universität wien

MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

„Anthropogenic effects on *Posidonia oceanica* fields in Kvarner Bay (Croatia) inferred by a live-dead study of seagrass-associated molluscs"

verfasst von / submitted by

Roberto J. Piñeyro Partl BSc.

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien, 2020 / Vienna, 2020

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	UA 066 879
Studienrichtung lt. Studienblatt / degree programme as it appears on the student record sheet:	Masterstudium: Naturschutz und Biodiversitätsmanagement UG2002
Betreut von / Supervisor:	Univ.-Prof. Mag. Dr. Martin Zuschin
Mitbetreut von / Co-Supervisor:	Dr. Paolo Giulio Albano

Acknowledgements

First and foremost, a sincere thank you to Paolo Albano and Martin Zuschin for invaluable guidance and supervision throughout the entire project. I am much obliged to Robert Hofrichter and Alexander Heidenbauer for their generosity and making this project possible. Special thanks to Heinz Pfeiffer for the construction of the air-lift-sampler, Captain Orlić, for his unwavering support and skills on the water, and Fiona Straßer, Laura Waldner, and Lisa Gassen, for tireless assistance and good energy in the field and lab.

Finally, Sophie D., your patience is legendary.

This project was funded and supported by Marubis (Mariner Arten- und Biotopschutz e.V.) and MareMundi.

Table of Contents

1. Introduction *6*

2. Materials and methods *8*

2.1. Study area *8*

2.1.1. Stara Baška, Krk 8

2.1.2. Kormati islet, Plavnik 9

2.2. Sample collection *10*

2.2.1. Field sampling 10

2.2.2. Preliminary sorting and sieving 10

2.3. Sample processing *10*

2.4. Sample coverage *11*

2.5. LD fidelity attributes *11*

2.5.1. Richness 11

2.5.2. Evenness 12

2.5.3. Spearman's Rank-order Correlation 12

2.5.4. Taxonomic similarity 12

2.5.5. Non-metric multidimensional scaling 13

3. Results *13*

3.1. Live-dead comparisons 13

3.1.1. Abundance and richness 13

3.2. Fidelity of taxonomic composition 14

3.2.1. Habitat-scale fidelity 14

3.2.2. Replicate-scale fidelity 14

3.2.3. Field-scale differences in relative abundance 14

3.3. Distinguishing groups between and within meadows 15

3.3.1. Species found live-only 16

3.3.2. Species found dead-only 16

3.4. Fidelity of species richness and evenness 17

3.4.1. Habitat-scale (8 station samples) 17

3.4.2. Replicate-scale (24 replicate samples) 17

4. Discussion 17

4.1. Compositional LD fidelity matches pristine settings 17

4.2. Diversity may be affected by the leaf layer interface 18

4.2.1. *Differences in variability of LD fidelity (S and PIE)* 18

4.3. Between-habitat distinctions 18

4.3.1. Feeding guilds suggest differential habitat preferences 19

4.4. Confounding factors 19

4.4.1. Differential time-averaging effects 19

4.4.2. Intensity and timing of anthropogenic disturbance 19

4.4.3. Lifespan brevity bias and interspecies differences 20

4.5. Environmental assessments should be supplemented by live-dead studies 20

5. Conclusion *20*

List of illustrations

Tables

Table 1: Field sampling information indicating sampling date, depth, location, samples, and identification codes

Table 2: Study area impacts

Table 3: *Posidonia oceanica* meadow shoot density quadrats for sampled stations

Table 4: Sample codes and shoot-density-dependent health status

Table 5: Similarity of percentages test results

Table 6: PERMANOVA partitioning and analysis of molluscan communities sampled from *Posidonia oceanica*

Table 7: Sample overview of rank-order index, abundance, and richness at replicate-, habitat-, and field-scale

Figures

Figure 1: Map of study area

Figure 2: Boxplots representing averaged shoot densities by station and field

Figure 3: Barplots depicting station abundance and richness of living and death assemblages

Figure 4: Proportional abundances of the most abundant species in Krk and Kormati

Figure 5: Non-metric multidimensional scaling of samples

Figure 6: Live-dead agreement scatterplots; fidelity metrics: taxonomic similarity, rank-order agreement, evenness, richness

Appendixes

Appendix A: Species list of study area in systematic arrangement

Appendix B1: Ranked living and dead abundances – Krk

Appendix B2. Ranked living and dead abundances – Kormati

Abstract

Molluscan living (LAs) and death assemblages (DAs) were sampled from two separate *Posidonia oceanica* meadows in Kvarner Bay (Croatia) for a live-dead (LD) study of fidelity. Regarded as good bioindicators, *Posidonia* biocoenoses are sensitive to recent anthropogenic disturbances in the littoral zone. Problematically, limiting impact assessments to short observation windows (i.e., days to years) overlooks human activity prevalence across larger timeframes (i.e., decades to centuries). Durable biological material from previous communities (e.g., molluscan shells) help uncover pre-impact community states to distinguish between natural and anthropogenic community shifts over time. LD studies of fidelity quantitatively assess whether biological attributes (e.g., species richness, evenness, taxonomic similarity, rank-abundances) characterizing DAs (i.e., taxonomically identifiable, dead organic remains) and LAs, match. Assuming DAs are time-averaged, strong assemblage resemblance (LD agreement) suggests pristine habitat settings, whereas strong discrepancies (LD mismatch) indicate ecological change, likely caused by anthropogenic disturbances. The evaluated meadows are subject to different impact levels: Krk (impacted) was expected to produce lower LD agreement than Kormati. Although multivariate analyses confirm assemblages and fields are compositionally distinct, compositional agreement does not suggest sizeable impacts in either meadow. No indications of community assemblage turnover were revealed, and taxonomic similarity is elevated across all samples. Lastly, depressed DA diversity metrics could be influenced by taphonomic processes, but (low) time-averaging effects are more likely. Despite distinctive amounts of human presence, the LAs depict typical molluscan communities, implying resilience to moderate human activity.

Lebende (LAs) und tote (DAs) Molluskengemeinschaften wurden aus zwei separaten *Posidonia oceanica* Wiesen in der Kvarner Bucht (Kroatien) für einen lebend-tot Vergleich der Übereinstimmung beprobt. *Posidonia*-Biozönosen gelten als gute Bioindikatoren und reagieren empfindlich auf rezente anthropogene Störungen in der Litoralzone. Problematisch ist, dass durch die Beschränkung der Folgenabschätzung auf kurze Beobachtungszeiträume (d.h. Tage bis Jahre) die Prävalenz menschlicher Aktivitäten über größere Zeiträume (d.h. Jahrzehnte bis Jahrhunderte) übersehen wird. Widerstandsfähiges biologisches Material aus früheren Gemeinschaften (z.B. Molluskenschalen) hilft dabei, den Zustand der Gemeinschaft vor dem Eingriff zu ermitteln, um zwischen natürlichen und anthropogenen Veränderungen der Gemeinschaft im Laufe der Zeit zu unterscheiden. Solche lebend-tot - Studien bewerten quantitativ, ob biologische Attribute (z.B. Artenreichtum, Ausgeglichenheit, taxonomische Ähnlichkeit, Ranghäufigkeiten), die Todesvergesellschaftungen (d.h. taxonomisch identifizierbare, tote organische Überreste) und Lebendvergesellschaftungen charakterisieren, übereinstimmen. Unter der Annahme, dass die Todesvergesellschaftungen über längere Zeit akkumuliert und vermischt sind, deutet eine starke Übereinstimmung auf unberührte Habitatbedingungen hin, während starke Diskrepanzen auf ökologische Veränderungen hinweisen, die wahrscheinlich durch anthropogene Störungen verursacht wurden. Die untersuchten Wiesen sind unterschiedlichen Beeinträchtigungen ausgesetzt: Auf Krk (beeinträchtigt) war eine geringere lebend-tot-Übereinstimmung zu erwarten als auf Kormati. Obwohl multivariate Analysen bestätigen, dass sich die Vergesellschaftungen und Habitate in ihrer Zusammensetzung unterscheiden, deutet die gute Übereinstimmung in der Zusammensetzung nicht auf große Auswirkungen in beiden Wiesen hin. Es wurden keine Anzeichen für eine Fluktuation der Lebensgemeinschaften festgestellt und die taxonomische Ähnlichkeit ist in allen Proben hoch. Schließlich könnten die niedrigen Diversitätsmaße in den Todesvergesellschaftungen durch taphonomische Prozesse beeinflusst sein, aber (geringe) zeitliche Mittelungseffekte sind wahrscheinlicher. Trotz des ausgeprägten menschlichen Präsenz zeigen die Lebendvergesellschaftungen typische Mollusken-Gemeinschaften, was darauf hindeutet, dass sie gegenüber moderaten menschlichen Aktivitäten resistent sind.

1. Introduction

Conservation biology is a multidisciplinary field interfacing with numerous societal stakeholders, and as such is in a unique position to embed environmental concerns in policy, thus continually shaping societal habits (Dietl and Flessa 2011). The discipline focuses on characterizing and monitoring biodiversity, developing an understanding for natural and human-driven factors influencing it, to ultimately define and communicate conservation practices which safeguard the biological diversity, ecological integrity and health of ecosystems (Trombulak et al. 2004; Cardinale, Primack, and Murdoch 2020). Human influence on biodiversity is ubiquitous and longstanding, often pre-dating historical records. Problematically, conservation studies have traditionally relied on survey data limited to very short recent time-frames ranging between days and decades (Froyd and Willis 2008). Without suitable reference data, conservationists risk deemphasizing the actual amount of change caused by human impacts (Gilad et al. 2018); the significance of long-term ecological data has been widely stressed and addressed in conservation paleobiology (Dietl and Flessa 2011; Kidwell and Tomašových 2013; Dietl et al. 2015; Barnosky et al. 2017; Froyd and Willis 2008). The relatively new discipline has in the last two decades refined the quality of data available to applied ecology through insights gained from robust geohistorical data and practical paleontological methods (Willis and Birks 2006; Dietl and Flessa 2011; Dietl et al. 2015).

A disturbed region with promising conservation prospects

The Mediterranean basin is one of the hottest biodiversity hotspots globally boasting the 3rd highest number of endemic plants worldwide and marine ecosystems with a high percentage of endemic species, many of which are threatened and emblematic (Myers et al. 2000; Coll et al. 2010), not to mention important ecosystem service providers. One such endemic is the primary habitat investigated in this study, *Posidonia oceanica* meadows. Seagrasses are widely recognized as an indispensable umbrella species and regarded "among the most important and representative coastal ecosystems" of Europe (Buia, Gambi, and Dappiano 2004). Ecosystem services attributed to seagrasses provide a diverse range of goods and benefits with high economic value to humans (Campagne et al. 2014) – carbon sequestration being one of the more salient and momentous examples (Ricart et al. 2020). Concurrently, the Mediterranean is reported "among the most heavily impacted marine regions worldwide", largely due to longstanding pressures directly linked to persistent human activity, and climate change (United Nations Environment Programme Mediterranean Action Plan (UNEP/MAP), 2015). The Adriatic Sea in particular belongs to the most severely impacted areas of the region, whereas its eastern coastlines are among the most rapidly changing environments on global scale, mainly due to anthropogenic activity (Pikelj and Juračić 2013). Coastal zone development and utilization has greatly increased in recent decades and is expected to continue, further aggravating complex disturbance regimes, the effects of which are hard to pinpoint (Neumann et al. 2015; Nõges et al. 2016), not to mention predict.

The designation *habitat 1120* under the Habitats Directive (92/43/EEC), a centerpiece in Europe's nature conservation strategy, is meant to guarantee the livelihood of *P. oceanica* under the NATURA 2000 network. However, the ecosystem's ecological integrity remains a concern due to consistent degradation, largely linked to human activity (Holon et al. 2015; Pergent et al. 2015; Griffiths, Connolly, and Brown 2020). Currently, seagrass protection is largely deemed inconsistent worldwide (Griffiths, Connolly, and Brown 2020). European policy makers are increasingly addressing such shortcomings – the European Commission's (EC) new Biodiversity Strategy for 2030 outlines ambitious future emphases (e.g. strengthening the management and monitoring of protected areas) and explicitly schedules seagrass meadows as priority ecosystems deserving strict protection (European Commission 2020). In 2021 the EC will propose a legally binding Nature Restoration Plan to mend degraded and carbon-rich ecosystems, both terrestrial and marine. Considering these developments, conservationists are hard pressed to set broad-scale targets and place a premium on methods which can in fact address the long-term ecological integrity of key ecosystems under pressure.

Shifting baselines

Before delving into the details of this study, I briefly highlight the shifting baselines syndrome, a perceptual bias counterproductive to conservation efforts if kept unchecked, and live-dead (LD) agreement, a useful paleontological concept which conservationists can implement in response. The *shifting baselines syndrome* (SBS), coined by marine biologist Daniel Pauly in 1995, describes how our perception of the natural environment adjusts over time under ever-changing circumstances. Understanding the significance of the SBS underscores the true utility behind live-dead (LD)

fidelity studies (*sensu* Kidwell 2013) such as this one. Succinctly put, SBS describes *"…a gradual change in the accepted norms for the condition of the natural environment due to lack of past information or lack of experience of past conditions"* (Soga and Gaston 2018). As we grow accustomed to modified (impacted) environmental states our tolerance for further change continuously re-calibrates. A major implication for conservationists is obvious – conservation and restoration goals must continually incorporate the past to inform future direction meaningfully. Because the environment is under a constant state of fluctuation, arguing for rigid ecological "baselines" (i.e. a single set of reference conditions) is seen as problematic (Flessa 2002). Herein lies the merit of conservation paleobiology, and more specifically, taphonomic research and LD agreement (i.e LD fidelity): reliable historical data can be retrieved to gauge whether perceived ecological changes fall within the natural range of variability of a habitat or region, despite subjective standpoints (Willis and Birks 2006). Developments in the field of applied taphonomy over the last 20 years have been reviewed, and their applicability in conservation paleontology emphasized, by multiple studies (Kidwell and Tomasovych, 2013; Zuschin and Ebner, 2015; García-Ramos et al., 2016; Dietl et al., 2015).

The dead keeps track

Living assemblages (LA) are composed of individuals representing standing populations monitored through biological surveys. Correspondingly, death assemblages (DA), i.e. the taxonomically identifiable dead counterparts of LA, are robust and durable sources of biological information from recent communities (Kidwell 2013). Time-averaging is a central feature of DA, referring to the condensation (i.e. accumulation) of multiple generations of dead individuals into a single assemblage, generally resulting from slower burial rates than species productivity and associated death rates (Kidwell and Flessa 1995; Kidwell and Tomašových 2013). Time-averaged DAs, naturally accumulated over decades, centuries, or millennia, reflect temporally and spatially coarsened biological data, but retain ecological information, nonetheless. Molluscs are good DA taxa because of shell durability – they are persistent conveyors of information such as species identity, trophic guilds, dominance patterns, and habitat preferences (Dietl and Flessa 2011; Albano and Sabelli 2012).

Species occurrence in a DA directly demonstrates its existence in previous communities and informs of relative abundances (Kidwell and Flessa 1995). Importantly, DA are able to accurately depict regional diversity and composition, despite LA availability (Kidwell and Tomašových 2013; Zuschin and Ebner 2015). Ecological descriptors traditionally used by ecologists to characterize a living community can also be used on a DA (Kidwell 2013). Live-dead (LD) comparisons of fidelity use this equivalence to estimate how much information from a contemporary LA is captured by the corresponding DA. The extent to which assemblages match in abundance, composition, and diversity determine the measure of agreement: strong LD agreement suggests pristine conditions, whereas poor LD agreement (or LD mismatch) has proven to be a versatile proxy for ecological change caused by anthropogenic impacts (Kidwell 2009; Weber and Zuschin 2013; Dietl et al. 2015). Compositional changes in a LA shape the DA in the course of time, given the drivers of change are persistent or intense enough. Such a delay in information transfer is termed taphonomic inertia and is relevant to distinguishing natural from anthropogenic environmental changes in LD studies (Feser and Miller 2014).

Several live-dead studies have recently evaluated molluscan LD fidelity on seagrasses (Feser and Miller 2014; Reich 2014; Korpanty and Kelley 2014; Gilad et al. 2018; Challen Hyman et al. 2019), but *Posidonia oceanica* meadows remain comparably unexamined (Albano and Sabelli 2011). Seagrasses are assumed to be good geohistorical repositories of time-averaged information because of poor out-of-habitat transport and low sedimentation rates. This study compares the LD fidelity of molluscs sampled from two distinct *Posidonia oceanica* meadows in the impacted Northeastern Adriatic Sea. Meta-analyses and modelling indicate that LD mismatch in rank-abundances and taxonomic composition is a conservative indicator of human stress, such as eutrophication (Kidwell 2007, 2008, 2009; Kidwell and Tomašových 2013; Kidwell 2015). Although it is important to note that such stress levels are significantly larger than those subject to comparison in this study.

The aim is to determine whether contrasting levels of human activity are significant enough to generate LD agreement (or mismatch) which distinguishes the molluscan communities in question, besides the regional pressures depicted previously. Localized human activity (i.e., tourism and settlements) and geomorphological instability (i.e., erosion due to physical and anthropogenic parameters such as: geologic fabric, coastal slope, land use) were identified in one meadow site (Krk) (Ružić et al. 2015; 2019), while the other (Kormati) is sheltered by an uninhabited islet and otherwise withdrawn from regular human activity. I expect molluscan assemblages closest to populated areas (Krk) will generate poorer LD agreement than those

removed from permanent human activity (Kormati). I also anticipate higher seagrass shoot densities in the latter.

2. Materials and methods

2.1. Study area

The *Posidonia oceanica* meadows evaluated are in the upper sublittoral off the southernmost coastline of Krk, Croatia (table 1, fig. 1). The meadow most exposed to anthropogenic pressures is in the Stara Baška area on Krk island (KM field), subject to permanent dwellings and strong tourism (see table 2 for impacts summary). Kormati islet (KI field) is uninhabited and lies about 5 km west of Krk. In accordance with the monitoring protocol for *P. oceanica* beds used by Croatia's MedMPAnet case-study (RAC/SPA - UNEP/MAP, 2014), both meadows have homogenous cover and a minimum length of 1 km. Preliminary aerial and onsite assessments as well as data from the Croatian Agency for the Environment and Nature were used for site selection. The meadows are confirmed Sites of Community Importance (SCI) but have not been designated Special Areas of Conservation (SAC), according to the Habitats Directive (92/43/EEC). Under the Birds Directive (2009/147/EEC), both sites are classified as Special Protection Areas (SPA) within a larger Natura 2000 site encompassing the large North Adriatic islands (Cres, Krk, and Rab) and smaller surrounding islands. SPA designations should, at least in theory, provide a layer of protection which is not guaranteed for SCI under the Habitats Directive. No obvious protective measures could be noted at either study site.

Stations 1, 2, and 3 (KORMATI meadow) are located off the south-western coast of Kormati islet. Stations 4, 5, and 6 (KM meadow) are likewise on the south-western coast of Krk Island between Stara Baška and Oprna Bay, close to a recreational vehicle park and campsite (Škrila). Unforeseeable conditions in the field interfered with sampling efforts in station 6, so the sampling area was omitted along with station 1 for comparability.

2.1.1. Stara Baška, Krk

The Natura 2000 Standard Data Forms (SDF) stored in the EUNIS database (European Nature Information System) identify the main threats and pressures affecting Krk as: *fishing and harvesting aquatic resources* [F02] and *nautical sports* [G01.01]. However, this threats classification and code scheme (according to IUCN-CMP as presented by Salafsky et al., 2008a) is very conservative and falls short of a complete list of pressures. Year-round settlements and tourism have a strong effect on the area's coastal vulnerability (Ružić et al. 2015; 2019). A recent census conducted by the Croatian Bureau of Statistics recorded a total of 6,281 people in Krk (2011), but the Croatian Ministry of Tourism boasts an increase in the number of yearly visitors from 1,071,561 (2016) to 1,284,723 (2017), a 20% increase within a year (+213,162). Seeing as Krk is one of the most popular destinations in Croatia, and tourism rates in Croatia are on a rise, it can be expected that human activity will intensify.

The IUCN references a list of threats affecting *P. oceanica* meadows globally, several of which affect Krk. Those with low impact scores include *recreational activities, domestic and urban wastewater, soil erosion and sedimentation*, those with middle impact scores include *housing and urban areas, tourism and recreation areas, fishing and harvesting aquatic resources* (Pergent, G., Gerakaris, V., Sghaier, Y.R., Zakhama-Sraier, R., Fernández Torquemada, Y. & Pergent-Martini 2016). Significant coastal and cliff line retreat has been observed (1996-present) in the Stara Baška area (Krk site) and attributed to a very high

Table 1 Field sampling information indicating sampling date, depth, location, samples, and identification codes

Sample date	08.09.16	08.09.16	20.09.2016	21.09.2016
Depth	7-8 m	7-8 m	7-8 m	7-8 m
Longitude	14°34'04.1" E	14°34'34.7" E	14°40'34.7"E	14°40'13.9"E
Latitude	44°56'55.9" N	44°56'37.7" N	44°57'50.5"N	44°57'54.2"N
Samples	R4, R5, R6	R7, R8, R9	R10, R11, R12	R13, R14, R15
Field code	KI	KI	KM	KM
Station no.	2	3	4	5
Station code	KI2	KI3	KM4	KM5

Table 2 Study area impacts affecting evaluated meadows Kormati (KI) and Krk (KM). Impacts in table 2a are from the EUNIS database Natura 2000 standard forms. Table 2b revises these impacts based on field observations and incorporates a Coastal Vulnerability Index (CVI) as specified by Ružić et al. 2019, which evaluates a) geologic fabric, b) coastal slope, c) emerged beach width, d) significant wave height, and e) land use.

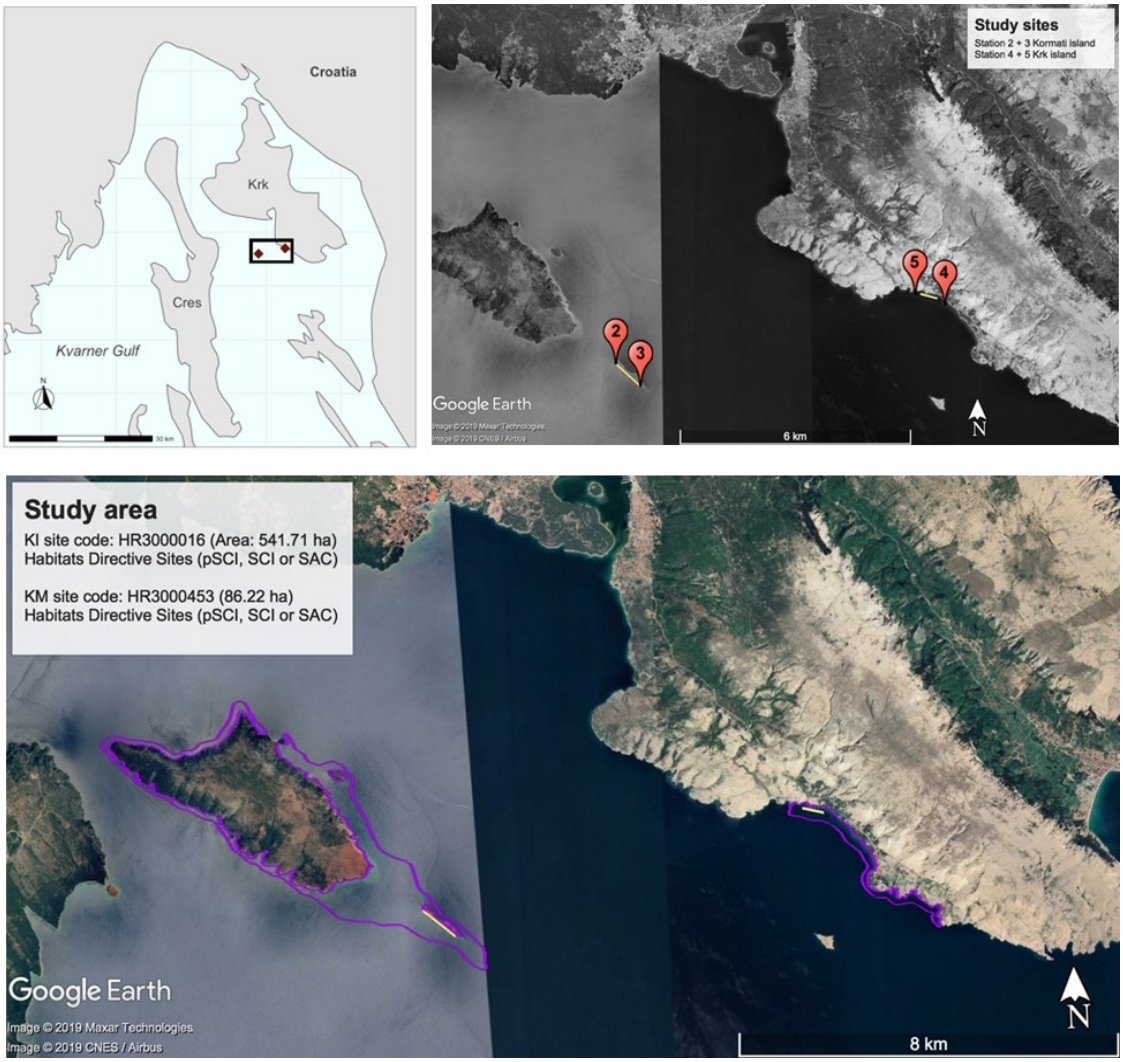
A – EUNIS impacts	**KI**	**KM**
Nautical sports	Medium	Low
Scuba diving, snorkeling	Medium	Medium
Fishing/harvesting aquatic resources	High	Medium
Anchoring	Low	Medium-high
B – EUNIS impacts *revised*	**KI**	**KM**
Nautical sports	Medium	Medium
Scuba diving, snorkeling	Medium	High
Fishing/harvesting aquatic resources	Low	High
Anchoring	Low	High
Housing and urban areas	NA	Low
Tourism / recreation areas	Low/NA	High
Domestic and urban wastewater	NA	Low - Medium
***Coastal Vulnerability Index**	Very low	Very High

coastal vulnerability index, determined by geologic fabric, coastal slope, beach width, wave height, and land use (Ružić et al. 2015; 2019). Because of the site's geomorphological features (i.e., low-resistance siliciclastic rocky coast, steep slopes, scarcely vegetated landscape) and hydrological catchment area, both torrential surface water and erosion are expected to increase sedimentation levels in Krk. Although *P. oceanica* reacts strongly to over-sedimentation (Manzanera, Pérez, and Romero 1998), these potential stressors have not been recorded as in the site's SDF.

2.1.2. *Kormati islet, Plavnik*

Kormati islet is within the aforementioned SCI (site code: HR3000016; site name: Podmorje Plavnika i Kormata) and part of the larger Plavnik area (541.9166 ha), which is recorded by Natura2000 as "one of the most representative sites for reefs" in the area (http://natura2000.eea.europa.eu-standarddataform). Plavnik island is about 1 km northwest of the Kormati islet and a popular tourist destination for day-trip tours and scuba-diving. Local boats generally set anchor and snorkel by the larger island of Plavnik because it provides better protection and recreational possibilities than Kormati (personal interviews; locals and sailors, 2016). Main threats and pressures listed for Kormati (according to its SDF) are like Krk: [F02] and [G01.01], and *scuba diving and snorkeling* [G01.07] is included as a low-impact pressure. The distance from Krk's coast, absence of permanent human presence, and its designation as a Special Protected Area (Natura 2000 site) suggest low levels of human disturbance in this location. The average wave height affecting Kormati has however

Figure 1 Map of study area showing the two studied meadows: Kormati field (sites 2 and 3) and Krk field (sites 4 and 5)



Source: Google Earth, 2019. *Study area,* Google Earth [online] Available through: https://earth.google.com/web/@44.959408,14.65703705,34734.52541009a,0d,35y,6.1821h,0.1691t,0.0005r?utm_source=earth7&utm_campaign=vine&hl=en [Accessed 01.06.2019]

been modelled to be 25% larger than in Krk (Ružić et al. 2015), so the contrast should be taken into account.

2.2. Sample collection

2.2.1. Field sampling

Field sampling was conducted by SCUBA divers across a 3-week time span in September 2016. Both fields were divided into three stations, each equidistant from another and along shallow isobaths at a depth of 7.5 m. Each station was quantitatively sampled for molluscan assemblages with 3 replicates (1 m^2 quadrats), which were placed at a minimum distance of 1 meter from each other. A total of 12 replicates from 4 stations were sampled for the molluscan data set. Additionally, 10 frames (40 x 40 cm) per station were used to count *P. oceanica* shoots in both fields, for a total of 40 quadrats. Shoot counts were then extrapolated to shoot density per square meter, a standard descriptor for Seagrass assessments (Pergent-Martini et al. 2005; Mayot, Boudouresque, and Leriche, 2005). The meadow's ecological status was inferred from the RAC/SPA - UNEP/MAP (2014) report, which specifies depth-dependent classes: bad, poor, moderate, good, and high (table 3). Layers within the 1 m^2 replicates were subject to separate sampling techniques following methods used by Albano and Sabelli (2011) and Buia et al. (2004). Leaf-layer organisms within replicates were collected directly from the leaves, the replicate area subsequently defoliated, and the exposed rhizome layer sampled separately by sediment extraction.

Molluscs ranging between 1-5 mm in size were targeted. A hand-net fitted with a 60 x 40 cm metal frame was used to sample the leaf layer: 20 strokes per replicate. The rhizome layer was sampled with a self-constructed air-lift suction sampler. The main components used to build this device are listed below:

- 6 exchangeable nets for the air-lift-sampler
- 6 exchangeable nets for the hand-nets
- 1 durable PVC pipe (length = 150 cm; diameter = 6 cm) pressurized air supply (i.e., SCUBA cylinders)
- 2-meter-long low-pressure hose equivalent to those used in diving regulators
- 1 adapter which connects the low-pressure hose to a hand valve
- 1 quarter-turn ball valve (hand-valve)
- 1 metal tube

As with recreational diving equipment, the scuba cylinder and low-pressure hose are connected via the 1st stage, but a hand-valve is mounted onto the hose's other end, instead of a 2nd stage. The valve is attached to the air-lift suction sampler and used to regulate the air flow between the air tank and a metal pipe, which redirects the air flow into the PVC pipe and out its posterior end. The metal pipe's entry-point was drilled at about 10 cm from the suctioning orifice, which ensures sufficient negative pressure build-up to suction sediment through the suction sampler and expulse it into the collection net. For a sketch outlining the basic principle of an air-lift suction sampler, refer to (Buia et al. 2004 pg. 168, fig. 11a)

The suction sampler facilitates efficient sediment extraction from the rhizome layer. Each replicate was sampled evenly and uninterruptedly for 100 bar (atm) air pressure, monitored with a submersible pressure gauge. Continuous, even, and uninterrupted hammering movements are necessary to dislodge hard-to-reach material, and thus minimize collection bias. Collection nets were custom built with hook-and-loop fasteners and press-studs for easy underwater exchangeability.

2.2.2. Preliminary sorting and sieving

The sampled material was sorted into subsets to represent targeted segments of the molluscan community. Replicate samples were sieved into separate size classes (< 1 mm, 1-5 mm, > 5 mm) and divided into taxonomic groups (molluscs, polychaetes, crustaceans, and remaining taxa). Only molluscs sized 1-5 mm (i.e., late juveniles and adults) were used for evaluation. The skeletal remains from early juveniles (< 1 mm) are less likely to persevere and thus do not represent the source live community as accurately, resulting in poorer LD agreement (Kidwell 2002, Albano and Sabelli 2011a). All specimens were identified to species-level when possible and reviewed by expert malacologists.

The leaf layer is mainly composed of living individuals, so little sorting is necessary, but samples do contain high amounts of leaf biomass and must be inspected, washed, and sieved thoroughly. The rhizome layer contained large amounts of sediment material and required extensive sorting. After sieving, preliminary sorting took place immediately to easily pick conspicuous living individuals. Further sorting through the material is time consuming and samples must be kept in fresh and aerated saltwater. All living individuals were stored in 95% ethanol for subsequent identification and DA samples were rinsed, dried, and stored for further processing in the lab.

2.3. Sample processing

The complete dataset used for quantitative measures in this LD study was compiled from 16 samples. The leaf and rhizome layers were sampled separately: 12

hand-net samples (leaf layer) and 4 air-lift-net samples (rhizome layer). One LA station sample constitutes 3 pooled replicate samples (R4:R6 [L-KI2], R7:9 [L-KI3], R10:R12 [L-KM1], R13:R15 [L-KM2]), whereas a DA subsample represents a full station after being fractioned (e.g., R4 [D-KI2], R7 [D-KI3], R10 [D-KM1], R14 [D-KM2]). DA samples were taken from the rhizome layer, from which subsamples were fractioned into the smallest possible volume necessary to extract 500-1000 molluscan fragments. Partitioning the DA allows for a reasonable amount of sediment and shells for study. Fragment preservation states determined whether empty shells and valves were kept for further identification. Shell fragments smaller than half the original element were also excluded to prevent double counts.

A total of 4581 skeletal elements were identified. DA bivalve and polyplacophoran counts were divided by 2 and 8 respectively (i.e. the taxon's complete number of skeletal elements) to render their abundances comparable to gastropods whose shell possesses a single element (Kowalewski et al. 2003). Following Chao's suggestion regarding species frequencies cut-off values, "abundant" species refer to those where $n_i > 10$, and "rare" species where $n_i \leq 10$. Species observed once (singletons) or twice (doubletons) are treated as "very rare" species. Whenever possible taxa were identified to species-level and confirmed by an expert malacologist.

2.4. Sample coverage

Sample coverage (completeness) was determined for station assemblages after pooling samples, using the iNEXT package to calculate diversity estimates (Chao and Jost 2012; Hsieh et al. 2016).

2.5. LD fidelity attributes

DA communities can be represented using diversity measures commonly used on LAs such as species richness, evenness, presence/absence, and relative abundances. Assemblage species composition can also be compared using metrics such as taxonomic similarity (Jaccard-Chao index) and rank-abundances of species (Spearman-rho coefficient of correlation). A quantitative assessment compares these biological attributes on cross-plots to visualize LD agreement variation at a very adaptable range of scales and groups (Kidwell 2013). When comparing Jaccard-Chao and Spearman rho metrics, values ranging within the upper right portion of the cross-plot are denoted "pristine", implying high LD agreement, and those in the opposite lower left portion "impacted", implying low LD agreement. Analogously, cross-plots for richness and evenness depict whether assemblages fall within the "expected" (upper-right quarter) or "unexpected" (lower-left quarter) range of LD agreement.

Squared distances between groups were visualized with NMDS ordination plots and differences in composition confirmed with PERMANOVA. Group differences were evaluated using both replicate samples (point-scale) and station samples (habitat-scale). Spatial scales were adopted from Kidwell and Tomasovych (2013): point scale = a sample comprising both living and dead individuals collected from a replicate sample; habitat scale = same depth replicate samples pooled by station. Field scale refers to pooled samples by meadow.

Statistical analyses were conducted with R (R Core Team, 2018) and the vegan package (Oksanen et. al 2019), as well as Past (Hammer and Harper, 2001). Figures were created with R's graphics package and ggplot2 (Wickham, 2016).

2.5.1. Richness

Raw species counts and sample-size-standardized counts were used to compare richness ratios for the LD assemblages in the study area. Assemblage comparisons were conducted by pooling LA replicates, subsampling DAs, and rarefying to LA sample sizes to correct for differences (Olszewski et al., 2007; Legendre and Legendre, 2012). The rarefy function in R's vegan package was used, described by Jari Oksanen and based on Hurlbert's (1971) formulation and the standard errors on Heck et al. (1975). Species richness and evenness were plotted

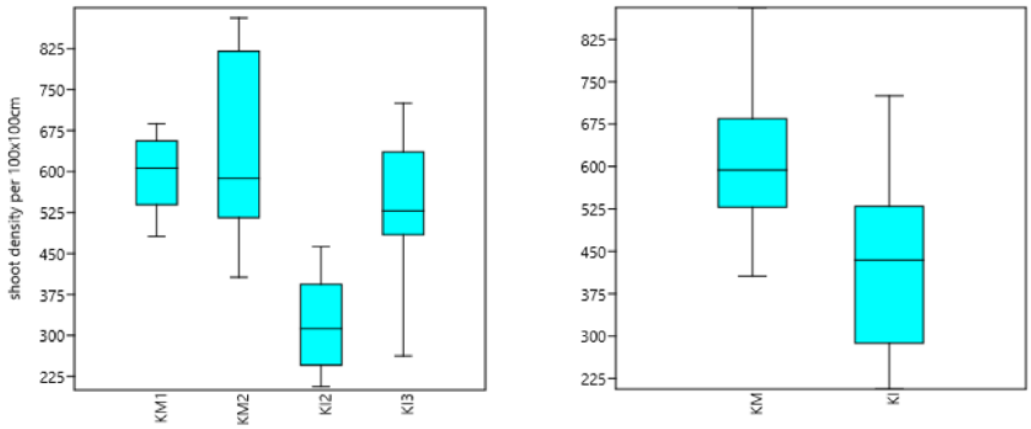
Table 3 *Posidonia oceanica* shoot density quadrats (SD1-10) at the sampled stations. Colors indicate the ecological health status for *Posidonia oceanica* meadows at a depth of 7.5 m as defined by the UNEP/MAP-RAC/SPA report (2011). Station- and field averages along 95% confidence intervals (95% CI) are indicated. Top table show reference values used for color coding.

Meadow status	SD/m²
High	>746
Good	746 to 584
Moderate	584 to 421
Poor	421 to 259
Bad	<259

	KM1	KM2	KI2	KI3
SD1	481	488	381	531
SD2	688	525	463	725
SD3	631	538	319	513
SD4	650	575	231	619
SD5	588	406	206	688
SD6	525	600	250	494
SD7	675	731	388	525
SD8	625	819	306	456
SD9	575	825	281	544
SD10	544	881	413	263
SD average	598	639	324	536
meadow health	Good	Good	Poor	Moderate

	KM	KI
Mean	618	430
95% CI.	561 - 676	359 - 501

Figure 2 Averaged shoot densities by station (left) and field (right). Boxplots show the sample median and the first and third quartiles, whiskers indicate shoot density minimum and maximum values



together by calculating differences in richness using $\Delta S = \log_{10}(\text{dead S}) - \log_{10}(\text{live S})$ (Olszewski et al., 2007; García-Ramos et al., 2016). Differences in species richness can be used as indicators for environmental change (Kidwell 2009).

2.5.2. *Evenness*

Along with richness, evenness is another common measure of diversity, which functions as a probability value that describes the likelihood of encountering the same species taken at random from a sample; it is useful when comparing communities. The amount of biological activity associated with a particular community state can also be inferred from evenness and provides insights when comparing living and death assemblages. Live-dead studies adopt the Probability of Interspecific Encounter (PIE) as a measurement of evenness (described in detail by Olszewski et. al, 2007) because of its convenient mathematical properties. Unlike ΔS, sample size differences do not affect ΔPIE and correcting for sample sizes is not necessary. Live-dead differences in evenness can thus be directly calculated by ΔPIE = PIE DA – PIE LA (Albano et al. 2016), so a positive ΔPIE value indicates that the DA is more even than the LA and the inverse for negative values.

2.5.3. *Spearman's Rank-order Correlation*

Spearman's correlation coefficient rho is a commonly used live-dead metric to assess for agreement in species relative abundances and is calculated with the non-parametric Spearman rank-order test. Resulting values range between -1 and 1, indicating to which degree species ranking within an assemblage compare to another. A rho coefficient of 1 indicates that sets of taxa belonging to different assemblages are ranked in the exact same order and is associated with pristine settings. A coefficient of -1 indicates the opposite, i.e. a low rho coefficient value indicates weak correlation between the set of ranks and is associated with impacted ecosystems (Albano et al. 2016); zero signals rank correlations do not fit a monotonic relationship (Legendre 2012). Species absent in both assemblages were removed prior to calculating for rho.

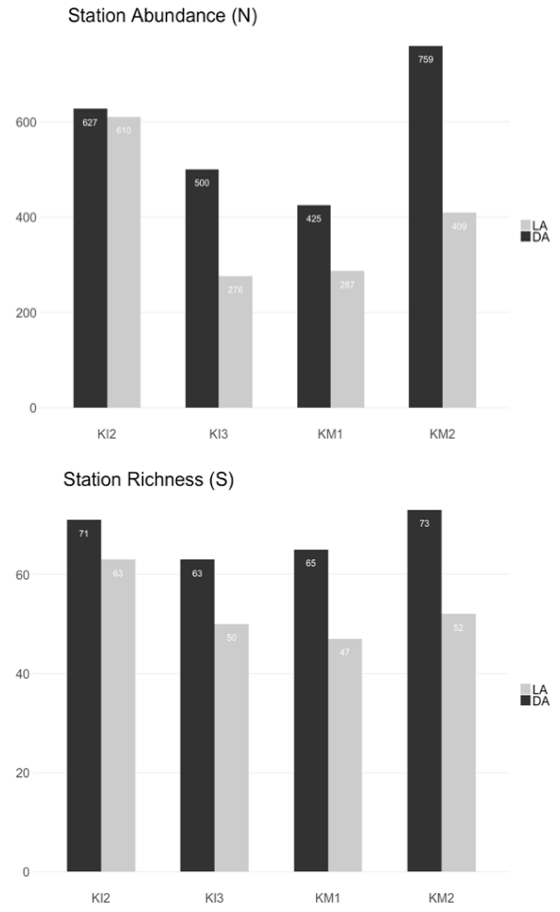
Table 4 Sample codes by station. Average shoot densities shown for stations and fields; confidence intervals are specified for the latter. *Posidonia oceanica* meadow health status is color-coded according to table 3b. Rhizome layer samples are in bold font

Field	Station	Sample	Code	Assemblage	Shoot density	Status
	2	R4-D	D-KI2	Dead	324	Poor
		R4	L-KI2	Live		
		R5	L-KI2	Live		
		R6	L-KI2	Live		
	3	R7-D	D-KI3	Dead	536	Moderate
		R7	L-KI3	Live		
		R8	L-KI3	Live		
		R9	L-KI3	Live		
KI		Average shoot density			430 (95% CI 359-501)	
	4	R10-D	D-KM1	Dead	598	Good
		R10	L-KM1	Live		
		R11	L-KM1	Live		
		R12	L-KM1	Live		
	5	R13	L-KM2	Live	639	Good
		R14-D	D-KM2	Dead		
		R14	L-KM2	Live		
		R15	L-KM2	Live		
KM		Average shoot density			618 (95% CI 560-676)	

2.5.4. *Taxonomic similarity*

Communities present in the same region or habitat are expected to have similar species composition. Taxonomic similarity between samples was estimated with the Jaccard index as modified by Chao et al. (2005), which evaluates species similarity between

Figure 3 Barplots depicting station abundance and richness of living (LAs) and death assemblages (DAs). Black bars = DAs, grey bars = LAs.



different-sized samples that may be undersampled or likely to capture various rare species (Chao et al. 2004). The Jaccard-Chao index of similarity produces more reliable results than the classic Jaccard and Sørensen indices when used on rich communities with a considerable proportion of rare species, as is generally the case for death assemblages.

2.5.5. Non-metric multidimensional scaling

Sample differences between LD assemblages and fields were visualized on two-dimensional space by performing Kruskal's non-metric multidimensional scaling (Kruskal 1964). Group associations were statistically evaluated by Non-parametric Permutational Multivariate Analysis of Variance (PERMANOVA) (McArdle and Anderson 2001). R's community ecology *vegan* package (version 2.5-6 Oksanen et al., 2019) provides the *adonis* function, which runs PERMANOVA with Bray-Curtis dissimilarity indices between groups. To ameliorate the overrepresentation caused by the most dominant species, relative abundances were transformed by the square root. The Similarity of Percentages routine (SIMPER, Clarke 1993) was used on relative abundances to determine to which extent species were responsible for observed dissimilarities between groups determined *a priori*. Lastly, zeros in the species matrix are kept for evaluation; omitting species occurring live-only or dead-only has been flagged as inappropriate practice as it incorrectly inflates live-dead agreement (Kidwell 2013).

3. Results

The study area's total abundance is 3893, of which 146 species were identified; 2311 (59.4%) dead and 1582 (40.6%) living individuals were collected in total. Very high sample coverage was obtained in both assemblages for each station (death assemblage: KI2 95%, KI3 96%, KM1 93% KM2 96%; living assemblage: KI2 96%, KI3 93%, KM1 95% KM2 97%).

Gastropod species predominate (66%) and constitute 63.2% of all shells. Bivalves make up 28% of species and 36.6% of the total abundance. Only 0.3% of the collected individuals are polyplacophorans and *Antalis vulgaris* is the only living Scaphopoda individual.

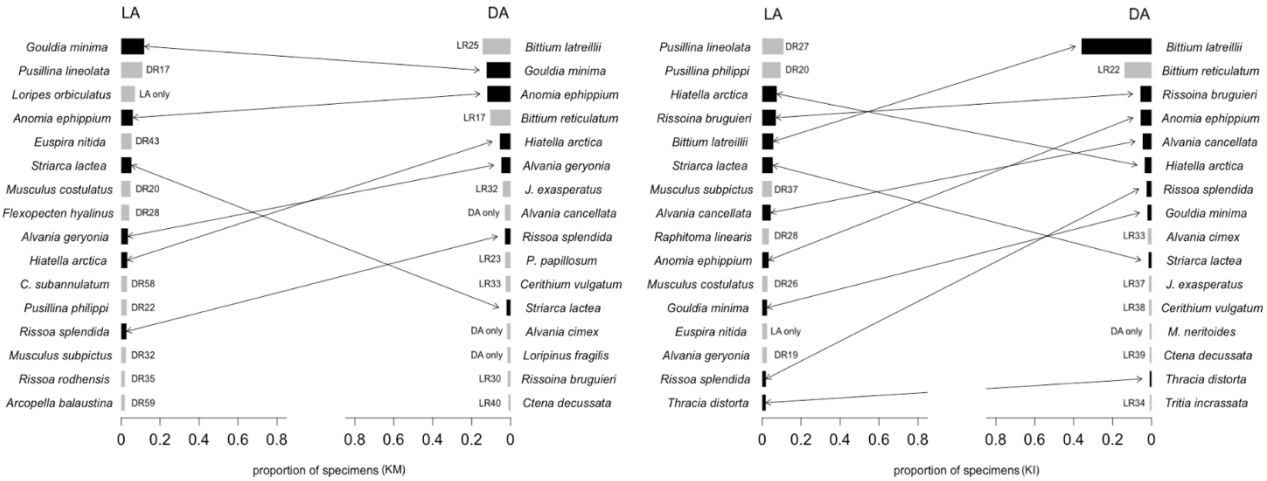
The mean shoot density (shoots/m^2) in Kormati was 430 (95% CI 359-501) and 618 in Krk (95% CI 560-676). See fig. 2 for shoot density averages by station and field. Field meadow cover means differ significantly by 189 shoots/m^2 (p-value < 0.001). The depth-dependent ecological health status was on average "poor" and "moderate" for Kormati stations and "good" in Krk stations (table 3, 4). Shoot densities ranged between 206-725 (KI) and 406-881 (KM), the lowest shoot densities were recorded in KI2 station.

3.1. Live-dead comparisons

3.1.1. Abundance and richness

The differences in richness and abundance between the DA and LA are smaller than expected, meaning the LA is particularly abundant (fig. 3). Sampled DA abundances are on average higher in Krk (D/L abundance ratio: KI = 1.27; KM = 1.70), but assemblages in KI2 (habitat-scale) were atypically equal (D/L KI2 = 1.03). The DA in both meadows is represented by 91 species, the LA in Kormati and Krk by 71 and 62 species, respectively (D/L richness ratios = KI 1.28; KM 1.47), and Taxonomic groups are more evenly represented in Krk than in Kormati. The DA is predominantly represented by gastropods (KI 80%; KM 56,1%), as is the LA in Kormati (64,8%). In contrast, dead bivalves in Krk make up roughly twice the proportion over Kormati (KI 19,8%; KM 43,8%) and living bivalves predominate (KI 34,8%; KM 53,7%). Polyplacophorans in both fields make up < 1% of

Figure 4 Proportional abundances of the most abundant species in Krk (left figure) and Kormati (right figure); Grey bars indicate species absent from the corresponding assemblage's list of top ranked species, black bars and arrows indicate common species. In each figure living assemblage species are on the left axis, death assemblage species on the right. Dead rank (DR) indicates the species rank position in the death assemblage; Live rank (LR) indicates the species rank position in the living assemblage.



species. The DA abundance structures show strong similarities: 16 species have a relative abundance ≥ 1%, separately both in Kormati (accounting for 84.4% of the assemblage's abundance) and Krk (accounting for 82.6% of abundance).

3.2. Fidelity of taxonomic composition

Most of the species in the LA are detected by the DA across all sites; several of the 15 most abundant LA species are also present in the DA (fig. 4), more so in Kormati assemblages (KI 9; KM 6), but proportional abundances do not match strongly.

3.2.1. Habitat-scale fidelity

All station samples fall within the pristine range of values for rank-order agreement ($x > 0$), but only KM2 is statistically significant (p = 0.012). Spearman rho values range in Krk from 0.018 (KM1) to 0.266 (KM2), and in Kormati from 0.131 (KI2) to 0.117 (KI3). Taxonomic similarity is high in all stations (Jaccard-Chao range: 0.704 [KI3] to 0.865 [KM2]) and highest in Krk.

3.2.2. Replicate-scale fidelity

At replicate scale, abundance rank correlations between assemblages again score mainly in the positive, but most replicates largely lack significance (excl. KM2.2 and KM2.3). Higher spatial resolution yields a wider value range and on average mildly decreases rank-order agreement in both fields. Spearman rho ranges from 0.019 to 0.213 in Kormati, and from –0.185 to 0.244 in Krk. The Jaccard-Chao index ranged from 0.583 to 0.866 in Kormati samples, and from 0.739 to 1 in Krk. Like the habitat-level results, KI3 again returns the lowest Chao. On the high end KM1 returns very high values (0.91 - 1), implying nearly identical assemblages in one of the replicates (KM1.3).

3.2.3. Field-scale differences in relative abundance

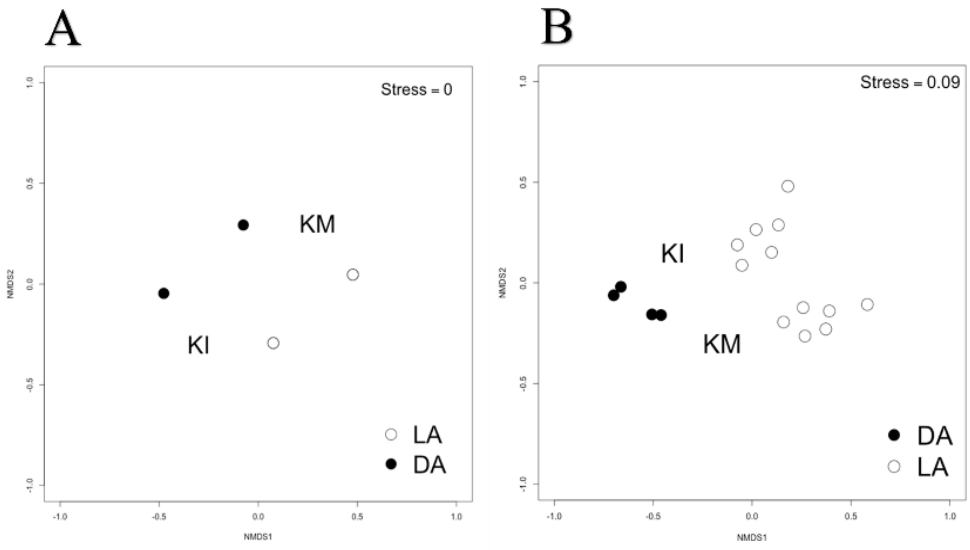
In Kormati, *B. latreillii* is notably the most abundant species in its assemblage; other top species are similarly abundant. This means 69.4% of the assemblage is largely represented by *B. latreillii* (35.9%) and closely related *B. reticulatum* (13.9%), followed more evenly distributed by *Rissoina bruguieri*, *A. ephippium*, *Alvania cancellata*, and *H. arctica*. Common species in the LAs top 6 are *H. arctica*, *R. bruguieri, and B. latreillii,* in that order, and otherwise *P. lineolata, P. phillipi,* and *S. lactea.* In Krk, 59.3% of the DA is represented more evenly by *B. latreillii*, *Gouldia minima*, *Anomia ephippium*, *B. reticulatum* (relative abundances between 10 – 15%),

Table 5 Similarity of percentages test results, indicating which species contributed most to the detected differences between assemblages in each field. Species absent from either assemblage are highlighted in **bold**

KM				DA	LA	
	Average	**SD**	**Ratio**	**Av.DA**	**Av.LA**	**Cum.%**
Bittium latreillii	0.0231	0.0019	12,3352	37%	9%	4%
Loripes orbiculatus	0.0223	0.0027	8,2817	0%	27%	9%
Pusillina lineolata	0.0207	0.0034	6,0931	8%	33%	13%
Euspira nitida	0.0159	0.0048	3,2939	4%	23%	16%
Bittium reticulatum	0.0158	0.0056	2,8286	32%	13%	19%
Alvania cancellata	0.0143	0.0015	9,5527	17%	0%	22%

KI				DA	LA	
	Average	**sd**	**ratio**	**Av.DA**	**Av.LA**	**Cum.%**
Bittium latreillii	0.0285	0.0063	4,5282	60%	26%	6%
Bittium reticulatum	0.0256	0.0071	3,67	37%	7%	11%
Pusillina lineolata	0.0233	0.0019	12,4534	6%	34%	15%
Pusillina philippi	0.018	0.004	4,5471	8%	29%	19%
Musculus subpictus	0.0148	0.0011	13,0514	5%	23%	22%
Euspira nitida	0.0127	0.0015	9,3443	0%	15%	24%

Figure 5 NMDS of living (LAs) and death assemblages (DAs), after resampling the death assemblages to the sample size of their respective living assemblages (100 randomizations). (A) NMDS run on station samples (B) NMDS run on replicate samples



H. arctica, and *Alvania geryonia*. Finally, *G. minima* and *A. ephippium* are likewise present in the corresponding LA's top 6, which also includes *P. lineolata, L. orbiculatus* (LA-only), *Euspira nitida [E. pulchella],* and *Striarca lactea*.

3.3. Distinguishing groups between and within meadows

Running nMDS on LA station samples returns two seemingly inconsistent ordination configurations. One plots a nearly equidistant rhombus-like spread between 4 points, which are actually 8 points overlapping (fig. 5a). The overlap occurs between habitat assemblages (e.g., DA-KI2 and DA-KI3) and the distance between points is minimal. The second configuration consistently plots samples on 0 along the y-axis (NMDS2 coordinate), tracing a straight line of data points. PERMANOVA identifies a significant difference between the LA and DA ($p < 0.05$) whereby 52% of the variation is attributed to assemblages. Evaluating within-field (n = 4) LD dissimilarities instead returns strongly insignificant p-values ($p = 0.333$).

These irregularities are due to few data points and are here addressed by using replicates instead of stations to increase the number of samples. The ordination now better distinguishes within- and between-group dissimilarities and reveals differences in community composition (fig. 5b), more pronounced between assemblages than between fields. DA points are more clustered than the LA points, indicating live-dead differences in temporal resolution. In contrast to LAs, because DAs are shaped by mixing across time, DAs are more similar to each other in terms of composition. PERMANOVA ascribes 34% of the observed variation to differences between assemblages ($F = 7.21$; $p = 0.001$). Dissimilarities based on field association show about half the effect size ($F = 3.15$; $p < 0.05$), but Kormati is discernable from Krk.

Table 6 PERMANOVA partitioning and analysis of molluscan communities sampled from Posidonia oceanica meadows. Samples were evaluated for group differences based on taxonomic composition at two levels: (A) station-scale and (B+C) replicate-scale. Evaluated groups: assemblages (LAs, DAs), fields (KI, KM), stations (KI2, KI3, KM1, KM2). Significance levels: p ≤ 0.05*, p ≤ 0.01**, p ≤ 0.001***

A	Station-scale				
Study area	Degrees of freedom	Sum of squares	Mean squares	*F*	*p*
Assemblage	1	0.3944	0.3944	6.5612	0.036*
Residuals	6	0.3607	0.0601		
Total	7	0.7551			
Field	1	0.1521	0.1521	1.5132	0.202
Residuals	6	0.6030	0.1005		
Total	7	0.7551			
B	Replicate-scale				
Study area	Degrees of freedom	Sum of squares	Mean squares	*F*	*P*
Assemblage	1	0.6625	0.6625	7.2112	0.001***
Residuals	14	1.2862	0.0919		
Total	15	1.9486			
Field	1	0.3578	0.3578	3.1482	0.006**
Residuals	14	1.5909	0.1136		
Total	15	1.9486			
Stations	3	0.4899	0.1633	1.3432	0.172
Residuals	12	1.4588	0.1216		
Total	15	1.9486			
C	Replicate-scale				
KI	Degrees of freedom	Sum of squares	Mean squares	*F*	*p*
Assemblage	1	0.3758	0.3758	5.2509	0.035*
Residuals	6	0.4294	0.0716		
Total	7	0.8051			
KM	Degrees of freedom	Sum of squares	Mean squares	*F*	*p*
Assemblage	1	0.3953	0.3953	6.0744	0.037*
Residuals	6	0.3905	0.0651		
Total	7	0.7858			

Of the 6 species contributing most to within-field LD dissimilarities, 4 coincide in both meadows: *B. latreillii, P. lineolata, B. reticulatum* and *E. nitida.* These species are either typically associated with or found among *P. oceanica* meadows. Additionally, *P. philippi* and *Musculus subpictus* attribute strongly to dissimilarities in Kormati, *L. orbiculatus* (live-only) and *Alvania cancellata* (dead-only) in Krk. See table 6a-c for PERMANOVA testing at several scales and appendix A, B for assemblage ranks.

3.3.1. *Species found live-only*

In Kormati, 20.2% of species (23 species) were found exclusively in the LA: 20 gastropods, 2 bivalves, and 1 scaphopod (i.e., *Antalis vulgaris*). The most abundant of these was the gastropod *Euspira nitida*, an infaunal carnivore and coarse sand-dweller which tolerates hypoxia and does not require stable sedimentary regimes (Huelsken et al. 2008; Gallmetzer et al. 2017). Despite a moderately low relative abundance (2.5% or 22 specimens) this gastropod is the 6th largest SIMPER contributor in Kormati (table 5), partly because it was found live-only. In Krk, 15.7% (17 species) were found live-only, 14 of which are gastropods, and 3 bivalves.

Among these LA-only species, 9 gastropods and 1 bivalve were found exclusively alive throughout the entire study area, and present in both assemblages. Notably *L. orbiculatus*, the only bivalve, accounts for 7% of the LA in Krk and ranks 3rd. *E. nitida* also has a stronger LA presence in Krk (5.2% or 37 specimens) and ranks 5th, although very rare (2) in the corresponding DA. Both are also the 2nd and 4th strongest SIMPER contributors to assemblage dissimilarities, respectively.

In Kormati, species that are considered both rare and entirely absent from Krk include gastropods *Haliotis tuberculata, Sticteulima jeffreysiana, Vitreolina curva, Typhinellus labiatus, Odostomella doliolum, Megastomia conoidea,* and *Raphitoma cf. locardi*, and the only scaphopod sampled, *Antalis vulgaris.* The bivalve *Arcopella balaustina* was only absent from the DA in Kormati but present in both Krk assemblages. Rare live-only species in Krk include gastropods *Acteon tornatilis, Roxaniella jeffreysi* and *Steromphala umbilicaris* (singletons).

3.3.2. *Species found dead-only*

Both fields reveal a similar number of species found dead only (DA-only: KI 43/114; KM 46/108); mostly gastropods, then bivalves, and a similarly low number of polyplacophorans. The gastropod to bivalve species ratio in Kormati (3,3:1) is more than double the ratio in Krk (1,4:1). Twenty-three gastropods (29.9%) and four bivalves (13.3%) were found DA-only exclusively

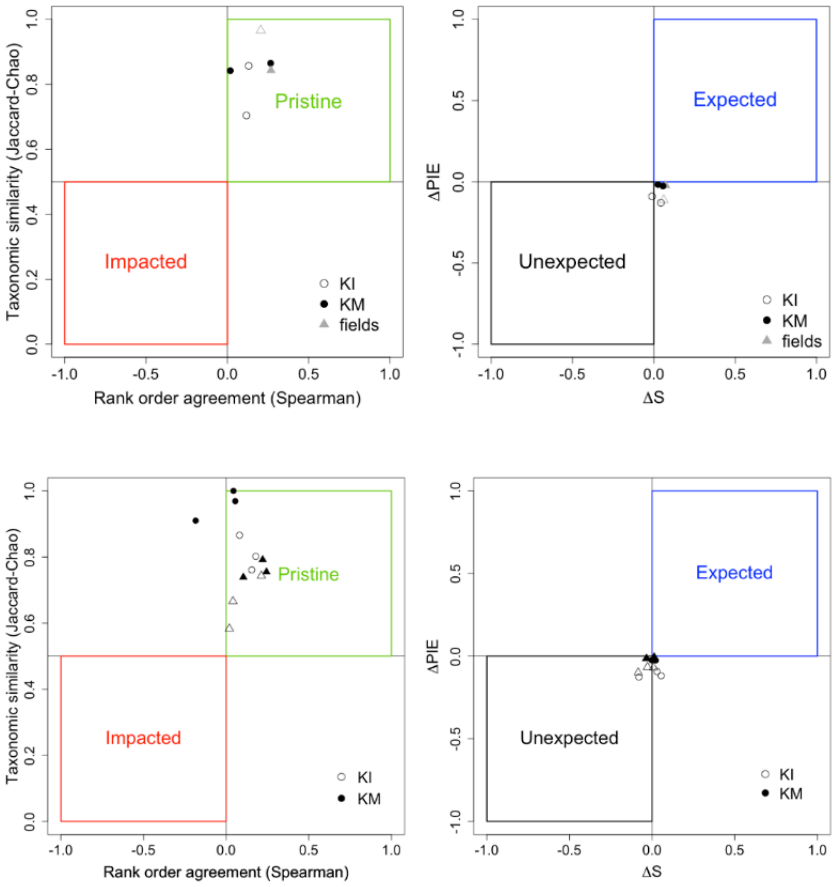


Figure 6 Live-dead agreement scatterplots; fidelity metrics used on x- and y-axis: Jaccard-Chao (taxonomic similarity), Spearman (rank-order agreement), ΔPIE (evenness), ΔS (richness). (A) Live-dead agreement at station-scale, (B) live-dead agreement at replicate-scale.

Table 7: Sample overview of rank-order index (Spearman rho), abundance (***n***), and richness (***S**obs*) at replicate-, habitat-, and field-scale. Ceiling applied on DA individuals at replicate-scale. Samples in **bold** font indicate significant Spearman rho values (significance level ≤ 5%).

				No. of specimen (***n***)		No of taxa (***S**obs*)	
Spatial scale	Sample	Spearman's rho	p value	DA	LA	DA	LA
Point (replicates)	KI2.1	0.155	0.15	627	165	71	44
	KI2.2	0.081	0.46	627	263	71	41
	KI2.3	0.179	0.11	627	182	71	36
	KI3.1	0.041	0.726	500	107	63	36
	KI3.2	0.019	0.875	500	81	63	27
	KI3.3	0.213	0.077	500	88	63	26
	KM1.1	-0.185	0.11	425	81	65	28
	KM1.2	0.055	0.644	425	130	65	34
	KM1.3	0.044	0.714	425	76	65	26
	KM2.1	0.104	0.348	759	122	73	35
	KM2.2	**0.244**	**0.028***	759	158	73	39
	KM2.3	**0.221**	**0.052***	759	129	73	32
Habitat (stations)	KI2	0.131	0.201	627	610	71	63
	KI3	0.117	0.293	500	276	63	50
	KM1	0.018	0.869	425	287	65	47
	KM2	**0.266**	**0.012***	759	409	73	52
Field (meadows)	KI			1127	886	91	71
	KM			1184	696	91	62

in Kormati, while thirteen gastropods (19.7%) and ten bivalves (27%) are exclusive to Krk. Of these species, *Alvania cancellata* is the most abundant, missing alive from Krk, and a main contributor to LD dissimilarity. Further abundant (sensu Chao) species include: *Pusillina marginata, A. cimex*, and *Loripinus fragilis*. In Kormati only *Melarhaphe neritoides* is abundant, but being an intertidal species, empty shells found in *Posidonia* meadows have most likely rolled off from the rocks above.

3.4. Fidelity of species richness and evenness

3.4.1. Habitat-scale (8 station samples)

At habitat scale, LD agreement scatterplots of stations reveal similarly distanced sample points (fig. 6a). Evenness (ΔPIE) and species richness (ΔS) metrics for LD agreement cluster station points around zero, leaning mildly towards a positive ΔS and negative ΔPIE. The latter ranges from -0.129 (KI2) to -0.017 (KM2) and ΔS ranges from -0.011 (KI3) to 0.056 (KM1).

3.4.2. Replicate-scale (24 replicate samples)

Instead evaluating LD agreement at replicate-scale, by pairing LA replicate samples with multiple identical DA station samples, allows for higher resolution (fig. 6b). Species richness and evenness depict a similar pattern of values minimally dispersed around zero and across replicates. But when compared to the 8-sample scatterplot, species richness shifts Kormati points into the bottom left 'unexpected' quadrant, and they are more dispersed. ΔPIE ranges from -0.127 to -0.004 and ΔS between -0.084 and 0.055, indicating similar evenness and richness in both living and death assemblages. The DA in Kormati is only marginally less even than the LA.

4. Discussion

4.1. Compositional LD fidelity matches pristine settings

The compositional agreement observed between assemblages does not suggest sizeable impacts in either meadow, contrary to initial expectations. In fact, the molluscan assemblages recorded depict stable regional communities typically associated with *Posidonia oceanica*.

Within-field distinctions between the LA and DA are detected by nMDS ordination at replicate-scale (fig. 5b), meaning centroids do not overlap. Cluster affiliation is distinctive and dissimilarities between groups are significant [PERMANOVA, (KI) F = 5.209, p = 0.035; (KM) F = 6.0744, p = 0.037) everywhere (table 6c). LA samples show larger spread than DA samples, an observation in line with compositional differences caused by natural temporal variability (Tomašových and Kidwell 2009). Temporal scale disparity is expected of non-averaged (LA) and time-averaged (DA) assemblages, the latter depicting a more homogenous signal due to the condensation of several non-contemporaneous generations (Kidwell 2013).

Rank-order agreement indicates there is no clear community assemblage turnover in either field; indeed, only KM2 samples return significant values (table 7). Elevated taxonomic similarity across samples does indicate the DAs account for most species in the living population (fig. 6). KI3 reveals the lowest congruence but is still within the range associated with pristine settings. These results match those obtained from temperate open-shelf data sets (median = 0.84) associated with minimal human activity (Kidwell 2008; Kidwell and Tomašových 2013). Such strong fidelity among molluscan assemblages strongly supports the notion that DAs are reliable sources to obtain regional species lists (Kidwell 2013).

LD agreement is on average mildly stronger at habitat-scale, a recognized scaling effect resulting from spatial coarsening (Kidwell and Tomašových 2013). However, evaluating compositional dissimilarities at habitat-level does not reveal significant LD differences within fields in multivariate space. The symmetrically distanced and seamlessly overlapping sample points visualized by the ordination plots are unexpected and inconsistent (fig. 5a). This lack of sample separation is probably due to computational limitations resulting from insufficient number of samples at this spatial scale (Kowalewski, personal communication, December 2020).

4.2. Diversity may be affected by the leaf layer interface

On average LD agreement for richness and evenness is marginally lower in Kormati, and LD agreement variation higher. This distinction is small but noticeable and could be a residue of taphonomic biases, which influence marine shelves more than they do lagoons and lakes (Tomašových and Kidwell 2011), and play a more decisive role in erosive coastline settings (Kidwell 2013).

Depressed DA values for ΔS and ΔPIE have been accredited to taphonomic vulnerability to damage and dead shell losses (Olszewski and Kidwell 2007), but these attributions seem unlikely in densely layered seagrass habitats. Most fidelity studies conducted on soft- or hard-bottom substrates assess LD agreement for substrates which are directly exposed to the water column. This is relevant insofar as seagrass rhizomes are considered hard substrates, albeit with a protective leaf layer buffer zone. I suspect postmortem transport is influenced by the leaf-layer interface, which may reduce within- and out-of-habitat shell movement (Albano and Sabelli 2011). The habitat's protective leaf canopy should soften the aforementioned effects on its DA by reducing both sediment stirring in the rhizome layer and mechanical stress caused by water currents close to the surficial layer, both which otherwise contribute to sediment relocation and shell deterioration.

Once dead shells precipitate into the rhizomes they essentially gain an additional protective layer at the sediment-water interface, possibly analogous to being buried below an otherwise exposed and potentially destructive interface (Kidwell 2013). Within-habitat incomplete ergodic mixing resulting from the non-uniform spread of dead shells, seems to better explain the depressed ΔS and ΔPIE observed (Olszewski and Kidwell 2007; Albano and Sabelli 2011). Low dispersal rates would lead to the incomplete homogenization of DAs and very localized shell retainment translates into patchy DAs which underrepresent local diversity.

Taphonomic processes aside, time-averaging alone is expected to generate depressed beta diversity in DAs (Albano and Sabelli 2011; Tomašových and Kidwell 2010b); time-averaging effects are discussed below in further detail.

4.2.1. *Differences in variability of LD fidelity (S, PIE)*

Richness and evenness scatterplots also depict the degree to which LD agreement varies within fields, suggesting that samples in Kormati are mildly less consistent in their LD agreement. Wave simulations of the region found that wave height averages around Kormati islet are significantly higher (~25%) than close to Krk (Ružić et al. 2015), suggesting elevated hydro-mechanical stress. Stronger water movement exacerbated by lower average shoot densities suggest more exposure to postmortem transport. Additionally, the islet in Kormati does not offer much wave protection; the islet has roughly the same length as the meadow, is adjacent to a narrow channel on the Plavnik side and open water on the other.

By contrast, Krk is protected by a continuous coastline with several recesses (bays), dampening the hydro-mechanical effects. Rougher conditions could intensify postmortem shell loss and explain part of the variability observed

4.3. Between-habitat distinctions

DA centroids show that compositional differences are substantially larger between habitats than within. This is impressive because it suggests the DAs echo compositional patterns observed in the LAs, picking up on larger dissimilarities between molluscan communities which are indeed farther apart geographically. Such spatial resolution has been observed frequently in DAs and discussed in detail (Kidwell 2013).

Diversity and abundance profiles confirm most species are common to both DAs. Relative abundance comparisons by class (i.e., Bivalvia, Gastropoda,

Scaphopoda) reveal some differences though. Of the 15 most abundant DA species 12 are common to both locations, but Krk bivalves represent a much larger portion of the assemblage (KM 36.3%; KI 14.9%). Kormati assemblages are abounded by gastropods while the abundance structure in Krk is comparatively equal among taxa; living bivalves in Krk are even mildly more abundant than the gastropods. Additionally, the number of abundant bivalve species is higher in Krk (n ≥ 10 species in KM 9, KI 6), suggesting better habitat suitability over Kormati.

4.3.1. Feeding guilds suggest differential habitat preferences

Taking species abundances into account, trophic guilds reveal microalgal grazers (i.e., gastropods) predominate the top 15 species cohorts in Kormati, while suspension feeders (i.e., bivalves) predominate in Krk. Since most bivalve species are filter feeders, many of which are epifaunal, lower shoot densities in Kormati could be responsible for lower bivalve incidence. Several studies have confirmed the positive effect elevated seagrass biomass and shoot densities have on bivalve abundances, for instance through increased protection from predation (e.g. Orth, Heck, and van Montfrans 1984). In addition, strong coastal vulnerability in Krk suggests the potential for terrigenous input is much higher, which should directly influence nutrient particle availability in the surrounding water body. Bivalves' capacity to extract nutrients from the water column is remarkable (Petersen et al. 2019), and filter feeders could benefit from elevated particulate nutrient availability.

4.4. Confounding factors

As previously noted, live-dead results obtained initially suggest moderately pristine conditions, or the absence of strong human disturbance, assuming DAs are time-averaged. However, temporal scales are unclear and the following sources of interpretative entanglement, recognized as important factors affecting LD fidelity, should be examined:

1. Differential time-averaging across meadows
2. Intensity of anthropogenic disturbance
3. Taxonomic biases

4.4.1. Differential time-averaging effects

One scenario assumes the DA is younger than impacts on the LA, resulting in assemblage equilibration. Bearing in mind how persistent human activity has been in the region, it is possible that pressures are longstanding. In other words, the DA reflects post-impact conditions and thus fails to reflect previous ecological states and shifts. Samples were not dated in this study, so it is uncertain to which extent time-averaging characterizes each DA. A shorter time-averaging window implies shorter DA response lags to new input from the LA (i.e., lower taphonomic inertia). This would explain the condensed LD fidelity results obtained for diversity metrics, especially in Krk samples. Under this premise the DA is partial to short-term fluctuations in the LA, readily depicting similar community attributes. Differential time-averaging effects across meadows (i.e., lower time-averaging window in Krk) would also help explain the high taxonomic similarity observed, contrary to original predictions.

Lastly, as time-averaging increases dominance patterns in the DA tend to decrease (i.e., evenness increases), meaning the most abundant species alternate to depict shared dominance in the DA (Kidwell 2013; Kidwell and Tomašových 2013). Judging from dominance patterns, time-averaging is low in the DAs. Observed evenness was very similar across assemblages in Krk, and in Kormati dominance is even lower in the LA. That being said, levelled ranks can result from multiple LA abundance structures sequentially mixing in the course of time. Flatter rank-abundance distributions (i.e., a decrease in proportional abundances particularly of top-ranking species) with longer rare species tails (e.g., resulting from long-term recording of infrequent species), are observed in the DAs, attributes associated with time-averaging (Tomašových and Kidwell 2010a; Kidwell 2013).

4.4.2. Intensity and timing of anthropogenic disturbance

Actual disturbance levels in the study area should ideally be re-examined for further interpretative scrutiny. From the current study two observations emerge: 1) considering the conservative nature of LD fidelity studies, evaluated impacts may have been overestimated. In other words, anthropogenic stressors may have been too mild to produce LD disagreement. Molluscan LD mismatch obtained from global meta-analyses resulted from strong anthropogenic eutrophication, the magnitude of which is considerably higher than in this study (Kidwell 2013). The same findings substantiate that nearly half of the habitats impacted by human activity also generate good LD agreement, comparable with results from pristine habitats. This leads to the second observation: 2) despite distinctive amounts of human presence, the LAs depict molluscan biocoenoses typical of *P. oceanica* meadows (Albano, personal communication, 2020). This is interesting because it suggests said molluscan communities may simply be resilient to moderate human activity.

4.4.3. Lifespan brevity bias and interspecies differences

Bittium latreillii and *B. reticulatum* are closely related taxa, microalgal feeders, and typical *Posidonia oceanica* species (Russo, Fraschetti, and Terlizzi 2002; Albano and Sabelli 2011; 2012). Particularly the former is very abundant dead in Kormati, the relative abundance of which is about 2.5 times larger than in Krk (51 found alive in Kormati and 6 in Krk). Such dominance patterns may be linked to short life cycles, estimated at around 18 months for *B. latreillii* (Russo, Fraschetti, and Terlizzi 2002). High generational throughput coupled with shell durability lead to swift shell accumulation in the DA. Spearman rho metrics lack significance in this study, but gastropod lifespan biases on hard substrates have been identified as important taphonomic processes influencing variation in population turnover (Albano and Sabelli 2011) and interspecies differences among feeding guilds. This is evident when comparing carnivores to microherbivores; the former live longer on average and tend to dominate DAs, while the latter are shorter-lived and predominate LAs (Kidwell 2013).

4.5. Environmental assessments should be supplemented by live-dead studies

Conservation paleobiology has provided insight in multiple areas of analysis relevant to environmental research and biodiversity management: detecting and predicting anthropogenic impacts, documenting baselines conditions, distinguishing native from alien species, defining dynamic management targets based on historical variability ranges, comparing biodiversity estimates across temporal scales, selecting and designing optimal areas for conservation efforts, and prioritizing strategy efficacy in conservation (for a comprehensive list see Dietl et al. 2015). Vast amounts of useful data are veiled from conservationists who disregard paleontological methods and the biological records they provide access to. As the field of conservation paleobiology grows and methods are refined, live-dead fidelity analyses should increasingly permeate strategic planning and decision-making at early stages of project development. Environmental assessments provide such an opportunity.

The Strategic Environmental Assessment (SEA), a preemptive protocol required by European law (SEA Directive 2001/42/EC) to minimize environmental impacts from public plans and programs (e.g. fisheries, coastline development, water management, waste management, tourism), focuses largely on identifying and predicting impacts, collecting baseline data, and monitoring environmental effects (OECD 2006); precisely the type of data live-dead fidelity studies can provide. A 2017 follow-up report on the implementation efficacy of the SEA directive emphasizes how different member state experiences and challenges have been depending on the quality and availability of information (European Commission, 2017). Provided time-averaging data is available, live-dead studies can enhance SEA procedures both in terms of data availability, e.g. by tapping into geohistorical archives otherwise unavailable to traditional surveys, and data quality, e.g. by adding geohistorical context to present conditions (Dietl et al. 2015). Importantly, a SEA must also be enforced if requested under the Habitats Directive, which as mentioned previously is relevant to this study area.

5. Conclusion

The biological attributes used to compare *Posidonia* meadows based on molluscan LD fidelity reveal similar patterns across spatial scales. Richness and evenness metrics depict neither strong agreement nor mismatch, rank-order coefficients do not reveal species turnover, and the degree to which assemblages coincide taxonomically is rather high in most samples. Within- and between field variation is lower in the DA; species composition variation and beta diversity tend to be smaller in DAs than LAs, tendencies which can be attributed to temporal coarsening due to time-averaging (Tomašových and Kidwell 2009). The DAs reflect contemporary communities to some degree and may suggest ecological integrity, but the pressures identified do not distinguish Krk from Kormati as expected. This was initially unexpected considering that meta-analyses consistently identify human activity as the single most important factor influencing LD agreement (Kidwell 2007; Tomašových and Kidwell 2009; Kidwell 2013; Kidwell and Tomasovych 2013), but LD fidelity studies are indeed conservative by nature. Average shoot densities are not consistent with LD results and expectations (i.e., Krk densities are higher), but the meadow cover adequately sustains molluscs associated with *Posidonia*. Although seagrass loss is an important driver of LD mismatch (Kidwell 2007), anthropogenic impacts associated with such discordance (e.g., eutrophication) must be substantial, and are stronger than those identified in the study sites. Taphonomic processes do not play as important a role in predicting LD discordance as time-averaging, but their effect is detectable (Kidwell 2013). Denser meadows in Krk may thus be responsible for weaker within-habitat shell transport and shell damage than in Kormati, producing a mildly more consistent LD agreement profile. Naturally, this observation requires further investigation. Taxonomic

structures and feeding guilds suggest differences in habitat preferences, implying the Krk sediment regime favors bivalves and Kormati favors gastropods, but additional information is needed to determine the drivers.

I conclude that living molluscan communities are more resilient to moderate anthropogenic influence than expected, provided meadow cover is sufficient to sustain them. Shoot densities appear to be good indicators for anthropogenic stress and good predictors of LD agreement in molluscs. Despite mixed results, the sampled molluscan assemblages are diverse, and the DAs likely represent local and regional diversity well, validating *Posidonia oceanica* habitats as biodiversity hotspots and potential reservoirs of past biological information.

Supporting Information

Appendix A. Species list of study area in systematic arrangement

Appendix B1. Ranked living and dead abundances – Krk

Appendix B2. Ranked living and dead abundances – Kormati

Cited literature

Albano, Paolo G., Nadezhda Filippova, Jan Steger, Darrell S Kaufman, Adam Tomašových, Michael Stachowitsch, and Martin Zuschin. 2016. "Oil Platforms in the Persian (Arabian) Gulf: Living and Death Assemblages Reveal No Effects." *Continental Shelf Research* 121 (June): 21–34. https://doi.org/10.1016/j.csr.2015.12.007.

Albano, Paolo G., and Bruno Sabelli. 2011. "Comparison between Death and Living Molluscs Assemblages in a Mediterranean Infralittoral Off-Shore Reef." *Palaeogeography, Palaeoclimatology, Palaeoecology* 310 (3–4): 206–15. https://doi.org/10.1016/j.palaeo.2011.07.012.

———. 2012. "The Molluscan Assemblages Inhabiting the Leaves and Rhizomes of a Deep Water Posidonia Oceanica Settlement in the Central Tyrrhenian Sea." *Scientia Marina* 0 (0): 721–32. https://doi.org/10.3989/scimar.03396.02c.

Barnosky, Anthony D., Elizabeth A. Hadly, Patrick Gonzalez, Jason Head, P. David Polly, A. Michelle Lawing, Jussi T. Eronen, et al. 2017. "Merging Paleobiology with Conservation Biology to Guide the Future of Terrestrial Ecosystems." *Science*. https://doi.org/10.1126/science.aah4787.

Buia, M. C., M.C. Gambi, and M. Dappiano. 2004. "Seagrass Systems." *Biologia Marina Mediterranea* 11 (November): 133–83.

Campagne, Carole Sylvie, Jean Michel Salles, Pierre Boissery, and Julie Deter. 2014. "The Seagrass Posidonia Oceanica: Ecosystem Services Identification and Economic Evaluation of Goods and Benefits." *Marine Pollution Bulletin* 97 (1–2): 391–400. https://doi.org/10.1016/j.marpolbul.2015.05.061.

Cardinale, Bradley J, Richard B Primack, and James D Murdoch. 2020. *Conservation Biology*. Sunderland, MA New York Oxford: Sinauer Associates Oxford University Press. https://ubdata.univie.ac.at/AC15624479.

Challen Hyman, A., Thomas K. Frazer, Charles A. Jacoby, Jessica R. Frost, and Michał Kowalewski. 2019. "Long-Term Persistence of Structured Habitats: Seagrass Meadows as Enduring Hotspots of Biodiversity and Faunal Stability." *Proceedings of the Royal Society B: Biological Sciences* 286 (1912). https://doi.org/10.1098/rspb.2019.1861.

Chao, Anne, Robin L. Chazdon, Robert K. Colwell, and Tsung-Jen Shen. 2004. "A New Statistical Approach for Assessing Similarity of Species Composition with Incidence and Abundance Data." *Ecology Letters* 8 (2): 148–59. https://doi.org/10.1111/j.1461-0248.2004.00707.x.

Coll, Marta, Chiara Piroddi, Jeroen Steenbeek, Kristin Kaschner, Frida Ben Rais Lasram, Jacopo Aguzzi, Enric Ballesteros, et al. 2010. "The Biodiversity of the Mediterranean Sea: Estimates, Patterns, and Threats." *PLoS ONE* 5 (8). https://doi.org/10.1371/journal.pone.0011842.

Dietl, Gregory P., and Karl W. Flessa. 2011. "Conservation Paleobiology : Putting the Dead to Work." *Trends in Ecology & Evolution* 26 (1): 30–37. https://doi.org/10.1016/j.tree.2010.09.010.

Dietl, Gregory P., Susan M. Kidwell, Mark Brenner, David A. Burney, Karl W. Flessa, Stephen T. Jackson, and Paul L. Koch. 2015. "Conservation Paleobiology: Leveraging Knowledge of the Past to Inform Conservation and Restoration." *Annual Review of Earth and Planetary Sciences* 43 (1): 79–103. https://doi.org/10.1146/annurev-earth-040610-133349.

European Commission. 2020. "Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions, EU Biodiversity Strategy for 2030, European Commission."

Feser, K. M., and A. I. Miller. 2014. "Temporal Dynamics of Shallow Seagrass-Associated Molluscan Assemblages in St. Croix, U.S. Virgin Islands: Toward the Calibration of Taphonomic Inertia." *Palaios* 29 (5): 218–30. https://doi.org/10.2110/palo.2013.103.

Flessa, Karl W. 2002. "Conservation Paleobiology," 2002.

Froyd, C. A., and K. J. Willis. 2008. "Emerging Issues in Biodiversity & Conservation Management: The Need for a Palaeoecological Perspective." *Quaternary Science Reviews* 27 (17–18): 1723–32. https://doi.org/10.1016/j.quascirev.2008.06.006.

García-Ramos, D. A., Paolo G. Albano, M. Harzhauser, W. E. Piller, and Martin Zuschin. 2016. "High Dead-Live Mismatch in Richness of Molluscan Assemblages from Carbonate Tidal Flats in the Persian (Arabian) Gulf." *Palaeogeography, Palaeoclimatology, Palaeoecology* 457. https://doi.org/10.1016/j.palaeo.2016.06.006.

Gilad, Ehud, Susan M. Kidwell, Yehuda Benayahu, and Yael Edelman-Furstenberg. 2018. "Unrecognized Loss of Seagrass Communities Based on Molluscan Death Assemblages: Historic Baseline Shift in Tropical Gulf of Aqaba, Red Sea." *Marine Ecology Progress Series* 589: 73–83. https://doi.org/10.3354/meps12492.

Griffiths, Laura L., Rod M. Connolly, and Christopher J. Brown. 2020. "Critical Gaps in Seagrass Protection Reveal the Need to Address Multiple Pressures and Cumulative Impacts." *Ocean and Coastal Management* 183 (September 2019). https://doi.org/10.1016/j.ocecoaman.2019.104946.

Hammer, Ø., Harper, D.A.T., Ryan, P.D. 2001. PAST: Paleontological Statistics software package for education and data analysis. Palaeontologia Electronica 4(1): 9pp.

Holon, F., P. Boissery, A. Guilbert, E. Freschet, and J. Deter. 2015. "The Impact of 85 Years of Coastal Development on Shallow Seagrass Beds (Posidonia Oceanica L. (Delile)) in South Eastern France: A Slow but Steady Loss without Recovery." *Estuarine, Coastal and Shelf Science* 165: 204–12. https://doi.org/10.1016/j.ecss.2015.05.017.

Kidwell, Susan M. 2002. "Mesh-Size Effects on the Ecological Fidelity of Death Assemblages: A Meta-Analysis of Molluscan Live-Dead Studies." *Geobios* 35 (SUPPLEMENT): 107–19. https://doi.org/10.1016/S0016-6995(02)00052-9.

———. 2007. "Discordance between Living and Death Assemblages as Evidence for Anthropogenic Ecological Change." *Proceedings of the National Academy of Sciences* 104 (45): 17701–6. https://doi.org/10.1073/pnas.0707194104.

———. 2008. "Ecological Fidelity of Open Marine Molluscan Death Assemblages: Effects of Post-Mortem Transportation, Shelf Health, and Taphonomic Inertia." *Lethaia*. https://doi.org/10.1111/j.1502-3931.2007.00050.x.

———. 2009. "Evaluating Human Modification of Shallow Marine Ecosystems: Mismatch in Composition of Molluscan Living and Time-Averaged Death Assemblages." *Conservation Plaeobiology: Using the Past to Manage for the Future* 15: 113–39.

———. 2013. "Time-Averaging and Fidelity of Modern Death Assemblages: Building a Taphonomic Foundation for

Conservation Palaeobiology" 56 (1970): 487–522. https://doi.org/10.1111/pala.12042.

———. 2015. "Biology in the Anthropocene : Challenges and Insights from Young Fossil Records" 112 (16). https://doi.org/10.1073/pnas.1403660112.

Kidwell, Susan M., and Karl W. Flessa. 1995. *The Quality of the Fossil Record: Populations, Species, and Communities*. *Annual Review of Ecology and Systematics*. Vol. 26. https://doi.org/10.1146/annurev.es.26.110195.001413.

Kidwell, Susan M., and Adam Tomašových. 2013. "Implications of Time-Averaged Death Assemblages for Ecology and Conservation Biology." *Annual Review of Ecology, Evolution, and Systematics* 44 (1): 539–63. https://doi.org/10.1146/annurev-ecolsys-110512-135838.

Korpanty, Chelsea A, and Patricia H Kelley. 2014. "Molluscan Live – Dead Agreement in Anthropogenically Stressed Seagrass Habitats : Siliciclastic versus Carbonate Environments." *Palaeogeography, Palaeoclimatology, Palaeoecology* 410: 113–25. https://doi.org/10.1016/j.palaeo.2014.05.014.

Kowalewski, Michal, Monica Carroll, Lorraine Casazza, Neal Gupta, Bjarte Hannisdal, Austin Hendy, Richard Krause, et al. 2003. "Quantitative Fidelity of Brachiopod-Mollusk Assemblages from Modern Subtidal Environments of San Juan Islands, USA." *Journal of Taphonomy* 1 (1): 43–65.

Legendre, Pierre. 2012. "05 Multidimensional Semiquantitative Data." *Numerical Ecology*, 195–218. https://doi.org/10.1016/B978-0-444-53868-0.50008-3.

Legendre, Pierre, and Louis Legendre. 2012. *Numerical Ecology Chapter 6. Developments in Environmental Modelling*. Vol. 24. https://doi.org/10.1016/B978-0-444-53868-0.50008-3.

Manzanera, M., M. Pérez, and J. Romero. 1998. "Seagrass Mortality Due to Oversedimentation: An Experimental Approach." *Journal of Coastal Conservation* 4 (1): 67–70. https://doi.org/10.1007/BF02806491.

Mayot, Nicolas, Charles François Boudouresque, and Agathe Leriche. 2005. "Unexpected Response of the Seagrass Posidonia Oceanica to a Warm-Water Episode in the North Western Mediterranean Sea." *Comptes Rendus - Biologies* 328 (3): 291–96. https://doi.org/10.1016/j.crvi.2005.01.005.

McArdle, Brian H, and Marti J Anderson. 2001. "Fitting Multivariate Models To Community Data : A Comment on Distance-Based Redundancy Analysis." *Ecology* 82 (1): 290–97. https://doi.org/10.1109/CIP.2010.5604124.

Neumann, Barbara, Athanasios T. Vafeidis, Juliane Zimmermann, and Robert J. Nicholls. 2015. "Future Coastal Population Growth and Exposure to Sea-Level Rise and Coastal Flooding - A Global Assessment." *PLoS ONE* 10 (3). https://doi.org/10.1371/journal.pone.0118571.

Nõges, Peeter, Christine Argillier, Ángel Borja, Joxe Mikel Garmendia, Jenică Hanganu, Vit Kodeš, Florian Pletterbauer, Alban Sagouis, and Sebastian Birk. 2016. "Quantified Biotic and Abiotic Responses to Multiple Stress in Freshwater, Marine and Ground Waters." *Science of the Total Environment* 540: 43–52. https://doi.org/10.1016/j.scitotenv.2015.06.045.

OECD. 2006. "Applying Strategic Environmental Assessment," September. https://www.oecd.org/environment/environment-development/37353858.pdf.

Oksanen, Jari, F. Guillaume Blanchet, Michael Friendly, Roeland Kindt, Pierre Legendre, Dan McGlinn, Peter R. Minchin, R. B. O'Hara, Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens, Eduard Szoecs and Helene Wagner (2019). vegan: Community Ecology Package. R package version 2.5-6. https://CRAN.R-project.org/package=vegan

Olszewski, Thomas D., and Susan M. Kidwell. 2007. "The Preservational Fidelity of Evenness in Molluscan Death Assemblages." *Paleobiology* 33 (1): 1–23. https://doi.org/10.1666/05059.1.

Orth, Robert J., Kenneth L. Heck, and Jacques van Montfrans. 1984. "Faunal Communities in Seagrass Beds: A Review of the Influence of Plant Structure and Prey Characteristics on Predator-Prey Relationships." *Estuaries* 7 (4): 339–50. https://doi.org/10.2307/1351618.

Pergent-Martini, C., V. Leoni, V. Pasqualini, G.D. Ardizzone, E. Balestri, R. Bedini, A. Belluscio, et al. 2005. "Descriptors of Posidonia Oceanica Meadows: Use and Application." *Ecological Indicators* 5 (3): 213–30. https://doi.org/10.1016/j.ecolind.2005.02.004.

Pergent, G., Gerakaris, V., Sghaier, Y.R., Zakhama-Sraier, R., Fernández Torquemada, Y. & Pergent-Martini, C. 2016. "IUCN Posidonia Oceanica." Posidonia Oceanica (Errata Version Published in 2018). The IUCN Red List of Threatened Species e.T153534A135156882. 2016. https://www.iucnredlist.org/species/153534/135156882#bibliography.

Pergent, Gérard, Christine Pergent-Martini, Aymeric Bein, Marine Dedeken, Pascal Oberti, Antoine Orsini, Jean-François Santucci, and Frederic Short. 2015. "Dynamic of Posidonia Oceanica Seagrass Meadows in the Northwestern Mediterranean: Could Climate Change Be to Blame?" *Comptes Rendus Biologies* 338 (7): 484–93. https://doi.org/10.1016/j.crvi.2015.04.011.

Petersen, Jens Kjerulf, Marianne Holmer, Mette Termansen, and Berit Hasler. 2019. "Nutrient Extraction Through Bivalves." In *Goods and Services of Marine Bivalves*, edited by Aad C Smaal, Joao G Ferreira, Jon Grant, Jens K Petersen, and Øivind Strand, 179–208. Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-96776-9_10.

Pikelj, Kristina, and Mladen Juračić. 2013. "Eastern Adriatic Coast (EAC): Geomorphology and Coastal Vulnerability of a Karstic Coast." *Journal of Coastal Research* 29 (4): 944–57. https://doi.org/10.2112/JCOASTRES-D-12-00136.1.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reich, S. 2014. "Gastropod Associations As a Proxy for Seagrass Vegetation in a Tropical, Carbonate Setting (San Salvador, Bahamas)." *Palaios* 29 (9): 467–82. https://doi.org/10.2110/palo.2013.071.

Ricart, Aurora M., Paul H. York, Catherine V. Bryant, Michael A. Rasheed, Daniel Ierodiaconou, and Peter I. Macreadie. 2020. "High Variability of Blue Carbon Storage in Seagrass Meadows at the Estuary Scale." *Scientific Reports* 10 (1): 1–12. https://doi.org/10.1038/s41598-020-62639-y.

Russo, Giovanni Fulvio, Simonetta Fraschetti, and Antonio Terlizzi. 2002. "Population Ecology and Production of Bittium Latreillii (Gastropoda, Cerithidae) in a Posidonia Oceanica Seagrass Bed." *Italian Journal of Zoology* 69 (3): 215–22. https://doi.org/10.1080/11250000209356462.

Ružić, Igor, Čedomir Benac, Ivan Marović, Suzana Ilić, Čedomir Benac, and Ilic Suzana. 2015. "A Stability Assessment of Coastal Cliffs Using Digital Imagery." *Acta Geotechnica Slovenica* 12 (2): 25–35. https://doi.org/10.1007/s11420-014-9422-8.

Ružić, Igor, Sanja Dugonjić Jovančević, Čedomir Benac, and Nino Krvavica. 2019. "Assessment of the Coastal Vulnerability Index in an Area of Complex Geological Conditions on the Krk Island, Northeast Adriatic Sea." *Geosciences (Switzerland)* 9 (5). https://doi.org/10.3390/geosciences9050219.

Salafsky, N, D Salzer, A J Stattersfield, C Hilton-Taylor, R Neugarten, S H M Butchart, B Collen, et al. 2008. "A Standard Lexicon for Biodiversity Conservation: Unified Classifications of Threats and Actions." *Conservation Biology : The Journal of the Society for Conservation Biology*. https://doi.org/10.1111/j.1523-1739.2008.00937.x.

Soga, Masashi, and Kevin J. Gaston. 2018. "Shifting Baseline Syndrome: Causes, Consequences, and Implications." *Frontiers in Ecology and the Environment* 16 (4): 222–30. https://doi.org/10.1002/fee.1794.

Tomašových, Adam, and Susan M. Kidwell. 2009. "Fidelity of Variation in Species Composition and Diversity Partitioning by Death Assemblages: Time-Averaging Transfers Diversity from Beta to Alpha Levels." *Paleobiology* 35 (1): 94–118. https://doi.org/10.1666/08024.1.

———. 2010a. "Predicting the Effects of Increasing Temporal Scale on Species Composition, Diversity, and Rank-Abundance Distributions." *Paleobiology* 36 (4): 672–95. https://doi.org/10.1666/08092.1.

———. 2010b. "The Effects of Temporal Resolution on Species Turnover and on Testing Metacommunity Models." *American Naturalist* 175 (5): 587–606. https://doi.org/10.1086/651661.

———. 2011. "Accounting for the Effects of Biological Variability and Temporal Autocorrelation in Assessing the Preservation of Species Abundance." *Paleobiology* 37 (2): 332–54. https://doi.org/10.1666/09506.1.

Trombulak, Stephen C., Kristian S. Omland, Julie A. Robinson, Jeffrey J. Lusk, Thomas L. Fleischner, Glenn Brown, and Meg Domroese.

2004. “Principles of Conservation Biology: Recommended Guidelines for Conservation Literacy from the Education Committee of the Society for Conservation Biology.” *Conservation Biology* 18 (5): 1180–90. https://doi.org/10.1111/j.1523-1739.2004.01851.x.

United Nations Environment Programme Mediterranean Action Plan (UNEP/MAP). 2015. “Adriatic Sea: Ecology (Draft Report).”

Weber, Kristina, and Martin Zuschin. 2013. “Delta-Associated Molluscan Life and Death Assemblages in the Northern Adriatic Sea: Implications for Paleoecology, Regional Diversity and Conservation.” *Palaeogeography, Palaeoclimatology, Palaeoecology* 370: 77–91. https://doi.org/10.1016/j.palaeo.2012.11.021.

Wickham H (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. ISBN 978-3-319-24277-4, https://ggplot2.tidyverse.org

Willis, K. J., and H. J.B. Birks. 2006. “What Is Natural? The Need for a Long-Term Perspective in Biodiversity Conservation.” *Science* 314 (5803): 1261–65. https://doi.org/10.1126/science.1122667.

Zuschin, Martin, and Claudia Ebner. 2015. “Compositional Fidelity of Death Assemblages from a Coral Reef Associated Tidal-Flat and Shallow Subtidal Lagoon in the Northern Red Sea.” *Palaios* 30 (3): 181–91. https://doi.org/http://dx.doi.org/10.2110/palo.2014.032.

Appendix A Species list of study area in systematic arrangement following Bouchet et al. (2017) for the gastropods and Bouchet et al. (2010) for the bivalves. Only one scaphopod specimen was found, *Antalis vulgaris.*

				Death assemblage				Living assemblage			
Class	**Family**	**Genus**	**Species**	**KI2**	**KI3**	**KM1**	**KM2**	**KI2**	**KI3**	**KM1**	**KM2**
Bivalvia	Mytilidae	Modiolula	*Modiolula phaseolina*	1	0	0	0	4	1	0	2
Bivalvia	Mytilidae	Modiolus	*Modiolus barbatus*	3	2	0	3,5	0	1	3	8
Bivalvia	Mytilidae	Musculus	*Musculus costulatus*	2,5	2	0,5	10	16	8	16	17
Bivalvia	Mytilidae	Musculus	*Musculus subpictus*	2	1	2	1,5	29	15	6	11
Bivalvia	Arcidae	Arca	*Arca noae*	0,5	0	0,5	0,5	0	0	0	0
Bivalvia	Arcidae	Barbatia	*Barbatia barbata*	2,5	1	0	0	0	0	0	0
Bivalvia	Noetiidae	Striarca	*Striarca lactea*	10,5	7	7,5	17,5	29	19	3	33
Bivalvia	Anomiidae	Anomia	*Anomia ephippium*	25	39	75,5	65,5	23	6	11	31
Bivalvia	Anomiidae	Pododesmus	*Pododesmus patelliformis*	0	2,5	0	0	0	0	0	0
Bivalvia	Pectinidae	Flexopecten	*Flexopecten hyalinus*	0	1	2	3	3	1	17	12
Bivalvia	Pectinidae	Mimachlamys	*Mimachlamys varia*	1	2,5	0	0,5	0	0	0	0
Bivalvia	Pectinidae	Talochlamys	*Talochlamys multistriata*	0	0	0	0,5	0	0	0	0
Bivalvia	Limidae	Lima	*Lima lima*	0,5	0	0	0	0	0	0	0
Bivalvia	Limidae	Limaria	*Limaria hians*	1	0	0	1	0	1	0	0
Bivalvia	Lucinidae	Ctena	*Ctena decussata*	6	5,5	1	12,5	3	0	0	2
Bivalvia	Lucinidae	Loripes	*Loripes orbiculatus*	0	0	0	0	11	1	25	24
Bivalvia	Lucinidae	Loripinus	*Loripinus fragilis*	1	2,5	4,5	14,5	0	1	0	0
Bivalvia	Lucinidae	Lucinella	*Lucinella divaricata*	0,5	1	4,5	2,5	0	0	0	0
Bivalvia	Trapezidae	Coralliophaga	*Coralliophaga lithophagella*	0	0	0,5	0	0	0	0	0
Bivalvia	Cardiidae	Papillicardium	*Papillicardium papillosum*	0,5	2	7,5	25,5	2	3	3	4
Bivalvia	Cardiidae	Parvicardium	*Parvicardium exiguum*	0	0	3	0	0	0	0	0
Bivalvia	Cardiidae	Parvicardium	*Parvicardium scabrum*	0	0	0	0,5	0	0	0	0
Bivalvia	Cardiidae	Parvicardium	*Parvicardium scriptum*	5	5,5	0,5	3,5	1	0	2	4
Bivalvia	Chamidae	Chama	*Chama gryphoides*	0,5	0	0	0	0	0	0	0
Bivalvia	Chamidae	Pseudochama	*Pseudochama cf.*	0	0	2	0	0	0	0	0
Bivalvia	Chamidae	Pseudochama	*Pseudochama gryphina*	0	0	1	1	0	0	0	0
Bivalvia	Galeommatidae	Galeomma	*Galeomma turtoni*	0,5	0	0	0,5	0	0	0	0
Bivalvia	Lasaeidae	Hemilepton	*Hemilepton nitidum*	0	0	0	0,5	0	0	0	0
Bivalvia	Lasaeidae	Kellia	*Kellia suborbicularis*	0	0,5	0	0	10	5	1	0
Bivalvia	Lasaeidae	Kurtiella	*Kurtiella bidentata*	0,5	0	0	2	0	1	1	0
Bivalvia	Lasaeidae	Tellimya	*Tellimya ferruginosa*	0	0	0,5	0	0	0	0	0
Bivalvia	Tellinidae	Arcopella	*Arcopella balaustina*	0	0	0,5	0,5	2	0	3	10
Bivalvia	Tellinidae	Moerella	*Moerella donacina*	0,5	0	1,5	1	0	0	0	0
Bivalvia	Veneridae	Gouldia	*Gouldia minima*	15	9,5	37,5	108,5	8	14	21	61
Bivalvia	Veneridae	Irus	*Irus irus*	1,5	4	0,5	1	0	1	0	0
Bivalvia	Veneridae	Pitar	*Pitar rudis*	0	0	0	1	0	0	0	2
Bivalvia	Veneridae	Timoclea	*Timoclea ovata*	0	0	0	1	0	0	0	0
Bivalvia	Veneridae	Venus	*Venus casina*	0	0	0	3,5	0	0	0	0
Bivalvia	Veneridae	Venus	*Venus verrucosa*	1,5	1,5	2	4	3	4	1	7
Bivalvia	Hiatellidae	Hiatella	*Hiatella arctica*	21	19	20	45,5	54	12	11	11
Bivalvia	Thraciidae	Thracia	*Thracia distorta*	7,5	3,5	4	7	8	8	4	7
Gastropoda	Patellidae	Patella	*Patella ulyssiponensis*	0	1	0	0	0	0	0	0
Gastropoda	Fissurellidae	Diodora	*Diodora graeca*	0	2	0	1	0	0	0	0
Gastropoda	Fissurellidae	Emarginula	*Emarginula huzardii*	1	1	0	0	0	0	0	0
Gastropoda	Fissurellidae	Emarginula	*Emarginula octaviana*	0	1	0	0	0	0	0	0
Gastropoda	Haliotidae	Haliotis	*Haliotis tuberculata*	0	0	0	0	1	1	0	0
Gastropoda	Scissurellidae	Scissurella	*Scissurella costata*	1	0	0	1	1	0	0	0
Gastropoda	Trochidae	Clanculus	*Clanculus corallinus*	0	3	0	0	0	0	0	0
Gastropoda	Trochidae	Clanculus	*Clanculus cruciatus*	1	3	0	0	0	0	0	0
Gastropoda	Trochidae	Gibbula	*Gibbula ardens*	0	0	2	1	0	0	0	0
Gastropoda	Trochidae	Gibbula	*Gibbula fanulum*	0	0	0	2	0	0	0	0
Gastropoda	Trochidae	Gibbula	*Gibbula guttadauri*	0	1	0	0	0	0	0	0
Gastropoda	Trochidae	Gibbula	*Gibbula turbinoides*	1	0	0	0	0	0	0	0
Gastropoda	Trochidae	Jujubinus	*Jujubinus exasperatus*	4	12	23	25	1	2	1	2
Gastropoda	Trochidae	Jujubinus	*Jujubinus striatus*	4	2	0	0	0	0	0	0
Gastropoda	Trochidae	Steromphala	*Steromphala umbilicaris*	0	0	0	0	0	0	0	1

Gastropoda	Trochidae	Steromphala	*Steromphala varia*	0	2	0	0	0	0	0	0
Gastropoda	Phasianellidae	Tricolia	*Tricolia pullus*	0	1	4	1	8	4	0	0
Gastropoda	Phasianellidae	Tricolia	*Tricolia speciosa*	0	0	0	0	3	2	0	0
Gastropoda	Cerithiidae	Bittium	*Bittium latreillii*	245	160	53	117	23	28	3	3
Gastropoda	Cerithiidae	Bittium	*Bittium reticulatum*	82	75	40	84	11	0	10	2
Gastropoda	Cerithiidae	Cerithium	*Cerithium protractum*	0	0	0	0	1	0	2	1
Gastropoda	Cerithiidae	Cerithium	*Cerithium vulgatum*	6	9	11	19	2	1	1	2
Gastropoda	Epitoniidae	Epitonium	*Epitonium clathrus*	0	1	0	0	0	0	0	0
Gastropoda	Littorinidae	Melarhaphe	*Melarhaphe neritoides*	8	4	0	0	0	0	0	0
Gastropoda	Naticidae	Euspira	*Euspira nitida*	0	0	1	1	17	5	23	14
Gastropoda	Triphoridae	Marshallora	*Marshallora adversa*	1	0	2	6	1	2	2	7
Gastropoda	Triphoridae	Metaxia	*Metaxia metaxa*	1	1	0	0	1	1	0	0
Gastropoda	Triphoridae	Monophorus	*Monophorus perversus*	0	0	0	0	1	0	3	0
Gastropoda	Cerithiopsidae	Cerithiopsis	*Cerithiopsis sp.3*	0	0	0	0	1	1	0	1
Gastropoda	Cerithiopsidae	Cerithiopsis	*Cerithiopsis sp.5*	0	1	0	0	0	0	0	0
Gastropoda	Cerithiopsidae	Cerithiopsis	*Cerithiopsis tubercularis*	1	0	0	3	13	1	0	2
Gastropoda	Rissoidae	Alvania	*Alvania beanii*	2	2	0	3	0	0	0	0
Gastropoda	Rissoidae	Alvania	*Alvania cancellata*	31	20	15	19	29	10	0	0
Gastropoda	Rissoidae	Alvania	*Alvania carinata*	1	0	3	1	0	0	0	0
Gastropoda	Rissoidae	Alvania	*Alvania cimex*	14	8	4	18	2	2	0	0
Gastropoda	Rissoidae	Alvania	*Alvania discors*	0	0	1	0	0	0	0	0
Gastropoda	Rissoidae	Alvania	*Alvania geryonia*	3	5	25	31	11	10	15	9
Gastropoda	Rissoidae	Alvania	*Alvania lactea*	3	0	0	0	0	0	0	0
Gastropoda	Rissoidae	Alvania	*Alvania lineata*	0	0	1	0	0	0	0	0
Gastropoda	Rissoidae	Alvania	*Alvania sp.1*	1	0	0	0	0	0	0	0
Gastropoda	Rissoidae	Crisilla	*Crisilla semistriata*	7	3	2	0	1	1	0	0
Gastropoda	Rissoidae	Manzonia	*Manzonia crassa*	6	0	3	5	0	2	1	0
Gastropoda	Rissoidae	Pusillina	*Pusillina inconspicua*	0	0	2	0	0	0	0	0
Gastropoda	Rissoidae	Pusillina	*Pusillina lineolata*	2	2	1	10	63	34	33	43
Gastropoda	Rissoidae	Pusillina	*Pusillina marginata*	3	3	4	7	0	0	0	0
Gastropoda	Rissoidae	Pusillina	*Pusillina philippi*	5	2	6	2	67	17	7	13
Gastropoda	Rissoidae	Rissoa	*Rissoa rodhensis*	2	2	1	2	5	2	6	7
Gastropoda	Rissoidae	Rissoa	*Rissoa splendida*	17	12	14	20	11	6	14	5
Gastropoda	Rissoidae	Rissoa	*Rissoa violacea*	0	2	0	1	7	1	3	2
Gastropoda	Rissoinidae	Rissoina	*Rissoina bruguieri*	33	32	8	9	47	15	0	4
Gastropoda	Caecidae	Caecum	*Caecum auriculatum*	4	0	1	0	0	0	0	1
Gastropoda	Caecidae	Caecum	*Caecum subannulatum*	1	0	0	1	8	1	8	13
Gastropoda	Caecidae	Caecum	*Caecum trachea*	0	0	2	1	0	0	2	3
Gastropoda	Eulimidae	Eulima	*Eulima glabra*	0	0	0	0	2	2	0	2
Gastropoda	Eulimidae	Parvioris	*Parvioris ibizenca*	0	0	0	0	10	2	2	1
Gastropoda	Eulimidae	Sticteulima	*Sticteulima jeffreysiana*	0	0	0	0	1	0	0	0
Gastropoda	Eulimidae	Vitreolina	*Vitreolina curva*	0	0	0	0	1	0	0	0
Gastropoda	Eulimidae	Vitreolina	*Vitreolina philippi*	0	0	1	0	7	0	2	3
Gastropoda	Calyptraeidae	Crepidula	*Crepidula unguiformis*	0	0	1	1	0	0	0	0
Gastropoda	Granulinidae	Granulina	*Granulina marginata*	0	2	0	0	0	0	0	0
Gastropoda	Nassariidae	Tritia	*Tritia incrassata*	7	4	3	7	2	2	0	1
Gastropoda	Pisaniidae	Pisania	*Pisania striata*	0	1	0	0	0	0	0	0
Gastropoda	Muricidae	Ocinebrina	*Ocinebrina aciculata*	1	0	1	1	1	0	0	0
Gastropoda	Muricidae	Typhinellus	*Typhinellus labiatus*	0	0	0	0	1	0	0	0
Gastropoda	Costellariidae	Pusia	*Pusia tricolor*	3	1	0	0	0	0	0	0
Gastropoda	Horaiclavidae	Haedropleura	*Haedropleura septangularis*	0	0	0	0	1	0	1	1
Gastropoda	Mangeliidae	Mangelia	*Mangelia attenuata*	0	0	0	0	0	0	1	2
Gastropoda	Mangeliidae	Mangelia	*Mangelia costulata*	0	1	0	0	0	0	0	0
Gastropoda	Mangeliidae	Mangelia	*Mangelia sp.4*	0	0	0	0	1	1	3	4
Gastropoda	Mangeliidae	Mangelia	*Mangelia stossiciana*	0	0	2	5	0	0	0	2
Gastropoda	Mangeliidae	Mangelia	*Mangelia vauquelini*	0	0	0	1	0	0	0	0
Gastropoda	Raphitomidae	Cyrillia	*Cyrillia linearis*	4	0	1	1	21	9	4	4
Gastropoda	Raphitomidae	Leufroyia	*Leufroyia concinna*	0	0	1	0	6	2	0	1
Gastropoda	Raphitomidae	Leufroyia	*Leufroyia leufroyi*	1	0	0	0	1	0	1	0
Gastropoda	Raphitomidae	Raphitoma	*Raphitoma cf. locardi*	0	0	0	0	1	0	0	0
Gastropoda	Raphitomidae	Raphitoma	*Raphitoma philberti*	1	0	0	1	1	0	0	1

Gastropoda	Raphitomidae	Raphitoma	*Raphitoma sp.1*	0	1	0	0	0	0	0	0
Gastropoda	Raphitomidae	Raphitoma	*Raphitoma sp.2*	0	1	0	0	0	0	0	0
Gastropoda	Raphitomidae	Raphitoma	*Raphitoma sp.3*	1	0	0	0	0	0	0	0
Gastropoda	Acteonidae	Acteon	*Acteon tornatilis*	0	0	0	0	0	0	1	0
Gastropoda	Rissoellidae	Rissoella	*Rissoella inflata*	0	0	0	0	5	5	1	2
Gastropoda	Tylodinidae	Tylodina	*Tylodina perversa*	0	1	0	0	0	0	0	0
Gastropoda	Retusidae	Retusa	*Retusa truncatula*	1	0	0	2	0	0	0	0
Gastropoda	Haminoeidae	Haminoae	*Haminoae sp.1*	0	0	0	1	0	0	0	0
Gastropoda	Haminoeidae	Roxaniella	*Roxaniella jeffreysi*	0	0	0	0	0	0	1	0
Gastropoda	Haminoeidae	Weinkauffia	*Weinkauffia turgidula*	0	0	1	0	0	0	3	0
Gastropoda	Philinidae	Philine	*Philine catena*	0	0	0	1	0	0	0	0
Gastropoda	Aplysiidae	Aplysia	*Aplysia sp.1*	0	0	1	0	0	0	0	0
Gastropoda	Siphonariidae	Williamia	*Williamia gussoni*	1	2	2	1	0	0	0	0
Gastropoda	Pyramidellidae	Eulimella	*Eulimella acicula*	0	0	1	0	0	0	0	0
Gastropoda	Pyramidellidae	Folinella	*Folinella excavata*	3	0	1	1	0	1	1	0
Gastropoda	Pyramidellidae	Megastomia	*Megastomia conoidea*	0	0	0	2	1	0	3	1
Gastropoda	Pyramidellidae	Megastomia	*Megastomia conspicua*	0	0	0	0	0	1	1	0
Gastropoda	Pyramidellidae	Odostomella	*Odostomella doliolum*	0	0	0	0	1	0	0	0
Gastropoda	Pyramidellidae	Parthenina	*Parthenina monozona*	1	0	0	0	0	0	0	0
Gastropoda	Pyramidellidae	Pyrgiscus	*Pyrgiscus jeffreysi*	0	0	0	2	0	0	0	0
Gastropoda	Pyramidellidae	Turbonilla	*Turbonilla acutissima*	0	0	0	1	0	0	0	0
Polyplacophora	Leptochitonidae	Leptochiton	*Leptochiton bedullii*	0	0	0,25	0	0	0	0	0
Polyplacophora	Leptochitonidae	Lepidopleurus	*Lepidopleurus cajetanus*	0,125	0,125	0,125	0	2	0	0	0
Polyplacophora	Chitonidae	Rhyssoplax	*Rhyssoplax corallina*	0,125	0	0	0	0	0	0	0
Polyplacophora	Chitonidae	Rhyssoplax	*Rhyssoplax olivacea*	0,375	0,125	0,5	0	0	0	0	0
Polyplacophora	Callochitonidae	Callochiton	*Callochiton septemvalvis*	0,125	0	0,125	0	1	0	0	2
Polyplacophora	Tonicellidae	Lepidochitona	*Lepidochitona caprearum*	0	0,125	0	0	0	0	0	0
Polyplacophora	Acanthochitonidae	Acanthochitona	*Acanthochitona fascicularis*	0,125	0,5	0,375	0,375	0	0	0	1
Scaphopoda	Dentaliidae	Antalis	*Antalis vulgaris*	0	0	0	0	1	0	0	0

Appendix B1 Krk (KM) living and death assemblage species list ranked (R) by abundance. Counts represent total uncorrected numbers of specimen (i.e., each fragment and disarticulated element is counted as 1 specimen). Death assemblage species ranks are additionally juxtaposed with their counterpart living ranks (LR), insofar as applicable. **Bold font** highlights live-only species with 10 or more specimens.

Living assemblage					Death assemblage					
Class	Genus	Species	Counts	R	Class	Genus	Species	Counts	R	LR
B	*Gouldia*	*minima*	82	1	G	*Bittium*	*latreillii*	170	1	21
G	*Pusillina*	*lineolata*	76	2	B	*Gouldia*	*minima*	147	2	1
B	***Loripes***	***orbiculatus***	**49**	**3**	B	*Anomia*	*ephippium*	142	3	4
B	*Anomia*	*ephippium*	42	4	G	*Bittium*	*reticulatum*	124	4	16
G	*Euspira*	*nitida*	37	5	B	*Hiatella*	*arctica*	66	5	10
B	*Striarca*	*lactea*	36	6	G	*Alvania*	*geryonia*	56	6	9
B	*Musculus*	*costulatus*	33	7	G	*Jujubinus*	*exasperatus*	48	7	24
B	*Flexopecten*	*hyalinus*	29	8	G	*Rissoa*	*splendida*	34	8	13
G	*Alvania*	*geryonia*	24	9	B	*Papillicardium*	*papillosum*	34	8	20
B	*Hiatella*	*arctica*	22	10	G	*Alvania*	*cancellata*	34	8	
G	*Caecum*	*subannulatum*	21	11	G	*Cerithium*	*vulgatum*	30	9	24
G	*Pusillina*	*philippi*	20	12	B	*Striarca*	*lactea*	26	10	6
G	*Rissoa*	*splendida*	19	13	G	*Alvania*	*cimex*	22	11	
B	*Musculus*	*subpictus*	17	14	B	*Loripinus*	*fragilis*	20	12	
B	*Arcopella*	*balaustina*	13	15	G	*Rissoina*	*bruguieri*	17	13	23
G	*Rissoa*	*rodhensis*	13	15	B	*Ctena*	*decussata*	14	14	25
G	*Bittium*	*reticulatum*	12	16	G	*Pusillina*	*lineolata*	11	15	2
B	*Modiolus*	*barbatus*	11	17	B	*Musculus*	*costulatus*	11	15	7
B	*Thracia*	*distorta*	11	17	B	*Thracia*	*distorta*	11	15	17
G	*Marshallora*	*adversa*	9	18	G	*Pusillina*	*marginata*	11	15	
G	*Cyrillia*	*linearis*	8	19	G	*Tritia*	*incrassata*	10	16	26
B	*Venus*	*verrucosa*	8	19	G	*Pusillina*	*philippi*	8	17	12
G	*Mangelia*	*sp.4*	7	20	G	*Marshallora*	*adversa*	8	17	18
B	*Papillicardium*	*papillosum*	7	20	G	*Manzonia*	*crassa*	8	17	26
G	*Bittium*	*latreillii*	6	21	B	*Lucinella*	*divaricata*	8	17	
B	*Parvicardium*	*scriptum*	6	21	G	*Mangelia*	*stossiciana*	7	18	25
G	*Caecum*	*trachea*	5	22	B	*Venus*	*verrucosa*	6	19	19
G	*Rissoa*	*violacea*	5	22	B	*Flexopecten*	*hyalinus*	5	20	8
G	*Vitreolina*	*philippi*	5	22	B	*Parvicardium*	*scriptum*	5	20	21
G	*Megastomia*	*conoidea*	4	23	G	*Tricolia*	*pullus*	5	20	
G	*Rissoina*	*bruguieri*	4	23	B	*Musculus*	*subpictus*	4	21	14
G	*Cerithium*	*protractum*	3	24	B	*Modiolus*	*barbatus*	4	21	17
G	*Cerithium*	*vulgatum*	3	24	G	*Alvania*	*carinata*	4	21	
G	*Jujubinus*	*exasperatus*	3	24	B	*Venus*	*casina*	4	21	
G	*Mangelia*	*attenuata*	3	24	G	*Rissoa*	*rodhensis*	3	22	15
G	*Monophorus*	*perversus*	3	24	G	*Caecum*	*trachea*	3	22	22
G	*Parvioris*	*ibizenca*	3	24	G	*Cerithiopsis*	*tubercularis*	3	22	25
G	*Rissoella*	*inflata*	3	24	G	*Alvania*	*beanii*	3	22	
G	*Weinkauffia*	*turgidula*	3	24	G	*Gibbula*	*ardens*	3	22	
G	*Callochiton*	*septemvalvis*	2	25	B	*Parvicardium*	*exiguum*	3	22	
G	*Cerithiopsis*	*tubercularis*	2	25	B	*Moerella*	*donacina*	3	22	
B	*Ctena*	*decussata*	2	25	G	*Williamia*	*gussoni*	3	22	
G	*Eulima*	*glabra*	2	25	G	*Euspira*	*nitida*	2	23	5
G	*Haedropleura*	*septangularis*	2	25	B	*Arcopella*	*balaustina*	2	23	15
G	*Mangelia*	*stossiciana*	2	25	G	*Cyrillia*	*linearis*	2	23	19
B	*Modiolula*	*phaseolina*	2	25	G	*Megastomia*	*conoidea*	2	23	23
B	*Pitar*	*rudis*	2	25	G	*Acanthochitona*	*fascicularis*	2	23	26
G	*Acanthochitona*	*fascicularis*	1	26	G	*Folinella*	*excavata*	2	23	26
B	*Acteon*	*tornatilis*	1	26	B	*Kurtiella*	*bidentata*	2	23	26
G	*Roxaniella*	*jeffreysi*	1	26	B	*Arca*	*noae*	2	23	
G	*Caecum*	*auriculatum*	1	26	G	*Crepidula*	*unguiformis*	2	23	
G	*Cerithiopsis*	*sp.3*	1	26	G	*Crisilla*	*semistriata*	2	23	
G	*Folinella*	*excavata*	1	26	G	*Gibbula*	*fanulum*	2	23	
G	*Steromphala*	*umbilicaris*	1	26	B	*Irus*	*irus*	2	23	
B	*Kellia*	*suborbicularis*	1	26	G	*Ocinebrina*	*aciculata*	2	23	
B	*Kurtiella*	*bidentata*	1	26	B	*Pseudochama*	*cf.*	2	23	
G	*Manzonia*	*crassa*	1	26	B	*Pseudochama*	*gryphina*	2	23	
G	*Megastomia*	*conspicua*	1	26	G	*Pusillina*	*inconspicua*	2	23	
G	*Leufroyia*	*concinna*	1	26	G	*Retusa*	*truncatula*	2	23	
G	*Leufroyia*	*leufroyi*	1	26	G	*Pyrgiscus*	*jeffreysi*	2	23	
G	*Raphitoma*	*philberti*	1	26	G	*Caecum*	*subannulatum*	1	24	11
G	*Tritia*	*incrassata*	1	26	G	*Rissoa*	*violacea*	1	24	22
G	*Alvania*	*beanii*			G	*Vitreolina*	*philippi*	1	24	22
G	*Alvania*	*cancellata*			G	*Weinkauffia*	*turgidula*	1	24	24
G	*Alvania*	*carinata*			G	*Callochiton*	*septemvalvis*	1	24	25
G	*Alvania*	*cimex*			B	*Pitar*	*rudis*	1	24	25
G	*Alvania*	*discors*			G	*Caecum*	*auriculatum*	1	24	26
G	*Alvania*	*lactea*			G	*Leufroyia*	*concinna*	1	24	26
G	*Alvania*	*lineata*			G	*Raphitoma*	*philberti*	1	24	26
S	*Antalis*	*vulgaris*			G	*Alvania*	*discors*	1	24	
G	*Aplysia*	*sp.1*			G	*Alvania*	*lineata*	1	24	
B	*Arca*	*noae*			G	*Aplysia*	*sp.*	1	24	
B	*Barbatia*	*barbata*			G	*Rhyssoplax*	*olivacea*	1	24	
G	*Cerithiopsis*	*sp.5*			B	*Coralliophaga*	*lithophagella*	1	24	
B	*Chama*	*gryphoides*			G	*Diodora*	*graeca*	1	24	
G	*Rhyssoplax*	*corallina*			G	*Eulimella*	*acicula*	1	24	
G	*Rhyssoplax*	*olivacea*			B	*Galeomma*	*turtoni*	1	24	
G	*Clanculus*	*corallinus*			G	*Haminoae*	*sp.1*	1	24	
G	*Clanculus*	*cruciatus*			B	*Hemilepton*	*nitidum*	1	24	
B	*Coralliophaga*	*lithophagella*			G	*Leptochiton*	*bedulii*	1	24	
G	*Crepidula*	*unguiformis*			G	*Lepidopleurus*	*cajetanus*	1	24	
G	*Crisilla*	*semistriata*			B	*Limaria*	*hians*	1	24	
G	*Diodora*	*graeca*			G	*Mangelia*	*vauquelini*	1	24	

G	*Emarginula*	*huzardii*			B	*Mimachlamys*	*varia*	1	24	
G	*Emarginula*	*octaviana*			B	*Parvicardium*	*scabrum*	1	24	
G	*Epitonium*	*clathrus*			G	*Philine*	*catena*	1	24	
G	*Eulimella*	*acicula*			G	*Scissurella*	*costata*	1	24	
B	*Galeomma*	*turtoni*			B	*Talochlamys*	*multistriata*	1	24	
G	*Gibbula*	*ardens*			B	*Tellimya*	*ferruginosa*	1	24	
G	*Gibbula*	*fanulum*			B	*Timoclea*	*ovata*	1	24	
G	*Gibbula*	*guttadauri*			G	*Turbonilla*	*acutissima*	1	24	
G	*Gibbula*	*turbinoides*			B	*Loripes*	*orbiculatus*			3
G	*Steromphala*	*varia*			G	*Mangelia*	*sp.4*			20
G	*Granulina*	*marginata*			G	*Cerithium*	*protractum*			24
G	*Haliotis*	*tuberculata*			G	*Mangelia*	*attenuata*			24
G	*Haminoae*	*sp.1*			G	*Monophorus*	*perversus*			24
B	*Hemilepton*	*nitidum*			G	*Parvioris*	*ibizenca*			24
B	*Irus*	*irus*			G	*Rissoella*	*inflata*			24
G	*Jujubinus*	*striatus*			G	*Eulima*	*glabra*			25
G	*Lepidochitona*	*caprearum*			G	*Haedropleura*	*septangularis*			25
G	*Leptochiton*	*bedulii*			B	*Modiolula*	*phaseolina*			25
G	*Lepidopleurus*	*cajetanus*			B	*Acteon*	*tornatilis*			26
B	*Lima*	*lima*			G	*Roxaniella*	*jeffreysi*			26
B	*Limaria*	*hians*			G	*Cerithiopsis*	*sp.3*			26
B	*Loripinus*	*fragilis*			G	*Steromphala*	*umbilicaris*			26
B	*Lucinella*	*divaricata*			B	*Kellia*	*suborbicularis*			26
G	*Mangelia*	*costulata*			G	*Megastomia*	*conspicua*			26
G	*Mangelia*	*vauquelini*			G	*Leufroyia*	*leufroyi*			26
G	*Melarhaphe*	*neritoides*			G	*Alvania*	*lactea*			
G	*Metaxia*	*metaxa*			S	*Antalis*	*vulgaris*			
B	*Mimachlamys*	*varia*			B	*Barbatia*	*barbata*			
G	*Ocinebrina*	*aciculata*			G	*Cerithiopsis*	*sp.5*			
G	*Odostomella*	*doliolum*			B	*Chama*	*gryphoides*			
G	*Parthenina*	*monozona*			G	*Rhyssoplax*	*corallina*			
B	*Parvicardium*	*exiguum*			G	*Clanculus*	*corallinus*			
B	*Parvicardium*	*scabrum*			G	*Clanculus*	*cruciatus*			
G	*Patella*	*ulyssiponensis*			G	*Emarginula*	*huzardii*			
G	*Philine*	*catena*			G	*Emarginula*	*octaviana*			
G	*Pisania*	*striata*			G	*Epitonium*	*clathrus*			
B	*Pododesmus*	*patelliformis*			G	*Gibbula*	*guttadauri*			
B	*Pseudochama*	*cf.*			G	*Gibbula*	*turbinoides*			
B	*Pseudochama*	*gryphina*			G	*Steromphala*	*varia*			
G	*Pusia*	*tricolor*			G	*Granulina*	*marginata*			
G	*Pusillina*	*inconspicua*			G	*Haliotis*	*tuberculata*			
G	*Pusillina*	*marginata*			G	*Jujubinus*	*striatus*			
G	*Raphitoma*	*cf locardi*			G	*Lepidochitona*	*caprearum*			
G	*Raphitoma*	*sp.1*			B	*Lima*	*lima*			
G	*Raphitoma*	*sp.2*			G	*Mangelia*	*costulata*			
G	*Raphitoma*	*sp.3*			G	*Melarhaphe*	*neritoides*			
G	*Retusa*	*truncatula*			G	*Metaxia*	*metaxa*			
G	*Alvania*	*sp.1*			G	*Odostomella*	*doliolum*			
G	*Scissurella*	*costata*			G	*Parthenina*	*monozona*			
G	*Sticteulima*	*jeffreysiana*			G	*Patella*	*ulyssiponensis*			
B	*Talochlamys*	*multistriata*			G	*Pisania*	*striata*			
B	*Tellimya*	*ferruginosa*			B	*Pododesmus*	*patelliformis*			
B	*Moerella*	*donacina*			G	*Pusia*	*tricolor*			
B	*Timoclea*	*ovata*			G	*Raphitoma*	*cf locardi*			
G	*Tricolia*	*pullus*			G	*Raphitoma*	*sp.1*			
G	*Tricolia*	*speciosa*			G	*Raphitoma*	*sp.2*			
G	*Turbonilla*	*acutissima*			G	*Raphitoma*	*sp.3*			
G	*Pyrgiscus*	*jeffreysi*			G	*Alvania*	*sp.1*			
G	*Tylodina*	*perversa*			G	*Sticteulima*	*jeffreysiana*			
G	*Typhinellus*	*labiatus*			G	*Tricolia*	*speciosa*			
B	*Venus*	*casina*			G	*Tylodina*	*perversa*			
G	*Vitreolina*	*curva*			G	*Typhinellus*	*labiatus*			
G	*Williamia*	*gussoni*			G	*Vitreolina*	*curva*			

Appendix B2 Kormati (KI) living and death assemblage species list ranked (R) by abundance. Counts represent total uncorrected numbers of specimen (i.e., each fragment and disarticulated element is counted as 1 specimen). Death assemblage species ranks are additionally juxtaposed with their counterpart living ranks (LR), insofar as applicable. **Bold font** indicates live-only species with 10 or more specimens.

Living assemblage					Death assemblage					
Class	Genus	Species	Counts	R	Class	Genus	Species	Counts	R	LR
G	*Pusillina*	*lineolata*	97	1	G	*Bittium*	*latreillii*	405	1	5
G	*Pusillina*	*philippi*	84	2	G	*Bittium*	*reticulatum*	157	2	19
B	*Hiatella*	*arctica*	66	3	G	*Rissoina*	*bruguieri*	65	3	4
G	*Rissoina*	*bruguieri*	62	4	B	*Anomia*	*ephippium*	64	4	10
G	*Bittium*	*latreillii*	51	5	G	*Alvania*	*cancellata*	51	5	8
B	*Striarca*	*lactea*	48	6	B	*Hiatella*	*arctica*	40	6	3
B	*Musculus*	*subpictus*	44	7	G	*Rissoa*	*splendida*	29	7	14
G	*Alvania*	*cancellata*	39	8	B	*Gouldia*	*minima*	25	8	12
G	*Cyrillia*	*linearis*	30	9	G	*Alvania*	*cimex*	22	9	25
B	*Anomia*	*ephippium*	29	10	B	*Striarca*	*lactea*	18	10	6
B	*Musculus*	*costulatus*	24	11	G	*Jujubinus*	*exasperatus*	16	11	26
G	***Euspira***	***nitida***	**22**	**12**	G	*Cerithium*	*vulgatum*	15	12	26

B	*Gouldia*	*minima*	22	12
G	*Alvania*	*geryonia*	21	13
G	*Rissoa*	*splendida*	17	14
B	*Thracia*	*distorta*	16	15
B	*Kellia*	*suborbicularis*	15	16
G	*Cerithiopsis*	*tubercularis*	14	17
B	***Loripes***	***orbiculatus***	**12**	**18**
G	***Parvioris***	***ibizenca***	**12**	**18**
G	*Tricolia*	*pullus*	12	18
G	*Bittium*	*reticulatum*	11	19
G	***Rissoella***	***inflata***	**10**	**20**
G	*Caecum*	*subannulatum*	9	21
G	*Leufroyia*	*concinna*	8	22
G	*Rissoa*	*violacea*	8	22
G	*Rissoa*	*rodhensis*	7	23
B	*Venus*	*verrucosa*	7	23
G	*Vitreolina*	*philippi*	7	23
B	*Modiolula*	*phaseolina*	5	24
B	*Papillicardium*	*papillosum*	5	24
G	*Tricolia*	*speciosa*	5	24
G	*Alvania*	*cimex*	4	25
G	*Eulima*	*glabra*	4	25
B	*Flexopecten*	*hyalinus*	4	25
G	*Tritia*	*incrassata*	4	25
G	*Cerithium*	*vulgatum*	3	26
B	*Ctena*	*decussata*	3	26
G	*Jujubinus*	*exasperatus*	3	26
G	*Marshallora*	*adversa*	3	26
B	*Arcopella*	*balaustina*	2	27
G	*Cerithiopsis*	*sp.3*	2	27
G	*Crisilla*	*semistriata*	2	27
G	*Haliotis*	*tuberculata*	2	27
G	*Lepidopleurus*	*cajetanus*	2	27
G	*Mangelia*	*sp.4*	2	27
G	*Manzonia*	*crassa*	2	27
G	*Metaxia*	*metaxa*	2	27
S	*Antalis*	*vulgaris*	1	28
G	*Callochiton*	*septemvalvis*	1	28
G	*Cerithium*	*protractum*	1	28
G	*Folinella*	*excavata*	1	28
G	*Haedropleura*	*septangularis*	1	28
B	*Irus*	*irus*	1	28
B	*Kurtiella*	*bidentata*	1	28
B	*Limaria*	*hians*	1	28
B	*Loripinus*	*fragilis*	1	28
G	*Megastomia*	*conoidea*	1	28
G	*Megastomia*	*conspicua*	1	28
B	*Modiolus*	*barbatus*	1	28
G	*Monophorus*	*perversus*	1	28
G	*Ocinebrina*	*aciculata*	1	28
G	*Odostomella*	*doliolum*	1	28
B	*Parvicardium*	*scriptum*	1	28
G	*Raphitoma*	*cf locardi*	1	28
G	*Leufroyia*	*leufroyi*	1	28
G	*Raphitoma*	*philberti*	1	28
G	*Scissurella*	*costata*	1	28
G	*Sticteulima*	*jeffreysiana*	1	28
G	*Typhinellus*	*labiatus*	1	28
G	*Vitreolina*	*curva*	1	28
G	*Acanthochitona*	*fascicularis*		
B	*Acteon*	*tornatilis*		
G	*Alvania*	*beanii*		
G	*Alvania*	*carinata*		
G	*Alvania*	*discors*		
G	*Alvania*	*lactea*		
G	*Alvania*	*lineata*		
G	*Aplysia*	*sp.1*		
B	*Arca*	*noae*		
G	*Roxaniella*	*jeffreysi*		
B	*Barbatia*	*barbata*		
G	*Caecum*	*auriculatum*		
G	*Caecum*	*trachea*		
G	*Cerithiopsis*	*sp.5*		
B	*Chama*	*gryphoides*		
G	*Rhyssoplax*	*corallina*		
G	*Rhyssoplax*	*olivacea*		
G	*Clanculus*	*corallinus*		
G	*Clanculus*	*cruciatus*		
B	*Coralliophaga*	*lithophagella*		
G	*Crepidula*	*unguiformis*		
G	*Diodora*	*graeca*		
G	*Emarginula*	*huzardii*		
G	*Emarginula*	*octaviana*		
G	*Epitonium*	*clathrus*		
G	*Eulimella*	*acicula*		
B	*Galeomma*	*turtoni*		
G	*Gibbula*	*ardens*		
G	*Gibbula*	*fanulum*		
G	*Gibbula*	*guttadauri*		
G	*Gibbula*	*turbinoides*		
G	*Steromphala*	*umbilicaris*		
G	*Steromphala*	*varia*		
G	*Granulina*	*marginata*		
G	*Haminoae*	*sp.1*		
B	*Hemilepton*	*nitidum*		

B	*Thracia*	*distorta*	12	13	15
B	*Ctena*	*decussata*	12	13	26
G	*Melarhaphe*	*neritoides*	12*	13	
G	*Tritia*	*incrassata*	11	14	25
B	*Parvicardium*	*scriptum*	11	14	28
G	*Crisilla*	*semistriata*	10	15	27
G	*Alvania*	*geryonia*	8	16	13
G	*Pusillina*	*philippi*	7	17	2
G	*Manzonia*	*crassa*	6	18	27
B	*Irus*	*irus*	6	18	28
G	*Jujubinus*	*striatus*	6	18	
G	*Pusillina*	*marginata*	6	18	
B	*Musculus*	*costulatus*	5	19	11
B	*Modiolus*	*barbatus*	5	19	28
G	*Pusillina*	*lineolata*	4	20	1
G	*Cyrillia*	*linearis*	4	20	9
G	*Rissoa*	*rodhensis*	4	20	23
B	*Venus*	*verrucosa*	4	20	23
B	*Loripinus*	*fragilis*	4	20	28
G	*Alvania*	*beanii*	4	20	
B	*Barbatia*	*barbata*	4	20	
G	*Caecum*	*auriculatum*	4	20	
G	*Clanculus*	*cruciatus*	4	20	
B	*Mimachlamys*	*varia*	4	20	
G	*Pusia*	*tricolor*	4	20	
B	*Musculus*	*subpictus*	3	21	7
B	*Papillicardium*	*papillosum*	3	21	24
G	*Folinella*	*excavata*	3	21	28
G	*Alvania*	*lactea*	3	21	
G	*Clanculus*	*corallinus*	3	21	
B	*Pododesmus*	*patelliformis*	3	21	
G	*Williamia*	*gussoni*	3	21	
G	*Rissoa*	*violacea*	2	22	22
G	*Lepidopleurus*	*cajetanus*	2	22	27
G	*Metaxia*	*metaxa*	2	22	27
G	*Acanthochitona*	*fascicularis*	2	22	
G	*Rhyssoplax*	*olivacea*	2	22	
G	*Diodora*	*graeca*	2	22	
G	*Emarginula*	*huzardii*	2	22	
G	*Steromphala*	*varia*	2	22	
G	*Granulina*	*marginata*	2	22	
B	*Lucinella*	*divaricata*	2	22	
B	*Kellia*	*suborbicularis*	1	23	16
G	*Cerithiopsis*	*tubercularis*	1	23	17
G	*Tricolia*	*pullus*	1	23	18
G	*Caecum*	*subannulatum*	1	23	21
B	*Modiolula*	*phaseolina*	1	23	24
B	*Flexopecten*	*hyalinus*	1	23	25
G	*Marshallora*	*adversa*	1	23	26
G	*Callochiton*	*septemvalvis*	1	23	28
B	*Kurtiella*	*bidentata*	1	23	28
B	*Limaria*	*hians*	1	23	28
G	*Ocinebrina*	*aciculata*	1	23	28
G	*Leufroyia*	*leufroyi*	1	23	28
G	*Raphitoma*	*philberti*	1	23	28
G	*Scissurella*	*costata*	1	23	28
G	*Alvania*	*carinata*	1	23	
B	*Arca*	*noae*	1	23	
G	*Cerithiopsis*	*sp.5*	1	23	
B	*Chama*	*gryphoides*	1	23	
G	*Rhyssoplax*	*corallina*	1	23	
G	*Emarginula*	*octaviana*	1	23	
G	*Epitonium*	*clathrus*	1	23	
B	*Galeomma*	*turtoni*	1	23	
G	*Gibbula*	*guttadauri*	1	23	
G	*Gibbula*	*turbinoides*	1	23	
G	*Lepidochitona*	*caprearum*	1	23	
B	*Lima*	*lima*	1	23	
G	*Mangelia*	*costulata*	1	23	
G	*Parthenina*	*monozona*	1	23	
G	*Patella*	*ulyssiponensis*	1	23	
G	*Pisania*	*striata*	1	23	
G	*Raphitoma*	*sp.1*	1	23	
G	*Raphitoma*	*sp.2*	1	23	
G	*Raphitoma*	*sp.3*	1	23	
G	*Retusa*	*truncatula*	1	23	
G	*Alvania*	*sp.1*	1	23	
B	*Moerella*	*donacina*	1	23	
G	*Tylodina*	*perversa*	1	23	
G	*Euspira*	*nitida*			12
B	*Loripes*	*orbiculatus*			18
G	*Parvioris*	*ibizenca*			18
G	*Rissoella*	*inflata*			20
G	*Leufroyia*	*concinna*			22
G	*Vitreolina*	*philippi*			23
G	*Tricolia*	*speciosa*			24
G	*Eulima*	*glabra*			25
B	*Arcopella*	*balaustina*			27
G	*Cerithiopsis*	*sp.3*			27
G	*Haliotis*	*tuberculata*			27
G	*Mangelia*	*sp.4*			27
S	*Antalis*	*vulgaris*			28
G	*Cerithium*	*protractum*			28
G	*Haedropleura*	*septangularis*			28
G	*Megastomia*	*conoidea*			28

G	*Jujubinus*	*striatus*	G	*Megastomia*	*conspicua*	28
G	*Lepidochitona*	*caprearum*	G	*Monophorus*	*perversus*	28
G	*Leptochiton*	*bedulii*	G	*Odostomella*	*doliolum*	28
B	*Lima*	*lima*	G	*Raphitoma*	*cf locardi*	28
B	*Lucinella*	*divaricata*	G	*Sticteulima*	*jeffreysiana*	28
G	*Mangelia*	*attenuata*	G	*Typhinellus*	*labiatus*	28
G	*Mangelia*	*costulata*	G	*Vitreolina*	*curva*	28
G	*Mangelia*	*stossiciana*	B	*Acteon*	*tornatilis*	
G	*Mangelia*	*vauquelini*	G	*Alvania*	*discors*	
G	*Melarhaphe*	*neritoides*	G	*Alvania*	*lineata*	
B	*Mimachlamys*	*varia*	G	*Aplysia*	*sp.1*	
G	*Parthenina*	*monozona*	G	*Roxaniella*	*jeffreysi*	
B	*Parvicardium*	*exiguum*	G	*Caecum*	*trachea*	
B	*Parvicardium*	*scabrum*	B	*Coralliophaga*	*lithophagella*	
G	*Patella*	*ulyssiponensis*	G	*Crepidula*	*unguiformis*	
G	*Philine*	*catena*	G	*Eulimella*	*acicula*	
G	*Pisania*	*striata*	G	*Gibbula*	*ardens*	
B	*Pitar*	*rudis*	G	*Gibbula*	*fanulum*	
B	*Pododesmus*	*patelliformis*	G	*Steromphala*	*umbilicaris*	
B	*Pseudochama*	*cf.*	G	*Haminoae*	*sp.1*	
B	*Pseudochama*	*gryphina*	B	*Hemilepton*	*nitidum*	
G	*Pusia*	*tricolor*	G	*Leptochiton*	*bedulii*	
G	*Pusillina*	*inconspicua*	G	*Mangelia*	*attenuata*	
G	*Pusillina*	*marginata*	G	*Mangelia*	*stossiciana*	
G	*Raphitoma*	*sp.1*	G	*Mangelia*	*vauquelini*	
G	*Raphitoma*	*sp.2*	B	*Parvicardium*	*exiguum*	
G	*Raphitoma*	*sp.3*	B	*Parvicardium*	*scabrum*	
G	*Retusa*	*truncatula*	G	*Philine*	*catena*	
G	*Alvania*	*sp.1*	B	*Pitar*	*rudis*	
B	*Talochlamys*	*multistriata*	B	*Pseudochama*	*cf.*	
B	*Tellimya*	*ferruginosa*	B	*Pseudochama*	*gryphina*	
B	*Moerella*	*donacina*	G	*Pusillina*	*inconspicua*	
B	*Timoclea*	*ovata*	B	*Talochlamys*	*multistriata*	
G	*Turbonilla*	*acutissima*	B	*Tellimya*	*ferruginosa*	
G	*Pyrgiscus*	*jeffreysi*	B	*Timoclea*	*ovata*	
G	*Tylodina*	*perversa*	G	*Turbonilla*	*acutissima*	
B	*Venus*	*casina*	G	*Pyrgiscus*	*jeffreysi*	
G	*Weinkauffia*	*turgidula*	B	*Venus*	*casina*	
G	*Williamia*	*gussoni*	G	*Weinkauffia*	*turgidula*	