool in implementing the management and conservation of biodiversity (Menz, Dixon, & Hobbs, 2013; Perring et al., 2015; Suding, 2011). A major challenge in restoration ecology is to evaluate the progress of re-created habitats towards desired ecological goals (sensu Zedler & Callaway, 2000). Historically, restoration schemes have primarily focused on the re-establishment of vegetation, hence adopting plant-based success criteria, e.g. plant morphometrics, vegetation cover, diversity and primary production (McAlpine et al., 2016). However, if restoration is expected to benefit the whole ecosystem, this approach could lead to simplistic and/or incomplete assessments, since it does not take into account fundamental ecological functions that cannot be easily inferred by vegetation status alone, such as the trophic role of recreated habitats for faunal assemblages and their capability to support biodiversity overall (Bourque & Fourqurean, 2014; Dolbeth, Cardoso, Grilo, Raffaelli, & Pardal, 2013; Fraser et al., 2015). Coastal and transitional water ecosystems pose additional challenges to the evaluation of restoration success, since many ecological compartments and processes are known to follow complex patterns of recovery and exhibit hysteresis after restoration (Borja, Dauer, Elliott, & Simenstad, 2010; Duarte et al., 2015; Elliott, Burdon, Hemingway, & Apitz, 2007). Nekton in transitional water ecosystems play a key role in mediating ecological processes and supporting ecosystem functions and services (Elliott & Hemingway, 2002; Kneib, 2000; McLusky & Elliott, 2004; Pérez-Ruzafa, Marcos, & Pérez-Ruzafa, 2011). Abundant and diverse nekton assemblages in estuaries and coastal lagoons are supported by seagrass meadows, which feature large proportions of habitat specialists as well as endangered and iconic species that utilize seagrass habitats for shelter, food and reproduction (Browne, Baker, & Connolly, 2008; Franco, Franzoi, Malavasi, Riccato, Torricelli, et al., 2006; Franzoi, Franco, & Torricelli, 2010; Scapin, Cavraro, et al., 2018; Shokri, Gladstone, & Jelbart, 2009; Vincent, Foster, & Koldewey, 2011). In addition, juveniles of many commercially important species are known to exploit seagrass beds in estuaries and coastal lagoons as nursery areas (Blandon & Zu Ermgassen, 2014; Pihl et al., 2006; Whitfield, 2016). Seagrass loss has been observed worldwide, due to both natural and human-induced pressures (Airoldi & Beck, 2007; Short et al., 2011; Waycott et al., 2009). In many Mediterranean coastal lagoons, seagrass meadows are threatened by eutrophication processes triggered by increased nutrient inputs from watersheds, and by sediment disturbance due to anthropogenic activities such as fishery, aquaculture, navigation and boat anchoring (Viaroli et al., 2008 and citations therein). The loss of seagrass beds has induced scientists and practitioners in many countries to directly intervene with restoration programmes (van Katwijk et al., 2015). However, there are still few examples of seagrass transplantations in the Mediterranean (Jahnke, Serra, Bernard, & Procaccini, 2015; Pirrotta et al., 2015; Pranovi, Curiel, Rismondo, Marzocchi, & Scattolin, 2000). In the Venice lagoon (Northern Adriatic Sea, Italy), a seagrass restoration programme (Seagrass RESTOration, “SeResto”; www.lifeseresto.eu; Facca et al., 2014) was started in 2014 in order to restore the status of the northern lagoon sub-basin, which was subject to extensive loss of *Zostera marina* and *Z. noltei* (Curiel, Checchin, Miotti, Pierini, & Rismondo, 2014; Sfriso, Facca, Ceoldo, & Marcomini, 2005). The project involved the transplantation of seagrass sods and rhizomes to trigger a natural process of re-colonization of shallow water substrata by *Z. marina* and *Z. noltei*. While restoration actions primarily targeted seagrasses, the project also acknowledged the need for evaluating the faunal communities exploiting seagrasses as habitat and playing a key role in maintaining overall ecosystem functionality. Together with the recreation of seagrass meadows, the scheme also aims to restore the associated nekton faunal assemblages, which are expected to progressively colonize the newly-created habitats and eventually become similar to those of natural seagrass beds (Facca et al., 2014; Scapin, Zucchetta, Facca, Sfriso, & Franzoi, 2016). Predicting species composition and dynamics in biological communities as a response of environmental factors is increasingly required by managers and conservationists in aquatic ecosystems, in order to counteract the degradation of biological resources and loss of biodiversity (Troia & Gido, 2013). Predictions carried out at the community level, by integrating the effects of both abiotic and biotic interactions, are particularly effective for management purposes, especially when applied to highly heterogeneous systems such as large rivers (Wilkes, Maddock, Link, & Habit, 2016) or coral reefs (Brokovich, Baranes, & Goren, 2006; Darling et al., 2017). Recently, a call for making restoration ecology a truly predictive science has been advocated (Brudvig, 2017). The use of forecasting techniques would help overcome some of the uncertainty associated with the assessment of restoration success, ultimately supporting the design and management of more effective habitat creation schemes (Brudvig et al., 2017; Suding, 2011). At the management level, predictive tools could be used to both define the specific goals of restoration schemes and, on such bases, assess the progress of restoration towards them (Beerens, Trexler, & Catano, 2017; Boumans, Burdick, & Dionne, 2002; Twilley, Rivera-Monroy, Chen, & Botero, 1998).

The goal of this paper is to propose a model-based approach to predict the characteristics of nekton assemblages to be expected in successfully restored seagrass habitats, and to assess the functionality of transplanted habitats for nekton by comparing predicted and observed assemblages. Three focal steps are involved in the analysis: i) models explaining the variability of nekton assemblages observed at natural seagrass sites are developed; ii) the target environmental and habitat scenarios expected at the end of the restoration process are defined, and the reference nekton assemblages expected according to such scenarios are predicted using the models developed in the first phase; iii) the nekton assemblages observed at a set of seagrass restoration sites are compared against the respective reference assemblages. The work highlights the relevance of a predictive approach in developing accurate management tools to define restoration goals and assess the restoration progress against them, in particular when evaluating the restoration of habitat functionality for associated fauna at the assemblage level.

2. Methods

2.1 Study area

The Venice lagoon is a large (approx. 550 km^2) transitional water body located in the northern Adriatic Sea and experiences a tidal range of ±0.50 m during spring tides (Umgiesser, Melaku canu, Cucco, & Solidoro, 2004). It is mostly composed of shallow water areas, with an average depth of 1.2 m (Molinaroli, Guerzoni, Sarretta, Cucco, & Umgiesser, 2007). The lagoon is connected to the sea by three sea inlets and subdivided into three sub-basins, created by the presence of two main watersheds. The northern sub-basin (Figure 1) is the widest (approx. 260 km^2), and on average it exchanges with the Adriatic Sea more than 1,000 m^3 s^{-1} through the Lido inlet (Ferrarin et al., 2013). This sub-basin is characterized by consistent freshwater inputs due to the presence of many tributaries (Solidoro, Cossarini, & Pastres, 2002). Such conditions produce strong environmental gradients within the sub-basin, with water salinity, trophic status, turbidity and sediment granulometry subject to relevant spatio-temporal variations. In addition, the northern sub-basin is characterized by the presence of a strong confinement gradient between the inlet and the mainland and by a higher degree of morphological and habitat heterogeneity compared with other lagoon areas. It features a mosaic of saltmarshes, intertidal flats, channels and subtidal shallows, the latter with or without seagrass meadows (Solidoro et al., 2010).

Seagrass transplant activities were carried out in 2014 at 17 sites. At each site, sods and rhizomes were transplanted within a 10 x 10 m square plot, to allow for standardized measures of habitat development among sites and over time (Facca et al., 2014).

2.2 Field data collection and sampling sites

Sampling scheme and definition of calibration and evaluation datasets

The sampling design included five natural seagrass sites located along a gradient of confinement (Sites N1-5; Figure 1). Site selection was dependent upon the different water and sediment physico-chemical conditions, floristic composition and habitat structure, in order to represent the heterogeneity of seagrass habitats found in the northern sub-basin. Nekton sampling was carried out on five occasions from late March to late June 2016, in order to coincide with the major epigeous growth phase of seagrasses (Sfriso & Ghetti, 1998) and the recruitment of most nektonic species found in the lagoon (Franco, Franzoi, Malavasi, Riccato, & Torricelli, 2006). Nektonic fauna, abiotic variables and habitat characteristics were recorded at each natural seagrass site on each sampling day employing the methods outlined below. Such data constituted the calibration dataset, employed for the development of the nekton assemblage models of the first phase of the work.

In addition, eight of the 17 sites transplanted in 2014 that were representative of the environmental variability in the whole northern sub-basin were included in the sampling design (Sites T1-8; Figure 1). Nekton sampling in these sites was carried out during spring 2014, 2015, 2016 and 2017 with the same methodology employed for the calibration dataset, allowing to track changes in nekton assemblages over time. Moreover, one additional natural seagrass site was also monitored in 2015, 2016 and 2017, and employed as a “control” site (Site C; Figure 1). This site exhibits environmental and vegetation conditions similar to those of the other natural seagrass sites, but was not included in the calibration dataset, hence providing the opportunity to test the predictive performances of the model developed, and allowing to track potential interannual changes in a natural habitat. Such data constituted the evaluation dataset, employed in the 3rd phase of this work.

Nekton sampling

Nekton assemblages were sampled in both calibration and evaluation datasets by seine netting, following the protocol described in Franco, Franzoi, Malavasi, Riccato, and Torricelli (2006). Specimens were identified at the species level, and abundance (number of individuals) was registered at all sites. Only for individuals belonging to the family Hippolytidae (Crustacea Decapoda), identification was limited to family level. All abundance data were expressed as density over an area of 100 m^2, allowing direct comparison between samples.

Abiotic variables

During nekton sampling, at sites included in the calibration dataset water temperature (°C), dissolved oxygen (DO, percentage of saturation), salinity (PSU) and turbidity (FNU) were measured with a multi-parameter probe (Hanna Instruments HI 9829). Chlorophyll-*a* (Chl-*a*) concentrations in water (µg/L) and surface sediments (µg/g) were quantified via fluorometry following Lorenzen (1966). As a measure of confinement,

Published: Aquatic Conserv: Mar Freshw Ecosyst. 2019;1–16.
DOI: 10.1002/aqc.3071

distance of each site from the Lido inlet (km) was calculated along the lagoon channel network. Finally, sediment grain-size (percentage of sand in the 10 cm top layer) and water residence times (days) were attributed to each sampling site from available data (ARPAV, 2012; Cucco et al., 2009; MAG.ACQUE - Selc, 2005; MAG.ACQUE - Thetis, 2005).

Habitat characterization

A set of seagrass habitat characteristics was also recorded at each site included in the calibration dataset. Total seagrass percentage cover was estimated at each site by visual census. Three to five replicate quadrats (0.25 x 0.25 m) allowed seagrass collection for morphological analyses along the transect of nekton sampling for a total of 52 samples. Canopy height (cm), shoot density (shoots m^{-2}), leaf area index (LAI, half-leaf area m^{-2}), epiphytal load (percent weight of all epiphyton relative to the 15 cm apical portion of leaves) and epigeous biomass (g m^{-2}) were measured separately for *C. nodosa*, *Z. marina* and *Z. noltei* and for each replicate. Values were then averaged per species, site and sampling date. Overall properties of the seagrass habitat were also calculated for each site and sampling date, by cumulating species values.

At the transplanted sites percentage cover was measured at the moment of transplantation (2014) and during the following three years, in order to track habitat development. Percentage seagrass cover was also estimated at the control site during each nekton sampling.

2.3 Data analysis

Model calibration

Two separate Principal Component Analyses (PCAs) were performed on standardized abiotic and habitat variables included in the calibration dataset, and the variable loadings on the PC axes were extracted. Abiotic and seagrass habitat properties of natural sites were summarized by considering the first two axes of each PCA. Negative binomial Generalized Linear Models (GLMs) were fitted to density of each species contributing to 97% of total density in the calibration dataset, while binomial GLMs were fitted to presence/absence of species present in at least 20% of observations. Different model formulations were considered, including different combinations of temporal, abiotic and habitat predictors (Table 1). Day of the year was included as continuous temporal variable; the first two principal components calculated on abiotic and habitat variables were included to represent abiotic and seagrass predictors respectively. The relative influence of abiotic and habitat predictors on structure of the nekton assemblage was then evaluated, comparing the different model formulations (Table 1) in a hierarchical framework, comparing the significance of the contribution of additive group of variables in comparison to the simpler model (Likelihood Ratio tests with 1000 bootstrap iterations). Following the approach of the *manyglm* software package (Wang, Naumann, Wright, & Warton, 2012), inference was carried out at the assemblage level by combining species-specific results in a global analysis. This allowed the investigation of two hypotheses on the different contribution of each type of predictor to the overall assemblage variability. Test t1 tested the hypothesis that habitat predictors would improve a model including only the temporal variability; test t2 tested the hypothesis that abiotic variables would improve a model already considering both temporal and habitat predictors (Table1). Ultimately, this method enabled us to disentangle the influence of habitat structure on nekton fauna, from the effect of day of sampling (test t1), and to investigate if physico-chemical and geographical characteristics of sites (i.e. abiotic variables) played an additional role (test t2). According to the results of the tests, the most parsimonious model formulation (i.e. that including the smallest number of relevant predictors) for both density and presence/absence was selected, and employed in the last phase of this work to evaluate the success of restoration for seagrass fauna recovery.

The predictive capabilities of the chosen model formulations were evaluated by calculating Spearman's r coefficients and Area Under the ROC Curve (AUC; Fielding & Bell, 1997) for GLMs based on species density and presence/absence respectively. To compute the coefficients, both the whole dataset (i.e. for all the species, using sampling sites and dates as replicates) and each species separately were considered. The evaluation statistics were calculated between observed and predicted values by means of a k-fold cross-validation (k=5; Hastie, Tibshirani, & Friedman, 2009).

Definition of target scenarios and prediction of reference assemblages

Published: Aquatic Conserv: Mar Freshw Ecosyst. 2019;1–16.
DOI: 10.1002/aqc.3071

In order to predict the reference assemblages, it was necessary to define the values of predictor variables as expected at the end of restoration process. The sets of such values are referred to as target scenarios in the following analysis.

Three target scenarios were defined for restoration sites, each one accounting for different floristic composition and habitat structure (Table 2). This allowed the setting of site-specific target environmental conditions, based on the different habitat characteristics that were designed for the restoration of each site. All sites were subjected to transplantation of *Z. marina* and *Z. noltei*, with different proportions of the two species (Facca et al., 2014). A greater proportion of *Z. noltei* was transplanted in shallower sites, with muddier and less oxygenated sediments and in closer proximity to saltmarshes. Conversely, deeper, more open and dynamic sites were restored using a greater proportion of *Z. marina*. Finally, at two sites both species were transplanted in similar proportions. Target scenarios were then constructed to match such variability, selecting for each seagrass variable the highest, the lowest or the average values recorded during the calibration phase, according to the specific scenario to be constructed (Table 2). Abiotic conditions were also included in target scenarios, and defined based on the assumption that, within the considered temporal range (three years after transplantation), temperature, salinity, %DO and sediment grain size would not be significantly influenced by the development of new seagrass habitat. In turn, the assumption was made that values of turbidity and Chl-*a* concentration in water and sediments would change as a response to changed habitat characteristics, and become similar to those observed at natural seagrass meadows in comparable condition of confinement within the study area. As a result, abiotic variables not influenced by seagrass restoration (i.e. temperature, salinity, %DO, sediment granulometry, distance from sea inlets and water residence time) were included in the three scenarios using values measured at each restoration site during each monitoring campaign. Variables expected to change as a consequence of seagrass restoration (i.e. turbidity and Chl-*a*), however, were included using average values measured at natural seagrass sites N4 and N5, the most similar to the restoration sites in terms of degree of confinement (Figure 1). In addition, a fourth target scenario was selected for the application of the model to the control site (Table 2). In order to match habitat characteristics found at the control site, the scenario included a mixed meadow with *Z. marina*, *Z. noltei* and *C. nodosa*. Following the same approach used to define the target scenario for transplantation sites, temperature, salinity, %DO, sediment granulometry, distance from sea inlets and water residence time were included in the scenario using values measured at the control site during each sampling day, whereas turbidity and Chl-*a* concentrations were included using average values measured at the calibration sites in closer proximity to the control site (N2 and N3; Figure 1). In all the scenarios, day of the year was used as a temporal variable (Table 2; see also Table 3 for scenarios selected for each restoration and control site).

For each site and year, both abundance and probability of presence of each species was predicted, using the selected GLM formulations and each site-specific scenario. The site-specific reference nekton assemblage, i.e. the one expected under target scenarios, was finally estimated by multiplying predicted density values by respective predicted probability of presence, following a two part modelling approach (Fletcher, Mackenzie, & Villouta, 2005; Martin et al., 2005; Welsh, Cunningham, Donnelly, & Lindenmayer, 1996). Species included in the analysis only either as density or probability of presence would therefore have a value of zero in the reference assemblage.

Applying the model-based approach to the evaluation dataset

In order to apply the developed predictive models to a real restoration case study, densities multiplied by probability of presence of nekton assemblage collected at each restoration site in each year were compared with the respective site-specific reference assemblage. A scatterplot of observed versus predicted log-transformed values in the evaluation dataset was produced for each restoration site to compare the expected and observed abundance. The absolute differences between log-transformed observed and predicted values of each species were averaged to visualize the yearly mean distance, and the relative standard error, of each restoration site from the reference conditions. This allowed the restoration trajectories of the whole nekton assemblage at each site to be tracked as a linear regression based on yearly mean distances and to eventually perform an evaluation of the success of seagrass transplantations for nekton fauna. The same procedure was applied to the control site.

3. Results

3.1 Abiotic and seagrass parameters at natural sites

Both abiotic variables and habitat characteristics varied markedly among natural seagrass sites included in the calibration dataset. The inclusion of sites located along a confinement gradient in the dataset resulted in major spatial differences in abiotic variables such as water turbidity, Chl-*a* in sediments, sediment grain-size, distance from inlet and water residence time. Overall, sites N1, N2 and N3 were characterized by coarser sediments (sand content >50%), smaller distances from the inlet (<5 km) and shorter residence times (<3 days) compared to N4 and N5. Also seagrass habitats exhibited noticeable differences among sites. *Z. marina* was dominant at more confined sites such as N4 and N5, which also exhibited higher overall seagrass cover, canopy height and leaf area index. Sites near the inlet were, on the whole, composed of mixed meadows featuring mainly *Z. noltei* in association with *C. nodosa* (present at several locations) and *Z. marina* (always as a minor component). Only N3 featured a pure *Z. noltei* meadow, with markedly lower percentage cover, canopy height, shoot density and leaf area index compared to other sites (see also Table S1 in Supporting Information).

PCAs were used to summarize the environmental variability observed in the calibration dataset (Figure 2). The first axis of PCA performed on abiotic variables (Figure 2a) explained 39% of variance, with the second axis explaining an additional 17% of variance. The first principal component showed a positive correlation with sediment grain size and a negative correlation with distance from inlet, water residence time, Chl-*a* concentration in sediments and turbidity, thus highlighting a major confinement gradient. As a result, sites such as N2 and N3, located in closer proximity to the sea inlet, were positively associated to the first axis, while more confined sites such as N4 and N5 showed a negative correlation with it. The second axis, being positively correlated with temperature and Chl-*a* concentration in water and negatively with DO and salinity, was mainly associated with the temporal dimension, with observations made in late spring and early summer at all sites being positively correlated with the axis.

PCA performed on seagrass variables (Figure 2b) explained 65% of variance with only two components. The first axis (40% of explained variance) showed a positive correlation with overall epiphytal load and most variables measured on *Z. noltei*. All variables measured on *Z. marina*, as well as overall percentage cover, canopy height, LAI and epigeous biomass were, in turn, negatively correlated with this axis. As a result, the first component enabled the separation of sites such as N1, N2 and N3, being positively correlated with the axis, from N4 and N5. The second axis (25% of explained variance) was positively correlated with all the variables related to *Z. noltei*, while it showed a strongly negative correlation with variables related to *C. nodosa*, as well as a slightly negative correlation with overall percentage cover, LAI and canopy height. The second component thus separated observations made at sites with presence of *C. nodosa* (i.e. at N1 and N2), showing negative correlation, from those featuring different proportions of *Z. marina* and *Z. noltei*, always without *C. nodosa*.

3.2 Model calibration

Thirteen species accounted for 97% of total nekton abundance (all sites and sampling days pooled) in the natural seagrass assemblage, including 11 fish and two decapods. In terms of presence/absence, 17 species were present at least in 20% of samples, including 12 fish, four decapods and 1 cephalopod (Table 4). The complete checklist of species caught in natural, transplantation and control sites is reported in Supporting Information (Table S2).

Likelihood Ratio tests among pairs of model formulations highlighted that seagrass habitat variables significantly explained both assemblage density ($p = 0.011$) and probability of presence ($p = 0.026$), when added to a model already including the temporal factor (t1). Conversely, the additional inclusion of abiotic variables to a model already accounting for temporal and habitat factors (t2) significantly explained only assemblage density ($p = 0.038$), with this test being non-significant ($p = 0.155$) for probability of presence. Therefore, the GLM formulation including all the considered predictors (temporal, habitat and abiotic factors; m2) was then selected as the best model explaining the variability in nekton density, and the formulation including only temporal and habitat factors (m1) was selected as the best model explaining the variability of species probability of presence.

Cross-validation enabled the identification of the species that were predicted more accurately (in terms of either density or presence/absence) by the models developed. Average Spearman's r coefficient values calculated for each species density ranged between 0.86 and -0.09 (Table 4). Species predicted more accurately in terms of density were *S. sprattus*, *S. abaster*, *S. typhle*, *N. ophidion* and *L. ramada*. The overall correlation calculated on the whole density dataset was 0.38 (sd: 0.08). Average AUC scores calculated for each species presence/absence ranged from 0.95 to 0.62, with only *A. boyeri* being associated to a model with null predictive capability (AUC = 0.5; Table 4). Species predicted more accurately in terms of probability of presence were *P. marmoratus*, *N. ophidion*, *S. pavo*, Hippolytidae, *K. panizzae*, *S. typhle* and *Z. ophiocephalus*. Overall AUC calculated on the whole presence/absence dataset was 0.72 (sd: 0.08).

3.3 Application to restoration sites

Restoration sites considered in the analysis were all characterized by a similar seagrass percentage cover immediately after the transplantation (*ca.* 0.6%), but exhibited markedly different rates of habitat development during the following years (Figure 3). During 2015, 2016 and 2017 vegetation cover vigorously increased at T3 and T8, which both showed 100% of site's area covered by plants since 2016. Also T6 showed good habitat development, reaching 100% of seagrass cover in 2017. T4 and T5 exhibited a more linear trend in habitat development, with cover steadily increasing up to ca. 40% and 50% in 2017 at the two sites, respectively. Habitat development at T7 started more slowly compared to the other sites, showing ca. 13% of seagrass cover in 2016 and 20% in 2017. On the contrary, transplanted seagrass established poorly at T1, showing only a slight increase in vegetation cover in 2017 (ca. 5%), and did not develop at all at T2. Plant cover measured at the control site was ca. 85% in 2015, 2016 and 2017. Consequently, both T1 and T2 were excluded from the evaluation of nekton recovery due to the insufficient habitat development during the analysis period.

Widespread and abundant species, such as *A. boyeri*, *K. panizzae* and *P. marmoratus*, but also locally abundant *C. crangon* and *A. fasciatus*, were found at greater densities than expected in the respective reference assemblages, hence being located above the regression line (diagonal) in scatterplots (Figure 4). On the contrary, Hippolytidae, *N. ophidion*, *S. typhle*, *S. abaster* and *L. aurata* were found, on the whole, at smaller densities than expected, hence being located below the regression line. Despite this general pattern, in some cases (namely at sites T3, T4 and T8 since 2015), *A. boyeri*, *S. abaster*, *S. typhle* and Hippolytidae were observed at densities more similar to the respective reference values compared to their densities at the other sites, hence being located closer to the regression line (Figure 4).

Nekton assemblage at control site C comprised relatively higher densities of *S. abaster*, *S. typhle*, *N. ophidion*, *P. adspersus* and Hippolytidae compared to restoration sites, with *S. pavo*, *Z. ophiocephalus* and *A. boyeri* additionally characterizing the assemblage (Figure 5). *A. boyeri*, *S. abaster*, *S. pavo* and *Z. ophiocephalus* were also the species observed with densities more similar to the respective reference values during all years. *N. ophidion* in 2016 and *P. adspersus* in 2017 were also observed with densities close to the respective reference conditions.

On average, the nekton assemblages observed at sites T3, T4 and T8 were characterized by shorter distance from the respective reference assemblages compared to the other sites (Figure 6), indicating conditions more similar to those expected in natural habitats. In turn, longer distance between observed and reference assemblages (hence conditions less similar to those expected) were detected at sites T5, T6 and T7, which also exhibited a higher degree of species variability compared to T3, T4 and T8 (see also Figure 4). On average, distance of nekton assemblage from the reference at the control site was constant among years, and comparable to that of sites T3, T4 and T8. Species variability at these sites was also comparable with that observed at the control site.

The linear trajectories calculated for T4, T5, T6 and T7 showed a steady response of nekton assemblages towards reference conditions, despite the above mentioned differences in average distance from reference between these sites. On the contrary, no clear patterns of progress could be detected for T3 and T8 (Figure 6). Overall, confidence intervals of linear trajectories for most restoration sites were larger compared to the control site, with the only exception being T8. Single species did not show clear trajectories, but with some exceptions, most notably, *S. abaster* at T4 and T8 and *P. marmoratus* at T4, T6 and T7 showed overall converging patterns towards reference conditions (see Figure S1 in Supporting Information for differences between observed and reference densities of individual species).

4. Discussion

4.1. Predicting reference conditions for seagrass nekton fauna

Any attempt to define or evaluate the state of highly dynamic environments such as transitional waters can be challenging. This is true for setting reference conditions in restoration programmes (Duarte et al., 2015), as well as for other ecological applications, such as the assessment of ecological status under the Water Framework Directive (Dir. 2000/60/EC; Elliott & Quintino, 2007). In the case study considered here, the strong gradients and high heterogeneity characterizing the northern area of the Venice lagoon (Solidoro et al., 2002) made it necessary to identify site-specific reference conditions to evaluate recovery of nekton fauna following habitat restoration. Seagrass transplantations were designed to match the site-specific environmental characteristics, involving the use of the most suitable species for each location (Facca et al., 2014), as suggested by van Katwijk et al. (2009). As a result, three target scenarios were considered in this study to reflect such differences, and site-specific reference conditions could be defined according to the expected physico-chemical, geographical and habitat properties of each restoration site. This enabled the overcoming of potential flaws in the commonly followed approach of directly comparing restored and reference habitats characterised by different environmental backgrounds (Brinson & Rheinhardt, 1996; Moorhead, 2013), and led to more accurate and realistic predictions of target assemblages and assessment of restoration progress at transplantation sites.

The calibration dataset employed in this study was specifically developed to encompass the variability in abiotic and seagrass characteristics that can be found in the northern Venice lagoon, as well as the seasonal variability in nekton distribution. Species composition and abundance of lagoon nekton assemblages can indeed vary markedly during spring, due to migration, reproduction and recruitment dynamics (Franzoi et al., 2010; Pérez-Ruzafa et al., 2007). Resulting models revealed a significant influence both of abiotic parameters and seagrass habitat structure at the assemblage level. However, the accuracy of model predictions varied markedly among species, as highlighted by cross-validation. Density and probability of presence of several species were predicted with good accuracy. As a result, such species can be reasonably included in the reference seagrass assemblage, if their predicted density or probability of presence is high, or excluded from it, if predicted values are low. Species predicted with high accuracy included both seagrass- and non-seagrass specialists (sensu Franzoi et al., 2010). *S. typhle* and *N. ophidion* were expected to occur with relatively high values of both density and probability of presence, suggesting a major contribution to the reference assemblages. Similarly, presence/absence of *S. pavo*, Hippolytidae and *Z. ophiocephalus* were predicted with high accuracy, hence the inclusion of such species in the reference assemblages can be inferred due to their relatively high probability of presence. *S. typhle* and *N. ophidion* are highly specialized pipefish that have developed morphological and behavioural adaptations to thrive in dense, highly-structured seagrass meadows (Franzoi et al., 2010; Malavasi et al., 2007; Scapin et al., 2018a). The peacock blenny (*S. pavo*), grass goby (*Z. ophiocephalus*) and hippolytid shrimps are other common species of seagrass habitats in Mediterranean coastal lagoons (d'Udekem d'Acoz, 1996; Franzoi et al., 2010; Scapin et al., 2016). Grass goby, in particular, select seagrass meadows as reproductive habitats since plant roots and rhizomes stabilize the roofs of burrows excavated by males as nests during the spring (Malavasi et al., 2002, 2005). In addition, the probability of presence of some typical non-seagrass species were predicted with high accuracy, including *P. marmoratus* and *L. ramada*. Both species are commonly found in Venice lagoon shallow waters, preferring unvegetated mud- and sandflats and saltmarsh habitats but sometimes found at the edge of seagrass patches (*P. marmoratus*) or in vegetated saltmarsh creeks (*L. ramada*) (Franco, Franzoi, Malavasi, Riccato, & Torricelli, 2006; Franco, Franzoi, Malavasi, Riccato, Torricelli, et al., 2006; Franco, Franzoi, Malavasi, Zucchetta, & Torricelli, 2012; Franzoi et al., 2010; Malavasi et al., 2005). This suggests that such species, despite not being seagrass specialists and being predicted to have relatively low abundances and probability of presence, can still be important when evaluating the nekton colonization of restored seagrass habitats in Mediterranean coastal lagoons.

The approach proposed in this work also allowed the tracking of the restoration trajectories for the whole nekton component associated to transplanted habitats, yielding a concise tool for accurate assessments at the assemblage level. It also allowed the identification of a pool of species that best discriminate transplanted habitats according to the degree of restoration success, including some syngnathids, peacock blenny, grass goby and some decapods. Verifying the presence and/or abundance of just these indicator species could be advantageous in more rapid assessment surveys of seagrass restoration schemes, avoiding the need to sample and characterize the whole nekton assemblage every time.

4.2. Assessing the progress rate of nekton fauna in transplanted seagrass habitats

The influence of environmental variables on seagrass nekton in estuarine and lagoon ecosystems has been widely studied, and distance to the sea, water quality and seagrass habitat structure are all recognised as major drivers of nekton distribution (Blaber & Blaber, 1980; Elliott & Hemingway, 2002; Franco, Franzoi, Malavasi, Riccato, & Torricelli, 2006; Lubbers, Boynton, & Kemp, 1990; Schultz, Kruschel, & Bakran-Petricioli, 2009; Taylor, Fry, Becker, & Moltschaniwskyj, 2017). The model approach followed in this study confirmed this evidence, with the predicted assemblages differing noticeably in both species presence and density among natural seagrass habitats employed for model calibration. The high degree of spatial variability in both abiotic variables and habitat parameters characterizing coastal lagoons, as emphasized in the present analysis, should be taken into account when restoring seagrass meadows in such heterogeneous ecosystems. For instance, location and design of transplantations must be planned on the basis of the known influence of environmental drivers on both seagrass and associated fauna, which should be taken into account in tools to guide the design of restoration plans (Short, Davis, Kopp, Short, & Burdick, 2002; Valle, Garmendia, Chust, Franco, & Borja, 2015; van Katwijk et al., 2009). Subsequently, as this study demonstrates, success criteria for seagrass fauna should be set allowing for the potential differences in the structure of the target assemblages. When natural and human-induced variability in environmental drivers prevents the selection of a suitable number of reference habitats for comparison with restored ones, it can be argued that predicting a set of site-specific reference conditions to match the variability in the local environmental context seems an adequate approach to assess the progress of restoration.

In the present study, the nekton assemblages at the investigated transplantation sites exhibited different degrees of similarity with the respective predicted reference conditions. For some sites, this broadly corresponded to the progress of habitat development after transplantation. Sites T3 and T4 in particular, exhibited high survival of seagrass sods and rhizomes, as well as a great increase in seagrass percentage cover, which would explain the better colonization by seagrass nekton observed there. In turn, despite the moderate to good seagrass development, other sites such as T5 and T6 exhibited poor colonization by target nekton assemblages, hence an overall lack of habitat functionality for fauna. This may be ascribed to additional environmental conditions at both local and seascape scale that, despite the presence of vegetation, are still unsuitable for seagrass nekton. Many seagrass species indeed rely on the complex trophic web supported by functional habitats, with physico-chemical conditions and habitat mosaic arrangements also playing an important role in addition to vegetation structure (Beck et al., 2003; Horinouchi, 2007; Jackson, Attrill, & Jones, 2006; Scapin, Zucchetta, Sfriso, & Franzoi, 2018; Whitfield, 2016).

While more time may be needed for nekton assemblages to resemble reference conditions (Scapin et al., 2015; Sheridan, Henderson, & McMahan, 2003), also poor reproduction and recruitment rates (Bell, Westoby, & Steffe, 1987) and scarce connectivity between restored and source habitats (Sogard, 1989) could be involved in the observed distance of nekton assemblages with respective reference conditions for some of the sites investigated. Indeed, the overall lack of consolidated natural meadows in the project area, the smaller dimensions of plants and seasonal leaf shedding in confined areas, together with the scarcity of deeper habitats that can enhance nekton survival in stressful conditions (e.g. during winter), may be among the seascape-scale factors implicated. In addition, convergence of some trajectories may have been masked by the marked interannual variability in weather conditions (hence in related abiotic parameters) in the Venice lagoon area during the study period. For instance, strong variations in winter and spring rainfalls (right before field surveys) from 2014 to 2017 (data from the regional environmental agency www.arpa.veneto.it; see Figure S2 in Supporting Information) determined highly variable river discharges, and major temporal differences in water physico-chemical parameters in the northern Venice lagoon. Hence salinity, nutrient concentrations, suspended solids and water transparency at restoration sites all exhibited noticeable temporal changes, as the environmental monitoring under the project SeResto revealed (see Figure S3 in Supporting Information). This may have contributed to the observed temporal oscillations in the annual average difference of nekton assemblages with respective reference conditions and, in addition to spatial heterogeneity among sites, determined the overall variability in the restoration outcomes. As Stuble, Fick, and Young (2017) pointed out for grassland habitats, outcomes of restoration efforts can vary dramatically according to yearly changes in weather conditions. The potential effects of unmanageable, although measurable, environmental contingencies should be considered also in seagrass habitat restoration, and appears to be crucial also for the recovery of associated fauna.

Interannual variability, together with the other potential factors discussed, resulted in yearly changes in assemblage structure, and subsequently in large errors of linear trajectories for most restoration sites. A higher degree of assemblage stability over time was in turn noted at the control site. Nekton at this natural site exhibited a relatively high degree of similarity (considering the limited dataset available for calibration and the amount of environmental determinants involved) with the expected conditions. It also remained relatively stable over the three years investigated, showing a smaller error associated to the temporal trend. Nekton assemblages of mature seagrass meadows are characterized by significantly more predictable temporal dynamics, compared to communities of bare or sparsely vegetated habitats. More structured habitats indeed buffer the effects of environmental stress and support communities that are less prone to abrupt changes (Cote, Gregory, Morris, Newton, & Schneider, 2013). The closer proximity of the control site to deeper meadows may also offer additional shelter and wintering habitats for nekton fauna, hence increasing assemblage stability over time. The dataset available for model calibration allowed the investigation of the spring assemblages in natural meadows during only one year. However, this limitation was partially overcome by including one additional natural habitats in the evaluation dataset, covering three years. This, as demonstrated here, allowed the potential interannual variability (at least part of) of nekton fauna to be taken into account. In addition, the use of a control site highlighted that a successfully restored seagrass habitat should promote stability in the nekton assemblage structure, hence fostering the long-term conservation of faunal diversity associated to seagrasses in coastal lagoons.

On the whole, the observed variability in the results of the assessment demonstrates the complex, non-obvious link between the success of seagrass transplantation and the subsequent recovery of associated nekton fauna, and highlights that not only structure, but also key ecological functions (i.e. support for specializsed nekton assemblages, in this case) should be taken into account by seagrass restoration schemes.

4.3. Future developments

The predictive methodology presented in this work, and the indicator based on distance to site-specific reference conditions, could be employed by managers and practitioners in routine assessments of future restoration schemes. While this work focused on structural aspects of nekton, it is suggested that future studies should aim to investigate also the response of functional attributes of faunal assemblages. Ecological and trophic guild composition, as well as species functional traits and their diversity (e.g. following Dolbeth et al., 2013), could be included as response variables in the proposed methodology, and predicted according to specific target scenarios. Incorporating functional aspects into predictive models would also provide insights into how biological communities and whole ecosystems function (Brudvig, 2017; Lavorel & Garnier, 2002). In addition, some functional aspects of ecosystems may be relatively more predictable than taxonomic composition itself (Brudvig et al., 2017), since they can result from many different combinations of redundant species (e.g. trophic guild composition). Therefore, focusing on functional features of nekton assemblages could result in more robust assessments of their recovery progresses.

Efforts should also be made to take into account the potential interannual changes in nekton assemblages of natural seagrass meadows. In this light, expanding the calibration dataset would help overcome the limitations of the present study, for which only one season of data from natural seagrass meadows was available. Multi-annual sampling schemes in candidate reference sites are therefore needed in coastal lagoons undergoing seagrass restoration, if more robust predictions of the recovery success are to be implemented. Including spatial variability at the seascape level, among different lagoon sub-basins and between lagoons within the same biogeographical region would allow for the potential effect of different habitat composition, configuration and connectivity to be taken into account (Jackson et al., 2006; Nagelkerken, Sheaves, Baker, & Connolly, 2015; Staveley, Perry, Lindborg, & Gullström, 2017), hence allowing more accurate predictions of nekton colonisation at transplanted seagrass meadows in coastal lagoons.

5. Acknowledgements

This work was partly funded by project LIFE12 NAT/IT/000331 – SERESTO (*Habitat 1150* (Coastal lagoon) recovery by SEagrass RESTOration. A new strategic approach to meet HD & WFD objectives*).

SeResto is funded by the European Union's LIFE+ financial instrument and contributes to the environmental recovery of a Natura 2000 site (SCI IT3250031– Northern Venice Lagoon/SPA IT3250046 – Venice lagoon).

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Tables

Table 1: GLMs formulations considered in this study, and summary of Likelihood Ratio tests performed between pairs of models. PC1 and PC2 refer to the first two axes extracted from PCAs performed on abiotic and habitat variables. For each model comparison, the predictors (abiotic or habitat) being tested are specified.

Model	Formula	Predictors included
m0	$Y_i \sim$ day of the year + intercept + ε_i	Temporal
m1	m0 + $PC1_{habitat}$ + $PC2_{habitat}$	Temporal + habitat
m2	m0 + $PC1_{habitat}$ + $PC2_{habitat}$ + $PC1_{abiotic}$ + $PC2_{abiotic}$	Temporal + habitat + abiotic
Test		**Testing the effect of:**

t1	m0 vs m1	*Habitat* predictors, when only temporal predictor was considered before
t2	m1 vs m2	*Abiotic* predictors, when both temporal and habitat predictors were considered before

Table 2: Target scenarios for the prediction of reference nekton assemblage-are defined for each seagrass species. Zma: parameters related to *Z. marina* and overall habitat parameters correlated with this species. Zno: parameters related to *Z. noltei* and overall habitat parameters correlated with this species. Cno: parameters related to *C. nodosa* and overall habitat parameters correlated with this species.

		Abiotic variables		**Seagrass habitat parameters (levels of values recorded)**		
Target scenarios	**Temporal variable**	**not influenced by restoration**	**influenced by restoration**	**Zma**	**Zno**	**Cno**
S1	Day of the year	Site-specific water and sediment parameters (measured during nekton sampling); site-specific distance from the inlet and water residence time	Average values of turbidity and chlorophyll-*a* in water and sediments measured at N4 and N5	highest	average	zero
S2				average	highest	zero
S3				average	average	zero
S4			Average values measured at N2 and N3	average	average	average

Table 3: Floristic composition of seagrass habitats designed for each transplantation site and respective scenario selected. Scenario selected for the control site is also shown.

Seagrass site	**Target seagrass habitat**	**Selected scenario**
Transplantation		
T3, T6, T7	*Z. marina* dominant	S1
T1, T2, T4	*Z. noltei* dominant	S2
T5, T8	Mixed meadow	S3
Control	**Observed habitat**	
C	*Z. marina, Z. noltei and C. nodosa* mixed meadow	S4

Published: Aquatic Conserv: Mar Freshw Ecosyst. 2019;1–16.
DOI: 10.1002/aqc.3071

Table 4: Average (and standard deviation) values of Spearman's coefficients and AUC calculated by means of cross-validation (k=5) on species constituting the calibration dataset and on the whole assemblage. For each species, the relative contribution to total density and the relative frequency of occurrence are also reported.
†Species not contributing to the 97% of total density
‡Species present in less than 20% of observations

Species	**Label**	**Contribution to total density (%)**	**Relative frequency (%)**	**Spearman's coefficient**	**AUC**
Aphanius fasciatus †	APFA	0.4	20		0.65 (0.02)
Atherina boyeri	ABO	37.5	96	0.27 (0.47)	0.50 (0)
Chelidonichthys lucerna †	CLU	0.2	20		0.66 (0.09)
Crangon crangon †	CCR	0.4	36		0.67 (0.2)
Hippolytidae	HIPPO	12.3	56	0.20 (0.48)	0.85 (0.21)
Knipowitschia panizzae	KPA	0.5	20	-0.09 (0.64)	0.81 (0.17)
Liza aurata	LAU	15.7	32	0.04 (0.28)	0.76 (0.21)
Liza ramada	LRA	7.4	24	0.38 (0.63)	0.73 (0.24)
Nerophis ophidion	NOP	2.8	68	0.40 (0.22)	0.89 (0.15)
Palaemon adspersus	PAD	2.7	76	0.16 (0.57)	0.62 (0.11)
Palaemon elegans †	PEL	0.4	60		0.69 (0.1)
Pomatoschistus marmoratus	PMA	2.2	56	0.06 (0.31)	0.95 (0.08)
Salaria pavo	SPA	0.5	56	-0.02 (0.33)	0.85 (0.22)
Sepia officinalis †	SOF	0.2	24		0.74 (0.17)
Sprattus sprattus ‡	SSP	3.0	16	0.86 (0.19)	
Syngnathus abaster	SAB	4.6	80	0.53 (0.34)	0.71 (0.22)
Syngnathus typhle	STY	6.8	72	0.50 (0.34)	0.81 (0.23)
Zosterisessor ophiocephalus	ZOP	0.6	40	0.23 (0.39)	0.80 (0.12)
Whole assemblage				0.38 (0.08)	0.72 (0.08)

Figure legends

Figure 1: Study area and location of sampling sites constituting the calibration and evaluation datasets.

Figure 2: Biplots of PCAs calculated on abiotic variables (A) and seagrass variables (B). Points are observations. Abiotic variables are abbreviated as follows. CHL_SED: Chl-*a* concentration in sediments; CHL_WAT: chlorophyll concentration in water; DIST: distance from sea inlet; DO: dissolved oxygen; SAL: salinity; SAND: sediment granulometry; T: temperature; T_RES: water residence time; TURB: turbidity. Seagrass variables were measured for *C. nodosa* (Cno), *Z. marina* (Zma), *Z. noltei* (Zno) and for the overall seagrass habitat (TOT), and are abbreviated as follows. B: epigeous biomass; C: canopy height; COP: percent cover; D: shoot density; EPI: epiphytal load; LAI: leaf area index.

Published: Aquatic Conserv: Mar Freshw Ecosyst. 2019;1–16.
DOI: 10.1002/aqc.3071

Figure 3: Seagrass percent cover measured in each year at restoration sites and independent control site. Values for the first year (2014) refer to the percent cover of sods and rhizomes actually transplanted.

Figure 4: Scatterplots of observed versus predicted log-transformed densities (multiplied by probability of presence) of nekton species at restoration sites. The distance of species plots from the regression line (diagonal) on y-axis is the difference from the reference species density. Species located above the diagonal are observed with greater densities than expected in the reference assemblage (blue segments), while those located below the regression line are observed with smaller densities than expected (red segments). Position of species located beyond the scale is indicated with an arrow. Key for species labels is provided in Table 4.

Figure 5: Scatterplots of observed versus predicted log-transformed densities (multiplied by probability of presence) of nekton species at the independent control site C. The distance of species plots from the diagonal on y-axis is the difference from the reference species density. Species located above the regression line (diagonal) are observed with greater densities than expected in the reference assemblage (blue segments), while those located below the regression line are observed with smaller densities than expected (red segments). Key for species labels is provided in Table 4.

Figure 6: Average difference between observed and reference log-transformed densities (multiplied by probability of presence) at restoration and independent control sites (error bars represent the standard error of the mean). Reference values are kept as zero to highlight the distance of each observed assemblage. The linear regression and 95% confidence intervals (shaded areas) are also shown.

Published: Aquatic Conserv: Mar Freshw Ecosyst. 2019;1–16.
DOI: 10.1002/aqc.3071