Unrecognized loss of seagrass communities based on molluscan death assemblages: historic baseline shift in tropical Gulf of Aqaba, Red Sea

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ABSTRACT: Anthropogenic stresses on the naturally oligotrophic Gulf of Aqaba over the last 50 yr are suspected to have had a strong impact on biota, but the status of benthic fauna on the extensive soft-sediment seafloors is unknown. This study represents the first research on possible anthropogenic impacts on benthic marine fauna other than corals in the Gulf of Aqaba, a region of exceptional biodiversity. Comparing the species and functional-group composition of the living bivalve community to dead-shell assemblages from the modern seabed (top 5 cm) at 15 and 30 m water depth, both proximal and distal to historic point sources of nutrients, reveals that the ecological baseline has shifted. Live–dead discordance is strongest in the area of former sewage outfall and fish farm operations where seagrass is now functionally absent, but molluscan trophic structure has changed significantly even at distal sites where seagrass is still moderately abundant. Chemosymbiont-bearing lucinid bivalves specialized to sandy seagrass dominate death assemblages but are scarce to absent in living assemblages, which are dominated instead by facultative deposit-feeding bivalves which prefer muddy sand or muddy seagrass, consistent with organic enrichment. Seagrass habitat has thus changed qualitatively even where it persists, and sites of seagrass loss have not recovered despite cessation of major pollution ≥10 yr ago. Although shells of dead-only species require geological age-dating to definitively establish human drivers, the documentation of significant habitat change and trophic restructuring makes a powerful case for adoption of paleontological analysis by environmental managers and conservation biologists.

KEY WORDS: Live–dead analysis · Bivalves · Anthropogenic modification · Paleoecology · Gulf of Aqaba · Eutrophication

INTRODUCTION

Human stresses on marine ecosystems are diverse, ranging from exploitation of species to climate change, and have been accelerating (Halpern et al. 2008, Doney et al. 2012). However, in most regions these stresses started many decades or centuries ago, usually long before any biological survey, and few areas have been monitored for more than the last few decades (e.g. Jackson et al. 2001, Kittinger et al. 2014, Kidwell 2015, Kosnik & Kowalewski 2016). In the absence of data acquired prior to human stresses, the extent of change, including local extinctions, is likely to be underestimated, as are the magnitude and types of efforts that might be required to restore a target taxon, community, or ecosystem to a more natural baseline. Such information gaps place a premium on approaches that can retroactively assess significant ecological change.

Skeletal and other biological remains from past generations, acquired from sediment cores or from surficial time-averaged 'death assemblages', are in-

creasingly appreciated as a basis for assessing whether the current state is outside the range of natural variability, and the direction and timing of significant past shifts (Rick & Lockwood 2013, Gallmetzer et al. 2017). Meta-analysis and modeling indicate that naturally time-averaged molluscan death assemblages from soft-sediment seafloors provide accurate samples of the average long-term composition and community structure of the local 'living assemblage' in natural settings, due to the summing of seasonal and inter-annual variability (Peterson 1977, Kidwell & Tomasovych 2013). Importantly, poor 'live–dead agreement' in species composition and abundance is limited almost exclusively to settings with known cultural stress(es), such as eutrophication or bottom-trawling: species or functional groups occurring 'dead-only' or disproportionately abundant as dead shells reflect past states, not dead shells transported from distant sources; taxa occurring 'alive-only' or more abundant alive than dead represent the relatively new, current state, not species with poor preservation (Kidwell 2007, 2008, Kidwell & Tomasovych 2013 and references therein, Weber & Zuschin 2013, Leshno et al. 2015). Only anthropogenic stress seems to be sufficiently strong and persistent to create significant live–dead discordance; the ecological change must also be recent relative to local rates of dead-shell burial and disintegration.

We used this approach to test for ecological change associated with cultural development in the northern Gulf of Aqaba, a region of exceptional biological, touristic, and economic importance (Loya 2004). Arid conditions restricted dense settlement and other development of the watershed until the 1950s. Sediment, nutrient, and pollution inputs have all increased since then: sewage run-off from Eilat was significant during the 1980s and 1990s (ceased in 1995) and commercial fish cages operated from 1995 to 2008, both focused at the mouth of the Wadi Arava (Kinnet canal) (Atkinson et al. 2001). We are unaware of any commercial exploitation of marine resources or direct stressors other than the fish cages. Water quality and coral reefs along the Israeli coastline south of Eilat (see Fig. 1) have been monitored since 2003 (Bongiorni et al. 2003, Wielgus et al. 2003, Bahartan et al. 2010), but these aspects of the Gulf ecosystem were suspected to have already shifted away from their natural ecological baselines, perhaps significantly (Loya 2004). In contrast, the past and present status of macrobenthic communities in the soft-sedimentary seafloors remain largely unstudied (Edelman-Furstenberg & Faershtein 2010), despite constituting the majority of the Gulf shelf ecosystem, and the status of

seagrass meadows is of particular concern (Winters et al. 2017).

Our analysis is the first test of cultural impacts on soft-sedimentary communities in the Gulf. Eutrophication is known elsewhere to decrease seagrass habitat via the attenuation of light by elevated planktonic populations (Burkholder et al. 2007), and to shift benthos to a more detritus-based and/or hypoxia-tolerant community owing to increased organic supply (e.g. Pearson & Rosenberg 1978, Diaz & Rosenberg 1995, Borja et al. 2000, Rossi et al. 2015). Anthropogenic eutrophication can leave an especially clear signal of live–dead discordance in the relative abundance of molluscan species and functional groups (Kidwell 2007, Ferguson & Miller 2007, Ferguson 2008, Korpanty & Kelley 2014, Leshno et al. 2015). The discordance documented in our samples indicates that bivalve communities of the Gulf of Aqaba have indeed changed significantly, with an almost total loss of seagrass near the former fish farms and a decline in sandy seagrass habitat and trophic restructuring across the studied area, consistent with organic enrichment. These significant changes could not have been recognized from living assemblages alone, and have important implications for conservation and management.

MATERIALS AND METHODS

Field work

Four study sites along the northern coastline of the Gulf at 15 and 30 m were sampled: 2 sites near the mouth of Wadi Arava, close to suspected point-sources of nutrients and other stress (former fish farm Sites FF15 and FF30), and 2 sites offshore of the Dan Hotel, distal to those point sources (DAN15 and DAN30) (Fig. 1). Each site was sampled 6 times over 1.5 yr (fall 2012 through winter 2014) for both living and death assemblages (Table 1). Fish farm seafloors were unvegetated, whereas seagrass was moderately abundant at DAN30 (20 to 60% by visual estimate) and had maximum abundance at DAN15 (>80%). This range is consistent with Winters et al. (2017). The sediment was muddy sand at all sites, varying from 10 to 35 weight-% particles <63 μm (Table 1).

During each visit, at least 3 spatially replicate samples were taken from the upper 5 cm of the seabed by SCUBA divers using a metal quadrat (40 × 30 × 5 cm), a common method in live–dead analysis (Kidwell 2013). As expected from other shallow marine set-
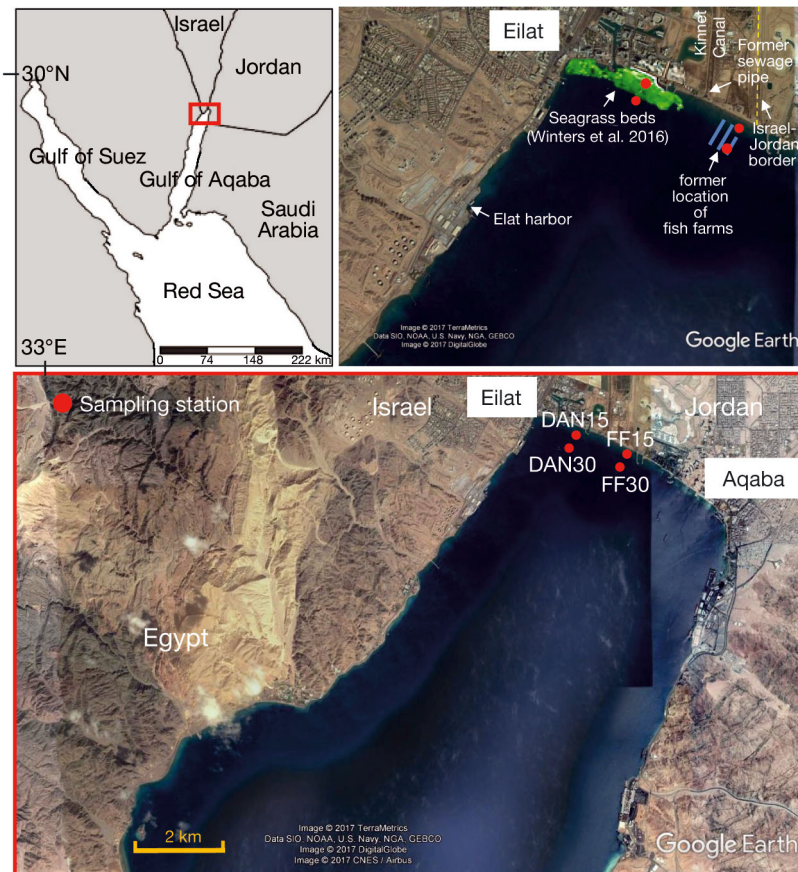
Fig. 1. Study sites in 15 and 30 m water near the Dan Hotel (DAN) and former fish farm (FF) area on the continental shelf of the Gulf of Aqaba near Eilat

live individuals. For death assemblages, all valves retaining at least one-half of their hinge line were counted, using a maximum-number-of-individuals protocol that assumes that each valve comes from a different living individual (Gilinsky & Bennington 1994). Taxonomic identifications followed regional authorities (Sharabati 1984, Oliver 1992, Bosch et al. 1995, Dijkstra & Knudsen 1998, Zuschin & Oliver 2003, Edelman-Furstenberg & Faershtein 2010, Huber 2010). Collections of live-collected and dead bivalves are archived at the Geological Survey of Israel.

To evaluate the ecological significance of live–dead discordance in species composition, each species was assigned to a functional group using information on feeding strategy and life position, mostly using Todd (2001) (see Table A1 in the Appendix). Species' habitat preferences draw on primary reports from the Gulf (mostly Mastaller 1979), elsewhere in the Red Sea (mostly Zuschin & Oliver 2003), and other parts of the Indo-Pacific Province (Table A1).

tings, dead shells were abundant but the density of living bivalves was extremely low (dead:live ratio ~10:1). To acquire statistically robust samples of live molluscs, quadrat samples were augmented by triplicate hauling of a small dredge (45 × 60 × 8 cm) along 30 m transects parallel to shore (Table 1), analogous to other studies (e.g. Staff et al. 1986). Supplementary dredging proved important: each quadrat yielded a mean (±SE) of only 6 ± 1 live bivalves >2 mm, contrasting with 37 ± 4 dredge^{-1} (Table 1). The pooled sample size site^{-1} visit^{-1} (~100 adult ind.) thus exceeded the minimum 20 individuals recommended for both live and dead samples (Kidwell 2013).

Laboratory analyses

Samples of living and death assemblages were sieved using a 2 mm mesh to focus on adult bivalves (Kidwell 2013), then preserved in ethanol and picked for individuals. Specimens with valves still articulated or with adhering soft tissue were counted as

Data analysis

All samples acquired in a season at a site (spatial replicates; a combination of quadrats and dredges for living assemblages) were pooled to produce site-level data on assemblage composition, as standard in benthic surveys. Species proportional abundances were used to reduce the effects of live–dead differences in raw sample sizes (Table 1).

Multivariate analyses of living and death assemblage composition were performed in PRIMER v.6 (Clarke & Warwick 1994) using site-level data (Table 1). Similarity percentage analysis (SIMPER) identified the taxa most responsible for live–dead differences (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m589p073_supp.pdf). ANOSIM was applied to site-level data (Table 1) to test for differences between sampling sites in living assemblages and in death assemblages (spatial variation in composition), and a similarity profile permutation test (SIMPROF) was applied to test for differences between seasons at each site (site-level

Table 1. Sampling site characteristics, number of spatial replicates site⁻¹ season⁻¹ (q: quadrat; dr: dredge), and number (N) of living (L) and dead (D) bivalve individuals. Dredging was not permitted at DAN15, thus a larger number of quadrat samples were collected. TOC: total organic carbon

Site and water depth (m)	Coordinates	Bottom seafloor type (top 5 cm)	Fall, Dec 2012 (N) L	Fall, Dec 2012 (N) D	Winter, Mar 2013 (N) L	Winter, Mar 2013 (N) D	Spring, May 2013 (N) L	Spring, May 2013 (N) D	Summer, Sep 2013 (N) L	Summer, Sep 2013 (N) D	Fall, Dec 2013 (N) L	Fall, Dec 2013 (N) D	Winter, Mar 2014 (N) L	Winter, Mar 2014 (N) D	Total ind. (all samples) L	Total ind. (all samples) D
DAN15	29° 32.69' N, 34° 57.83' E	Dense *Halophila*, 74% wt sand, 0.4–0.5% TOC	3q (13) 2dr (85)	3q (996)	3q (22)	3q (1141)	3q (29)	3q (1375)	3q (56)	3q (4847)	7q (81)	7q (1237)	10q (76)	3q (1244)	362	10840
DAN30	29° 32.62' N, 34° 57.72' E	Moderate *Halophila*, 66% wt sand, 0.3–0.5% TOC	3q (10) 3dr (92)	3q (579)	3q (19) 3dr (152)	3q (1244)	3q (8) 3dr (249)	3q (1302)	3q (2) 3dr (13)	3q (1333)	3q (2) 3dr (21)	3q (797)	3q (6) 3dr (56)	3q (915)	630	6170
FF15	29° 32.50' N, 34° 57.43' E	Low *Halophila*, 76% wt sand, 0.5% TOC	3q (16) 1dr (25)	3 q (962)	6q (13) 3dr (165)	6q (487)	3q (27) 3dr (134)	3q (1307)	3q (34) 3dr (26)	3q (2258)	3q (11) 3dr (90)	3q (497)	3q (21) 3dr (88)	3q (396)	650	5907
FF30	29° 32.45' N, 34° 57.27' E	Low *Halophila*, 92% wt sand, 0.4–0.5% TOC	3q (15) 3dr (144)	3q (52)	6q (6) 3dr (290)	6q (244)	3q (21) 3dr (184)	3q (314)	3q (20) 3dr (40)	3 (1118)	3q (2) 3dr (47)	3q (169)	3q (6) 3dr (110)	3q (487)	885	2384

temporal variation in composition) (see Table S2). We used non-metric multidimensional scaling (NMDS) to ordinate seasonal, site-level samples of living and death assemblages into groups without pre-specifying those groups, using the abundance-based Bray-Curtis similarity coefficient.

For live–dead comparison, we pooled seasonal samples at each site to approximate habitat-level data on living and death assemblages, comparable to other studies (Kidwell 2013) (Table 1). Live–dead discordance was measured using the Jaccard-Chao taxonomic similarity (J-C) index, a sample-size corrected measure of shared species, and Spearman's rank order coefficient (rho), which quantifies similarity in species' relative abundances (and thus community structure), in EstimateS 9.0.0 software and www.wessa.net/rankcorr.wasp, respectively.

RESULTS

Sampling yielded 2527 living and 25301 dead bivalve individuals, representing 161 bivalve taxa (see Table S1 in the Supplement). SIMPER indicated that 83% of observed live–dead difference in the study area was explained by 16 taxa (see Table S1, listed in Table A1 in the Appendix); each constituted ≥1% of living and/or dead individuals and together they comprised 79% of all living and 85% of all dead individuals.

Overall, living assemblages did not vary significantly in composition by season, but did differ among sites (see Table S2). Ordination revealed that living assemblages exhibited greater compositional variation among sites and seasons than death assemblages, being dispersed across a larger area of NMDS space (i.e. higher beta diversity; Fig. 2). The compositions of living and death assemblages were also distinct: neither centroid ('average composition') would fall within the range of the other set of samples. Death assemblages were characterized by abundant chemosymbiont-bearing lucinids (*Ctena divergens* and *Anodontia edentula*; Fig. 2A,B), whereas living assemblages were characterized by a scarcity of those taxa (Fig. 2A,B) and by the dominance of facultative deposit feeders, especially *Abra fragillima* (Fig. 2C) and *Tellina flacca* (Fig. 2D).

Bar graphs (Fig. 3) display live–dead differences for all key taxa by site. At each site, the discordance owes to 2 sets of species, each having distinct feeding modes and substrate preferences. One set of species was disproportionately more abundant alive than dead (black bars in Fig. 3). The most important taxa
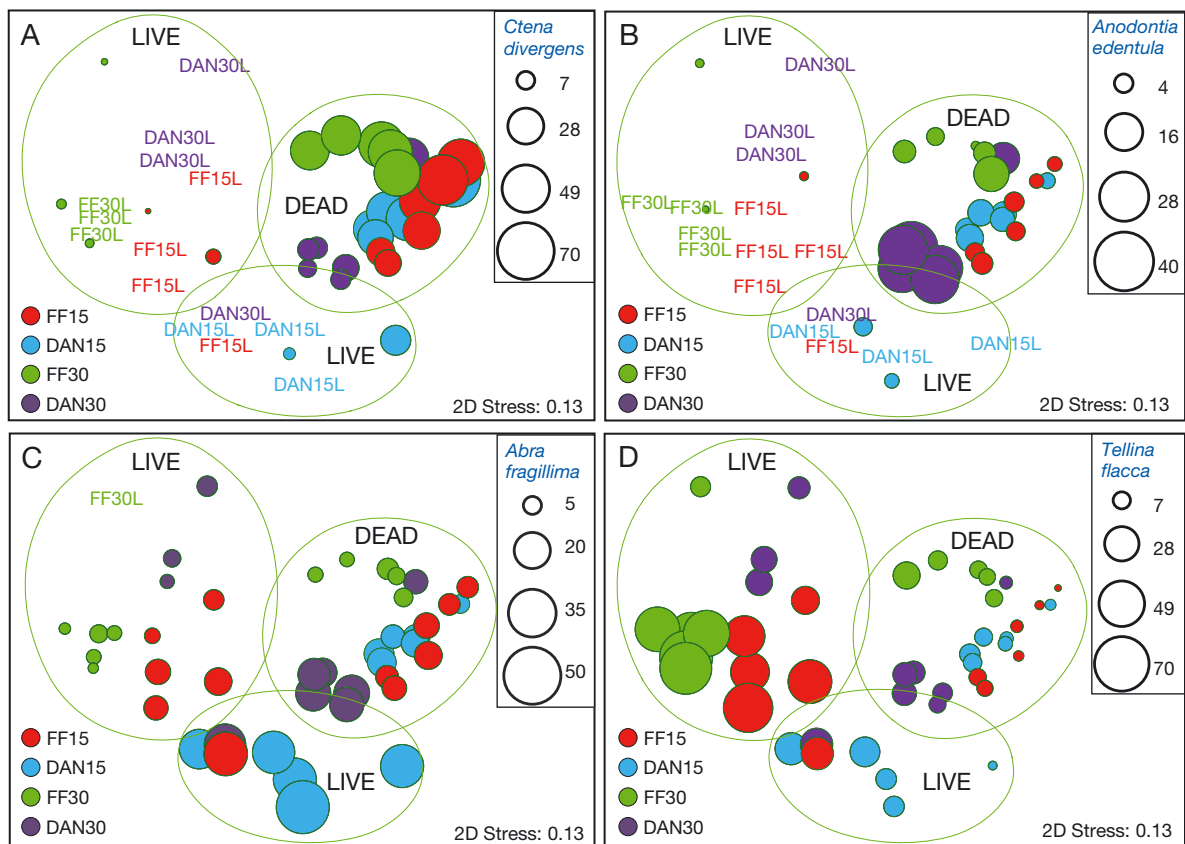
Fig. 2. Variation in living and death assemblage compositions based on non-metric multidimensional scaling (NMDS) using the proportional abundance-based Bray Curtis similarity coefficient. Each point reflects either the living (LIVE, L) or the death (DEAD, D) assemblage from a site (FF15, FF30, DAN15, DAN30) sampled during one season; ellipses enclose samples with ≥35% similarity. Each bubble plot (A–D) displays the proportional abundance of a different key species identified by SIMPER; abundances too small to appear as data points are indicated by site labels

in this set were facultative deposit-feeding tellinids (*T. flacca*, *Arcopagia isseli*), which constituted ~50% of all living individuals at the fish farm sites but fewer than 10% of dead shells. Facultative semelids (*A. fragillima*) and multiple infaunal suspension feeders were also disproportionately abundant alive at most sites.

The second set of species had the opposite polarity, occurring either 'dead-only' or disproportionately more abundant dead than alive. The most dramatic example is the chemosymbiont-bearing bivalve *C. divergens*, which constituted 39% of all dead shells and only 1% of all living individuals. The lucinid *A. edentula* and several infaunal suspension feeders showed a similar pattern (Fig. 3).

The strong live–dead differences in proportional abundance and presence–absence evident in Fig. 3 produces a spectrum of taxonomic similarity values (J-C index) and live–dead rank-order correlations (Spearman rho; Fig. 4). This range is similar to that observed among comparably sampled, habitat-level

live–dead data sets from other open shelves. Live–dead agreement by these measures was highest at DAN15, comparable to datasets from 'pristine' study areas with no known cultural nutrient inputs. Live–dead agreement was intermediate at DAN30 and FF30, comparable to values from study areas with definite cultural nutrient loading. Live–dead agreement was poorest at FF15, comparable to areas near strong point-sources of nutrients or other contaminants.

DISCUSSION

Live-dead discordance arises from ecological change rather than post-mortem bias

The lucinids *Ctena divergens* and *Anodontia edentula*, known to prefer sandy seagrass elsewhere (see Table A1 in the Appendix), dominated the death assemblages at all 4 sites but were essentially absent in living assemblages. In contrast, facultative deposit
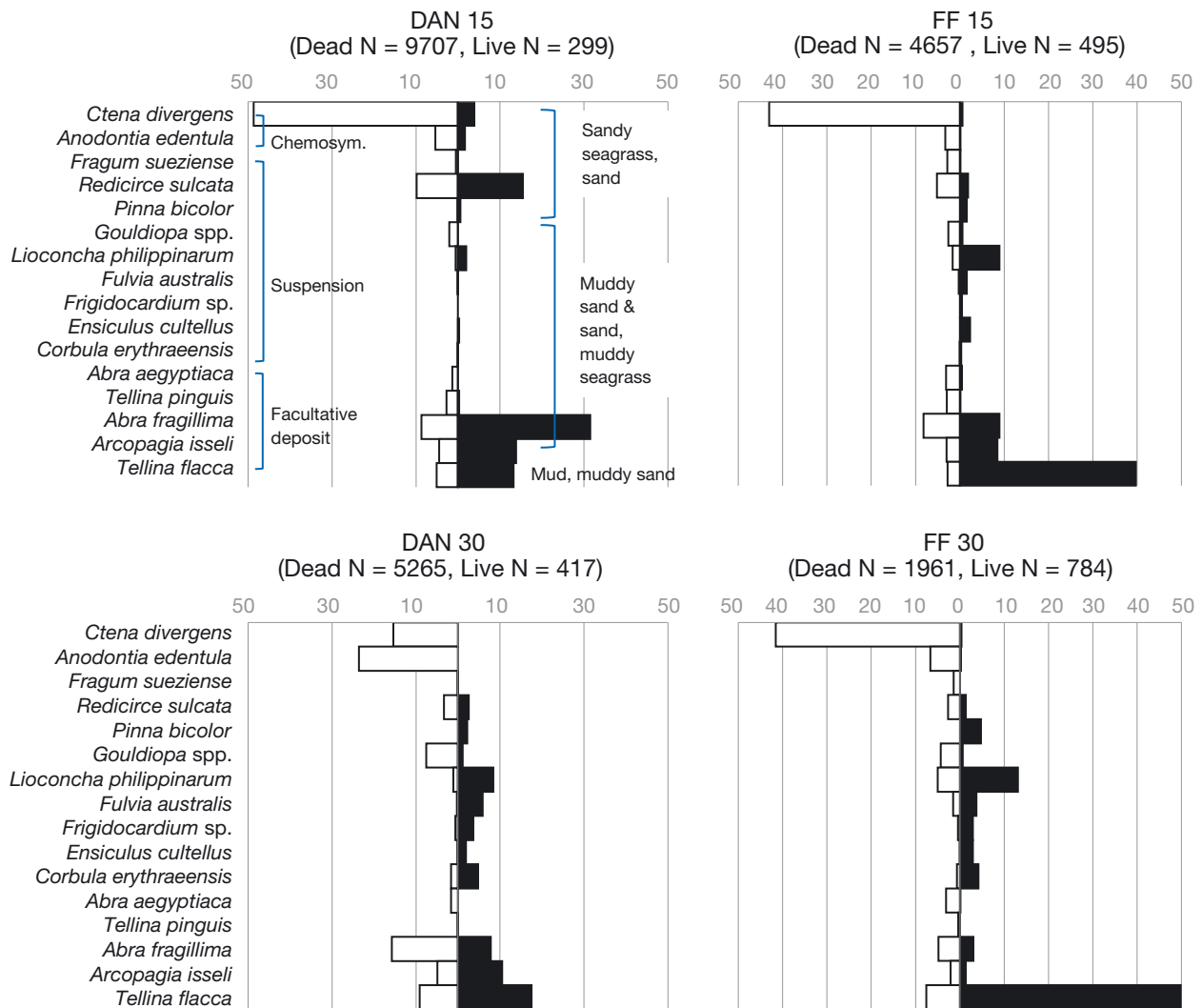
Fig. 3. Proportional abundances of species in death assemblages (white bars; scaled to the left of each graph mid-point) and living assemblages (black bars; scaled to the right) after pooling all seasonal samples at a site and focusing on the 16 taxa most responsible for live–dead discordance in the study area. Taxa are arranged by trophic group and habitat preference (see Table A1 in the Appendix). Fish farm sites (FF; right graphs) are proximal to historic point-sources of pollution, and Dan Hotel sites (DAN; left graphs) are distal. N: total number individuals in death or living assemblage

feeders (*Tellina flacca*, other tellinids, semelids) and multiple suspension feeders known from studies elsewhere to prefer non-vegetated seabeds or muddy seagrass (Table A1) were more abundant alive than dead. These contrasts suggest widespread loss of sandy seagrass habitat, with a shift to muddy seagrass or non-vegetated habitat, as well as increased organic matter supply to the seafloor. Such changes, whether caused by natural or anthropogenic forces or some combination, would represent a significant shift in the soft-sedimentary benthic community, and so alternative taphonomic explanations should be considered.

For example, the spatial homogeneity of the death assemblage composition, in contrast to strong differences in living assemblages among the same sites, might reflect natural spatial mixing of shells among sites, such as by storms. We consider this unlikely, given the low fetch for winds, their dominant southward flow, and the retarding effect of the sill at the mouth of the Gulf, which limit storm power (Drews 2015), and the rarity of significant 'out-of-habitat' transportation of shells on other open shelves, even narrow and steep ones (Kidwell 2008). Additionally, an earlier survey of death assemblages from 20 to 100 m on the Eilat shelf
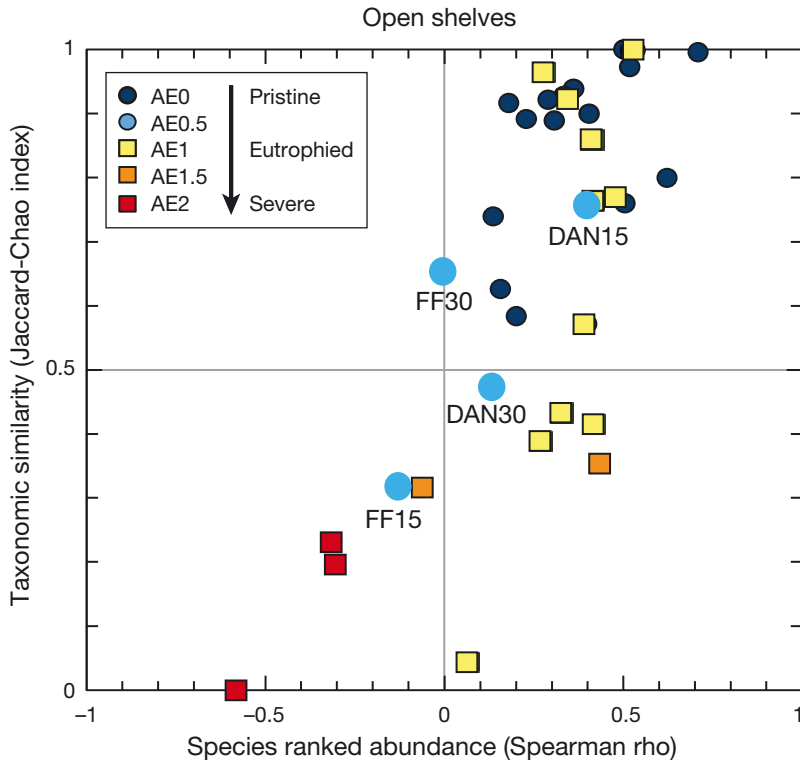
Fig. 4. Cross plot of taxonomic similarity (Jaccard-Chao) against the rank-order correlation of species' abundances (Spearman's rho) of living and death assemblages at the 4 study sites (large blue circles), calculated after pooling all temporal replicates, compared with data from a global meta-analysis of live–dead agreement in open shelf settings. Small icons are color-coded to reflect level of stress from anthropogenic eutrophication (AE) (adapted from Kidwell & Tomasovych 2013)

(Edelman-Furstenberg & Faershtein 2010) detected a bathymetric gradient in death assemblage composition, arguing against post-mortem homogenization, and did not encounter living assemblages rich in *Ctena* and/or *Anodontia* that might serve as a source for their widely distributed and abundant dead shells.

Live–dead discordance also cannot be explained by a failure of our sampling method to detect living species, given multiple spatial replicate samples per site during each of 6 replicate visits; the lack of appropriately sandy seagrass habitat is a more likely explanation. Nor is discordance likely to be an artefact of inter-species differences in post-mortem preservation (taphonomic bias). Even species that occurred abundantly dead-only at some sites were encountered living at others, and these species do not have particularly thick or robust shells that would promote exceptionally high preservation. Moreover, the most fragile-shelled and abundant of the living species, especially *T. flacca*, occurred dead at all sites.

We thus judge that observed live–dead discordance on the soft-sedimentary shelf of Eilat, reflecting strong spatial variation in living assemblages versus homogeneity in death assemblages, and strong live–dead differences in dominant species, indicates a genuine ecological change in the system.

Loss of Ctena and Anodontia signify loss in extent and quality of seagrass habitat

In addition to the shift in dominant species, the soft-sediment macrobenthic community has undergone a remarkable shift in trophic dominance (Fig. 3). The community is dominated by facultative deposit feeders today, even at vegetated sites (DAN 15 and DAN 30), whereas death assemblages indicate that chemosymbiont-bearing lucinid bivalves dominated the entire area in the recent past (within the window of time-averaging; see below).

The bivalve genera *Ctena* and *Anodontia* are both likely obligate chemosymbiotic bivalves (Taylor & Glover 2005) that evolved a symbiotic relationship with sulphide-oxidizing bacteria and seagrass under oligotrophic conditions, and are well-documented inhabitants of seagrass meadows globally (van der Heide et al. 2012). *Ctena* thrives in both *Halophila* and *Halodule* seagrass beds in the Gulf, whereas living *Anodontia* are limited to *Halophila* and more strictly sandy seabeds (Mastaller 1979, Table A1). Isotopic analysis shows that *A. edentula* relies on seagrass detritus even in sparsely or unvegetated sediment (Kon et al. 2015).

The decline in lucinid populations indicates both a reduction in seagrass cover, especially in the fish farm area, and a change in the quality of seagrass meadows that still exist (DAN area), which were previously sandier (≤10% mud). Today, *T. flacca* is the most abundant species alive at all 4 sites and prefers unvegetated sandy mud (50 to 90% mud) or muddy sand (10 to 49% mud) elsewhere, and many subsidiary suspension- and facultative deposit-feeding bivalves found more abundant alive than dead at one or more of our sites also prefer muddy sand and/or

muddy seagrass (Fig. 3, Table A1). Living assemblages were consistent with seagrass distribution during our fieldwork, with maximum seagrass abundance at DAN15, moderate abundance at DAN30, and least at FF15 and FF30 (Table 1) (authors' obs., see also Winters et al. 2017).

Timing and drivers of baseline shift

The scarcity of seagrass today in the fish farm area is the strongest pattern in seabed conditions and live–dead discordance is also greatest there. However, all sites have shifted to dominance by facultative deposit-feeding taxa, adapted to relatively high and/or variable organic-matter supply (e.g. Borja et al. 2000, Rossi et al. 2015), and so ecological change has been widespread. Both natural and anthropogenic factors might have contributed to these changes and are not mutually exclusive.

One potential driver is flood-derived siliciclastics from the mouth of the wadi. Such sediments have the potential to smother seagrass at the fish farm area: flood-delivered sediments are transported as hyperpycnal flows along the seabed rather than as a surface plume (Katz et al. 2015), magnifying their benthic effects. Flood-delivered sediment is a natural stressor, but its negative effects have almost certainly been increased anthropogenically by watershed development (decreased infiltration), the focusing of flood waters by the Kinnet canal since the 1960s, and higher contaminant loads from urbanization (Katz et al. 2015, Winters et al. 2017).

A second potential factor is organic enrichment, which can alter both trophic structure (toward deposit feeding; Pearson & Rosenberg 1978, Borja et al. 2000, Rossi et al. 2015) and the physical habitat (seagrass decline): nutrient addition initially fertilizes seagrass, but increasing planktonic populations eventually reduce water clarity (Burkholder et al. 2007). Urbanization and industrialization are widely accepted to have increased the flux of nutrients and organic material to the northern Gulf of Aqaba since the mid-20th century (e.g. Loya 2004). Water monitoring, starting in 2003, shows that nutrient levels near the mouth of the wadi are as high or higher than any other sampled site in the northern Gulf, with strong seasonal and inter-annual variation probably related to runoff, and with high ammonia when the fish farm operated (IUI 2017).

We thus suspect a combination of (1) culturally enhanced runoff, including greater nutrients, fostered by mid-20th century construction of the Kinnet

and watershed development, and (2) multiple decades of anthropogenic nutrient addition in coastal waters, first from sewage emissions (1980s to 1995) and then from fish farms (1990s to 2008), as the likely drivers of ecological change in benthic mollusc communities. The shells of key dead-only species are being radiocarbon-dated to establish when those populations started to decline. Bivalve death assemblages from the upper 5 to 15 cm of other tropical carbonate seabeds are dominated by shells produced during recent past decades (median age <50 to 100 yr) but commonly include shells from previous centuries due to bioadvection (Kidwell 2013, Kosnik et al. 2015), and so we suspect that Eilat-shelf death assemblages capture a similar, approximately centennial sample of past populations.

Live–dead discordance has been shown to be effective in revealing recent eutrophication in estuarine and open shelf settings including seagrass habitats, based both on meta-analysis (Kidwell 2007) and local studies. In tropical carbonate seagrass habitats, death assemblage composition equilibrates rapidly (within a decade) to natural variability in community composition (Ferguson & Miller 2007, Feser & Miller 2014, Korpanty & Kelley 2014), but live–dead discordance can persist for >20 yr where cultural pressure has driven community change (e.g. Ferguson 2008). These observations suggest that the community change implicit from live–dead discordance on the tropical Eilat shelf is indeed anthropogenic and occurred within recent decades. Moreover, the scarcity of seagrass in the fish farm area, despite cessation of sewage emissions >20 yr ago and removal of fish cages a decade ago, suggests slow ecological recovery.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

This unique live–dead analysis of bivalves in the Gulf of Aqaba provides insights that could not be acquired from living assemblages alone, and answers the first-order question of whether soft-sedimentary shelf communities have changed. We conclude three main points: (1) Communities and habitats have changed significantly, almost certainly within the 20th century. (2) The shift from baseline has been most severe near the mouth of the wadi, where the unvegetated seabed was formerly sandy seagrass. The scarcity of seagrass suggests considerable ecological inertia to recovery and possible hysteresis, given cessation of major nutrient inputs from sewage and fish farming 10 to 20 yr ago. Contaminants and

solid-sediment runoff from the Kinnet canal might be suppressing recovery. Even seagrass habitat at more distal sites is qualitatively different from that in the past: chemosymbiont-bearing lucinids known to prefer sandy seagrass conditions elsewhere in the Red Sea dominated the death assemblages at all 4 sites but are essentially absent in living assemblages, suggesting loss of this habitat type. And finally, (3) facultative deposit feeders adapted to higher and more variable organic-matter supply are significantly more abundant alive than dead everywhere, representing a significant change in community structure consistent with organic enrichment (anthropogenic eutrophication). The full spatial extent of this ecological change could be determined by testing additional sites on the Eilat/Aqaba shelf for live–dead discordance. We suspect, for example, that areas near phosphate-shipping harbors might be as severely impacted as the fish farm area, and that large intervening areas have probably experienced qualitative changes comparable to those observed near Dan Hotel.

Further analysis, particularly geological dating of the shells of dead-only species and down-core analysis, are needed to attribute changes to human agency definitively. However, even these initial data from surficial death assemblages provide novel regional insights into a global issue, and make a powerful case for adoption of paleontological analysis by environmental managers and conservation biologists. Live–dead discordance in species composition and abundance is a valuable means of testing for ecological change in areas lacking historic surveys or monitoring over appropriate periods.

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Appendix.

Table A1. Ecology of the 16 most abundant (>1% of total ind.) bivalve taxa arranged in the same order as in Fig. 3, by functional group (trophic group plus life habit) and then by habitat preference. Trophic group and life habit drawn mostly from Todd (2001); Chemo: chemosymbiont-bearing; Fac dep: facultative deposit (mixed deposit-suspension) feeder; Susp: obligate suspension feeder; Inf: infaunal; Byss: byssate as an adult. Habitat preference from (1) Mastaller (1979) based on living occurrences only; (2) Zuschin & Oliver (2003) based on dead occurrences unless noted otherwise; (3) Huber (2010); (4) J. J. ter Poorten (pers. comm.); (5) Ibrahim et al. (2015); (6) Nordlund & Gullström (2013). Quantitative grain size data for habitat types denoted by reference (2) are tabulated in Piller & Mansour (1990): sand and sand among corals has lowest weight-% mud, with mean of 5% (range 1 to 25%); sand with seagrass and 'seagrass' have a mean of 21 to 24% mud (3 to 50%); muddy sand has mean of 42% mud (17 to 77%); 'mud' is actually sandy mud, with mean of 76% (22 to 99%)

Taxon	Trophic group	Life habit	Habitat preference
Ctena divergens	Chemo	Inf	*Halodule* & *Halophila* sandy seagrass (1); sand, sandy gravel near mangroves, sandy seagrass, rare muddy sand with seagrass (2); locally large numbers in sand (3); seagrass near mangroves (5)
Anodontia edentula	Chemo	Inf	*Halophila* sandy seagrass (1); living muddy sand often among seagrass, dead in sand, sandy seagrass (2); large numbers in muddy sand seagrass (3); seagrass (6)
Fragum sueziense	Susp	Inf	*Halodule* sandy seagrass (1); sand, sandy seagrass (2); locally large numbers sand among corals (3 based on 4)
Redicirce sulcata	Susp	Inf	Sandy seagrass, sand, muddy sand, muddy sand with seagrass (2); sand (3)
Pinna bicolor	Susp	Semi-inf byss	Unvegetated 'soft sediment' (1); sand and gravel (3)
Gouldiopa spp.	Susp	Inf	Living muddy sand and sand; dead muddy sand, mud, sandy seagrass sand (2); sand & shelly gravel, muddy sand seagrass (3)
Lioconcha philippinarum	Susp	Inf	Living muddy sand and sand; dead muddy sand with seagrass, (2); clean and coral sand, rubble (3)
Fulvia australis	Susp	Inf	Muddy sand, muddy seagrass (2); large numbers sandy mud and rubble near reefs (3); can be on seagrass (4)
Frigidocardium sp.	Susp	Inf	cf. *F. torresi* per H. Meinis: sandy mud (3); muddy sand, not seagrass (4)
Ensiculus cultellus	Susp	Inf	Muddy sand (2); sandy and muddy (3)
Corbula erythraeensis	Susp	Inf byss	[Sandy] mud, muddy sand (2); sand, muddy sand (3)
Abra aegyptiaca	Fac dep	Inf	Muddy sand, [sandy] mud, muddy seagrass (2); sandy grass beds with muddy sand (3)
Tellina pinguis	Fac dep	Inf	Sand, muddy sand, seagrass (2); coral and fine sand (3)
Abra fragillima	Fac dep	Inf	Sand, muddy sand, seagrass (2); sand, shelly sand (3)
Arcopagia isseli	Fac dep	Inf	Muddy sand, muddy seagrass (2); coarse to fine sandy (3)
Tellina flacca	Fac dep	Inf	[Sandy] mud, muddy sand (2); muddy sand (3)