



Localized effects of offshore aquaculture on water quality in a tropical sea

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ABSTRACT

Aquaculture production has increased steadily in many tropical countries over the past few decades, although impact assessments have been frequently neglected. We investigated the impacts of an offshore barramundi fish farm on water quality in the southern-central Red Sea, a traditionally understudied tropical, oligotrophic, and semi-enclosed basin. Inorganic nutrients, particulate matter, chlorophyll-*a*, and heterotrophic bacteria were measured periodically over 8 months around the farm. Water down-current from the farm had, on average, more heterotrophic bacteria and chlorophyll-*a* than up-current (11% and 34% higher, respectively). Ratios of dissolved inorganic nitrogen:phosphorus down-current from the farm were lower than ratios up-current (mean 9.8 vs 16.0, respectively). Phosphate, inorganic nitrogen, and particulate matter showed patterns of enrichment associated with the farm after a fish feeding event. Strategies such as feed optimization and considering hydrodynamics in site selection may improve water quality for future fish farms in Saudi Arabia and other tropical countries.

1. Introduction

As the human population grows, so does our global demand for seafood. Increased fishing efforts and technological advances have allowed us to harvest wild fish at an industrial scale, leading to the over-exploitation of many wild stocks (Myers and Worm, 2003). It has been estimated that nearly 40 to 50% of tropical and temperate ecosystems exceed thresholds of overfishing (Link and Watson, 2019), and trends of decreasing fish size and declines in global fish landings have been observed globally (Pauly et al., 2005). Marine aquaculture has the potential to reduce the pressure on both wild fisheries and terrestrial agriculture. A study by Gentry et al., 2017a considered aquaculture to be a viable alternative to these traditional means of protein production after estimating that aquaculture could be used to produce the current global fish landings using only 0.015% of Earth's Ocean area. Between 1970 and 2006, global aquaculture production grew at a rate of 6.9% year⁻¹ (Bostock et al., 2010), and between 2016 and 2018 aquaculture accounted for 46% of global fish production (FAO, 2020).

While offshore aquaculture has great potential to meet our food security needs and reduce strain on over-exploited fisheries, it comes with a list of environmental concerns. Offshore aquaculture generally consists of cage cultures, which are fairly open systems that release waste

products (i.e., solid and chemical waste, therapeutics, harmful bacteria or pathogens, and farmed species escapees) directly into surrounding waters (Cao et al., 2007). One of the impacts associated with this discharge is organic matter enrichment, which is caused by the release of fecal material and uneaten feed from cages and is known to alter the biogeochemical processes and biotic communities in the surrounding environment (Holmer et al., 2008; Holmer et al., 2002). As a result of this nutritional input, marine fish farms have been shown to diminish water transparency and dissolved oxygen as a consequence of fish respiration, as well as enhance microbial, nutrient, and organic matter remineralization (Morata et al., 2015). These changes in water quality can adversely affect surrounding wildlife and the farmed animals themselves, including effects on the settlement and growth of benthic organisms such as corals (Koop et al., 2001; Nugues and Roberts, 2003; Villanueva et al., 2005) and seagrasses (Ticina et al., 2020).

The Red Sea is a warm, oligotrophic environment with no riverine nutrient inputs along its arid coastline, and is therefore low in major nutrients such as nitrogen, phosphorus, and silica (Raitos et al., 2013). Like in many other tropical regions where aquaculture is already well established or intensive, this low-nutrient environment is home to sensitive and valuable habitats including mangroves, coral reefs, and seagrass meadows (Hozumi et al., 2018). Excess nutrients and organic

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matter from aquaculture activities have been shown to affect the pelagic environment (Navarro et al., 2008), limit survivorship and growth rates of coral (Villanueva et al., 2005; Bongiorno et al., 2003), increase sea-grass decline (Delgado et al., 1997), and alter microbial communities in mangrove forests (Castine et al., 2009). Higher temperature waters are also known to affect biological processes, with warmer temperatures seen to enhance the metabolic rates of plankton and the degradation of organic carbon in mesopelagic waters (Regaudie-De-Gioux and Duarte, 2012; Kheirreddine et al., 2020). Therefore, it is critical to understanding how these processes associated with fish farms will affect this warm, markedly nutrient-deficient marine ecosystems.

This study aims to determine how a warm, oligotrophic pelagic ecosystem responds to localized inputs of organic matter and inorganic nutrients from an offshore fish farm. Seasonal sampling of the upper water column (down to 25 m deep) was performed around a set of barramundi (*Lates calcarifer*) fish farm cages in the southern-central Red Sea to measure indications of organic and inorganic nutrient enrichment. We hypothesized that signals of increased nutrients, organic matter or heterotrophic bacterioplankton abundance would be measured down-current from the farm at different times of the year. While other studies have examined the effluent from fish farms, few resolved the spatial and temporal extent to which effluent is detectable in the water column, and rather compare water sampled near the farm to a control site farther away from it. A gridded sampling design surrounding the farm allowed us to gain a better understanding of the dispersion of offshore fish farm effluent in coastal tropical waters.

2. Methods

2.1. Study site and sampling design

This study was conducted at an offshore fish farm in the southern-central Red Sea off the west coast of Saudi Arabia (Fig. 1). The farm (20.186°N, 40.048°E) was located approximately 20 km up-coast from

the town of Al Lith, Saudi Arabia. At the time of sampling, the farm consisted of 16 circular cages (40 m in diameter each) in which barramundi (*Lates calcarifer*) were being grown. Information regarding stocking densities, feeding rates, or other operational parameters of the farm was unavailable due to a lack of response or communication from the fish farm company. The fish farm sits approximately 5 km from the shore and is anchored in water that is roughly 75 m deep. A nearby coral reef (Shib al Jiffin) has its reef crest approximately 1 km inshore from the farm (Fig. 1).

The water column near the fish farm was sampled three times over the course of eight months (August 2017, December 2017, and March 2018) thus covering the seasonal cycle of this region of the Red Sea (Raitsos et al., 2013) with samples in the summer, winter, and spring. Stations were sampled over the course of two days for each sampling month. Niskin bottles were used to collect water samples at two depths (5 m and 25 m) at 12–13 stations during each sampling month (Fig. 1C). The water was collected to measure the concentration of: Dissolved nutrients including nitrite (NO_2^-), nitrate (NO_3^-), ammonium (NH_4^+), phosphate (PO_4^{3-}), silicate (SiO_2), and dissolved organic carbon (DOC); particulate matter including suspended particulate matter (SPM), particulate organic carbon (POC), and particulate organic nitrogen (PON); chlorophyll-*a* (Chl-*a*); and the abundance of heterotrophic bacteria.

2.2. Analytical methods

DOC quantifications were based on 40 mL samples of seawater filtered through a 0.2 μm pore-size Millipore filter on the boat. All materials used were acid-cleaned. Phosphoric acid was added after filtration for pH 1–2 preservation, and samples were stored at 4 °C. DOC analysis was done by high temperature catalytic oxidation (HTCO) using a Shimadzu TOC-L as described in Calleja et al., 2019. Reference materials of deep-sea carbon (42–45 $\mu\text{mol C L}^{-1}$) and low carbon water (1–2 $\mu\text{mol C L}^{-1}$), provided by University of Miami (D. A. Hansell laboratory), were used to monitor the accuracy of DOC concentration

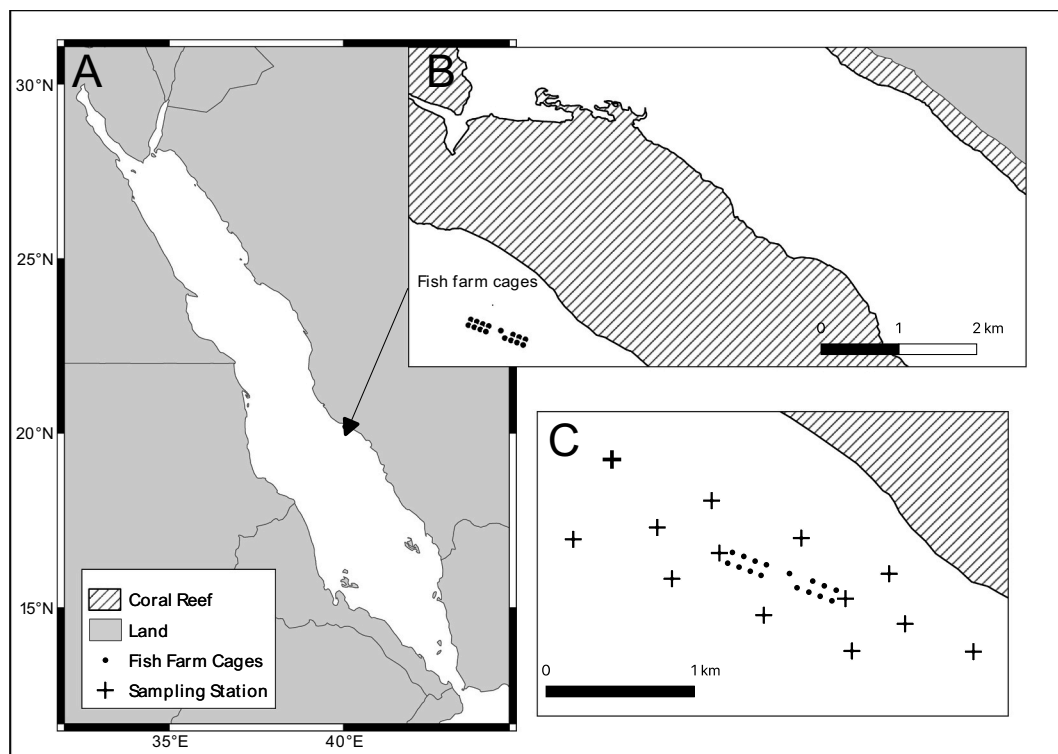


Fig. 1. Location and sampling design of studied fish farm. The fish farm is located in the southern-central Red Sea (A) in close proximity to coral reefs (B), and water samples were taken at various stations around the fish farm (C).

measurements. For NO_3^- , NO_2^- , PO_4^{3-} , and SiO_2 , 30 mL of 0.2 μm filtered seawater were stored at -20°C and measured colorimetrically using a Seal Analytical Segmented Flow Analyzer. NO_3^- was determined by cadmium reduction and a subsequent reaction with sulfanilamide under acidic conditions to form a diazo compound. NO_2^- was determined by reaction with sulfanilamide under acidic conditions to form a diazo compound. PO_4^{3-} was determined by a reaction with molybdate ion and antimony ion followed by a reduction with ascorbic acid. SiO_2 was determined by reduction in ascorbic acid to molybdenum blue. NH_4^+ concentrations were quantified fluorometrically on the same sampling day after dark incubations of 5 mL of 0.2 μm filtered seawater with 1.2 mL of working reagent (ophthalaldehyde solution). Incubations lasted 4–12 h and measurements were performed according to Birkicht, 2012. Samples were compared to ammonium chloride standards. Nitrogen:phosphorus ratios (dissolved inorganic nitrogen:soluble reactive phosphorus, or DIN:SRP) were calculated by summing the concentrations of NO_3^- , NO_2^- , and NH_4^+ and dividing it by PO_4^{3-} concentration in each sample. For the quantification of Chl-*a* concentrations, 2 L of seawater were filtered through Whatman GF/F filters; filters were stored in liquid nitrogen until being transferred to a -50°C freezer. Chl-*a* was extracted from the filters by soaking, sonicating, and vortexing filters in vials with 90% acetone solution for 24 h before measurement. The extract concentration was measured fluorometrically according to Holm-Hansen et al., 1965.

For SPM, POC, and PON quantifications 2 L of water were collected per site and stored in a cooler and then filtered in a laboratory through pre-weighed and ashed Whatman GF/F filters on the same sampling day. An extra 500 mL of fresh MilliQ filtered water was run through each filter to remove excess salts. Filters were frozen in liquid nitrogen and then stored at -50°C until analysis. To determine SPM concentration, filters were dried and weighed, and the original weight of the filter was subtracted to find the weight of the suspended particulate matter. POC and PON were measured by acidifying the GF/F filters with HCl and quantifying total carbon and nitrogen with a CHNS elemental analyzer (Thermo Scientific FLASH 2000 CHNS/O Analyzer). Dried and acidified filters were packed in silver foil disks before combustion in the elemental analyzer.

Heterotrophic bacterial cells were measured in unfiltered seawater samples preserved with 1% paraformaldehyde and 0.5% glutaraldehyde solution (final concentration). Bacterial samples were frozen in liquid nitrogen after sampling until returning to the lab, where they were stored at -80°C . Samples were analyzed with a BD FACSCanto II flow cytometer according to Gasol and Moran, 2015. The abundance and cellular properties (i.e., cell size and fluorescence after staining with SybrGreen) of low nucleic acid (LNA) and high nucleic acid (HNA) heterotrophic bacteria were analyzed using BD Paint-a-Gate™ software. Conversion of cell size to biomass was made assuming spherical shape and using the light scatter to cell diameter relationship of Calvo-Díaz and Morán, 2006 and the biovolume to carbon relationship of Gundersen et al., 2002. Hereafter and along the manuscript we use the term “bacteria” or “heterotrophic bacteria” as synonymous to “heterotrophic prokaryotes” since bacteria represents the major contribution of heterotrophic prokaryotes in surface oligotrophic waters (Karner et al., 2001).

Current velocities were measured in the study site using a CODE/DAVIS drifter. A drifter was deployed near the fish farms at the beginning of each sampling day and was retrieved when sampling was finished (drifters deployments lasted from 2 h 40 min to 7 h 15 min on different sampling dates). Drifter position and trajectory were measured using a Garmin inReach® GPS that logged and telemetered data via the Iridium satellite network. Current velocity measurements were used to contextualize the patterns of water quality variables in the study site and classify sampling stations as “up-current” or “down-current” from the fish farm at the time of sampling. This classification was then used to assess differences between the overall water quality in water that had and had not passed through the farm.

2.3. Statistical analysis

Changes in water quality due to the fish farm were assessed by comparing values of measured variables sampled up-current and down-current from the farm across all sampling months (March, August, and December) and sampling depths (5 m and 25 m). The Shapiro-Wilk test was used to test the data for normality, and either a Student's unpaired *t*-test or Mann-Whitney *U* test (R Studio) was used to compare the differences in water quality variables between all water sampled up- and down-current from the fish farm. The Student's unpaired *t*-test was applied to normally distributed data, and the Mann-Whitney *U* test was applied to non-normally distributed data. A *p*-value <0.05 indicated statistical significance.

For each water quality variable, generalized linear models (GLM) were created to assess whether location relative to the farm, sampling depth, or sampling month could be used as predictors of water quality variables. For each variable analyzed, the following model was created:

$$Y_i = \beta_0 + \beta_1(\text{Current relationship}) + \beta_2(\text{Sampling Depth}) + \beta_3(\text{Sampling month}) + \beta_4(\text{Distance from fish farm}) + \varepsilon_i$$

where Y_i is the concentration of each water quality variable, β_0 is the intercept (constant term), $\beta_1 \dots \beta_4$ are the slopes of relationship between relative water quality variable and current relationship (if the sampling station is up vs. down current from the fish farm), sampling depth (5 m or 25 m), sampling month (March, August, or December), and distance from fish farm (km), respectively. ε_i is the error term. GLMs were calculated using the “glm” function in R Studio (R Core Team, 2019).

Additionally, principal component analyses (PCA) and linear discriminant analyses (LDA) were run to compare water sampled up- and down-current from the fish farm in August as food delivery and fish feeding was observed in the fish cages during this period. PCAs were run using the “prcomp” function and the LDAs were run using the “lda” function from the MASS package, both in R Studio (R Core Team, 2019). Operational information was unavailable from the fish farm operators, so during most sampling months it was not possible to know when feeding had most recently occurred in the fish pens. Therefore, data from this month were used to assess the characteristics of water up- and down-current of an actively feeding fish farm. Variables used in both the PCA and LDA were: Chl-*a*; HNA, LNA, and total bacterial abundance; bacterial biomass; bacterial cell size; dissolved inorganic nutrients (NO_3^- , NO_2^- , NH_4^+ , PO_4^{3-} , SiO_2); particulate matter (SPM, POC, PON); DOC; DIN:SRP ratio; and POC:PON ratio. Water quality variables were also mapped using MATLAB R2017a to visually assess water quality differences up- and down-current from the farm.

3. Results

3.1. Water quality assessment up- and down-current from the fish farm

Differences between up- and down-current water quality were observed in several variables (Fig. 2). When values were pooled across all sampling months, DIN:SRP ratios were significantly lower in down-current water than in up-current water (9.8 vs 16.0). Chl-*a* and total heterotrophic bacterial abundance (LNA plus HNA heterotrophic bacterial cells) were significantly higher in samples collected down-current from the fish farm than those collected up-current with pooled data. Average Chl-*a* concentrations in water down-current from the farm were 34.3% higher than in up-current water ($0.42 \mu\text{g L}^{-1}$ vs $0.31 \mu\text{g L}^{-1}$), and bacterial abundance was 10.5% higher in down-current water ($2.96 \times 10^5 \text{ cells mL}^{-1}$ vs $2.68 \times 10^5 \text{ cells mL}^{-1}$). Water down-current from the farm also had higher minimum and maximum bacterial abundances, ranging from $1.46\text{--}4.32 \times 10^5 \text{ cells mL}^{-1}$ while bacterial abundance in up-current water ranged from $0.94\text{--}3.99 \times 10^5 \text{ cells mL}^{-1}$ through the study period. Values of all water quality variables in each individual sampling month and combining sampling months are given in Table S1.

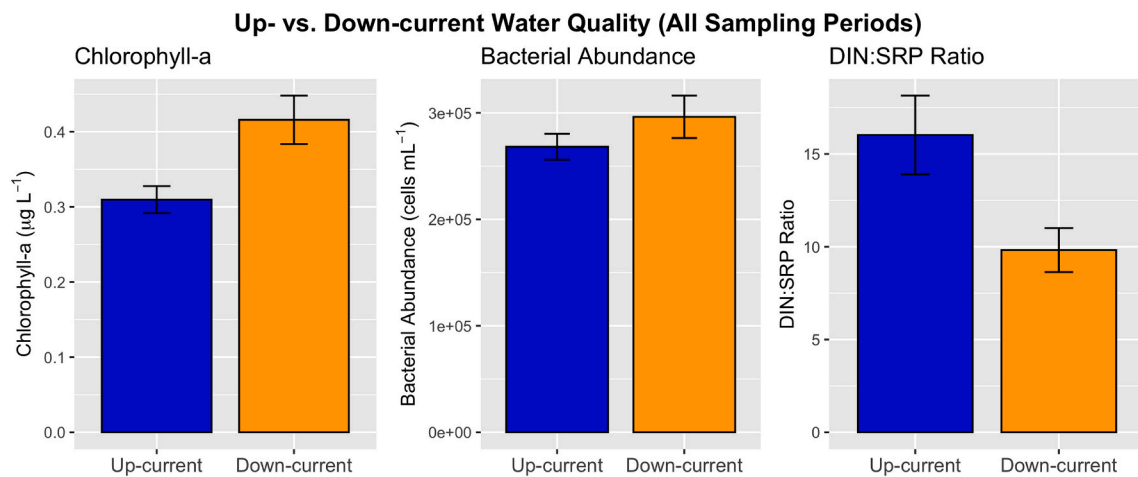


Fig. 2. Mean (\pm SE) water quality variables that were statistically significantly different between up- and down-current water samples pooled across all sampling months (p -value <0.05).

GLMs combining data from all sampling months indicated that whether water was sampled up- or down-current from the farm was a significant predictor of several water quality variables. Negative and statistically significant relationships (coefficient estimates) were found between a sample's up-current position and Chl-*a*, heterotrophic bacterial abundance, LNA bacterial abundance, and NO_2 (coefficients = -0.08 , $-19,118$, $-16,885$, and -0.03 , respectively). A positive and statistically significant relationship was found between a sample's up-current position and the DIN:SRP ratio (coefficient = 8.09). Deeper sampling depth (25 m) was also positively linearly related to Chl-*a*, LNA bacterial abundance, and NO_2 (coefficients = 0.14 , $12,178$, and 0.02 , respectively). Summaries of GLMs are given in Table S2.

3.2. Differences in water characteristics up- and down-current from the farm during a feeding event

In August (during a recorded fish feeding event), a number of additional water quality variables were statistically significantly different (p -value <0.05) between water up- and down-current from the fish farm. Mean concentrations were higher in down-current than up-current water for Chl-*a* (0.43 vs 0.25 $\mu\text{g L}^{-1}$), PO_4^{3-} (0.16 vs 0.08 $\mu\text{mol L}^{-1}$), SiO_2 (1.36 vs 0.96 $\mu\text{mol L}^{-1}$), POC (103.45 vs 72.18 $\mu\text{g L}^{-1}$), and PON (18.85 vs 13.82 $\mu\text{g L}^{-1}$) (Fig. 3). The DIN:SRP ratio was lower in down-current than up-current water (8.7 vs 19.5 , respectively) (Fig. 3). Directions of currents on each day are shown in Fig. 4.

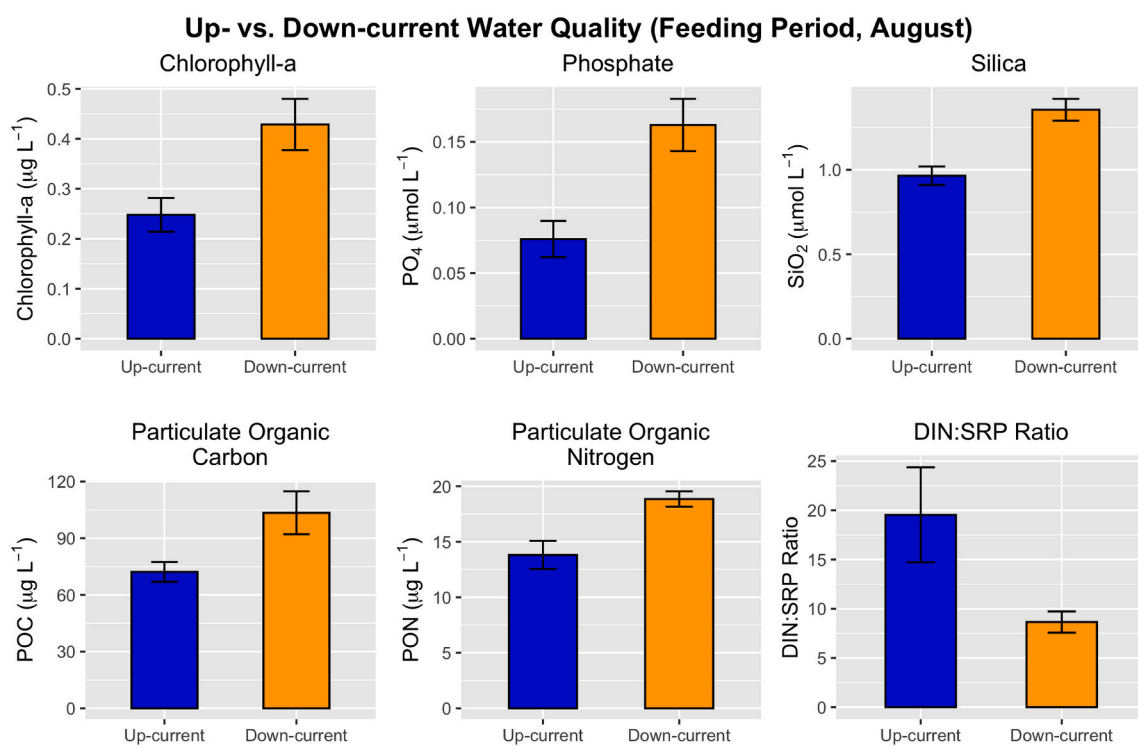


Fig. 3. Mean (\pm SE) water quality variables that were statistically significantly different between up- and down-current water samples in the August sampling month (p -value <0.05).

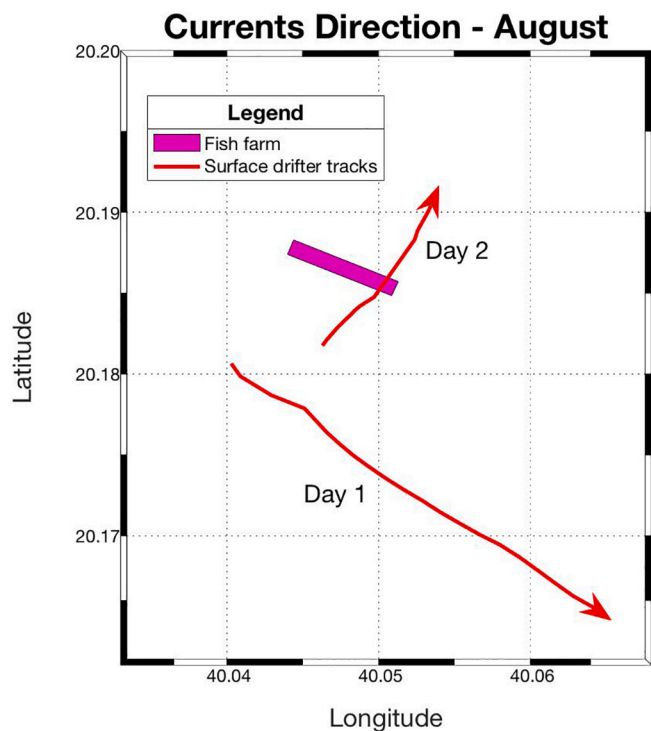


Fig. 4. Direction of surface currents (based on tracks of CODE/DAVIS drifter movement) on sampling dates in August. Average current velocities were 23 cm s^{-1} on Day 1 and 9 cm s^{-1} on Day 2.

A principal components analysis of the August measurements also separated stations sampled up- and down-current from the farm at both depths (Fig. 5). The first principal component (PC1) explains 48.2% of variance at 5 m and 37.7% of variance at 25 m. This shows a difference in the overall water characteristics between ambient water and water that has passed through the fish farm. This separation was only seen in the August sampling month, and not when measurements from all sampling months were combined.

Two up-current stations in August are grouped near the down-current stations in the PCA plots for both depths (Fig. 5). While these two stations were up-current from the fish farm, they were also the two closest up-current stations to the farm (approximately 200 m and 260 m from the edge of the fish farm). The down-current plus nearby stations are separated from other up-current stations along PC1. This grouping pattern is also seen in a linear discriminants analysis pooling samples taken from both depths in August (Fig. S1). Up-current water separates clearly from down-current/nearby water along LD1 (88.4% of separation), and down-current water separates slightly from nearby water along LD2 (11.6% of separation). This separation indicates a change in water quality, as measured by the variables tested at each station, between sites down-current/nearby and up-current from the farm.

Inputs of inorganic nutrients (NH_4^+ and PO_4^{3-}), as well as inputs of suspended particulate matter spatially associated with the farm were clearly visualized with a heat map of these variables during this feeding event (August sampling month) (Fig. 6). Concentrations of NH_4^+ were highest close (150 m) to the fish cages ($1.15 \mu\text{mol L}^{-1}$ at 5 m and $0.61 \mu\text{mol L}^{-1}$ at 25 m depth), and elevated values of NH_4^+ ($1.06 \mu\text{mol L}^{-1}$) were also detected in surface waters (5 m depth) up to approximately 800 m away from the edge of the fish farm cages. These values can be compared with an average NH_4^+ concentration of $0.32 \mu\text{mol L}^{-1}$ at 5 m depth and $0.15 \mu\text{mol L}^{-1}$ at 25 m depth for the entire sampling area during this period. A spike in the concentration of SPM was also present in the station closest to and down-current from the fish farm (0.78 mg L^{-1} at 5 m and 1.34 mg L^{-1} at 25 m, compared to an average of 0.36 mg L^{-1} at 5 m and 0.32 mg L^{-1} at 25 m for the entire sampling area that

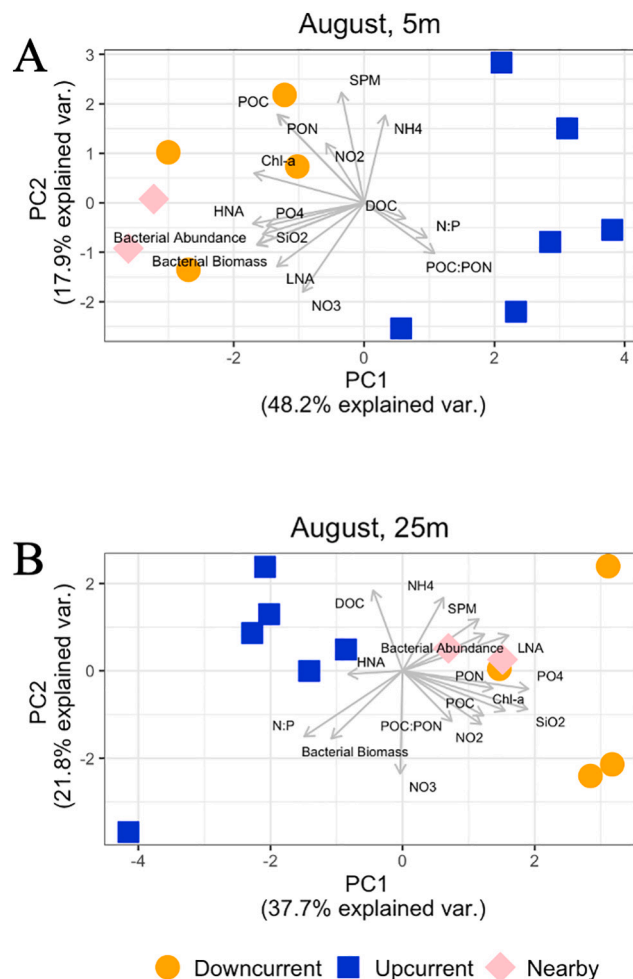


Fig. 5. Principal Component Analysis of water quality data at 5 m (A) and 25 m (B) in August. Stations are classified as down-current (orange dots), up-current (blue dots), and nearby (pink dots) from the fish farm at the time of sampling. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

month). Above-average concentrations of PO_4^{3-} ($0.17\text{--}0.23 \mu\text{mol L}^{-1}$) were detected at 25 m depth at stations 200–650 m away from the edge of the fish farm cages, while the average concentration of PO_4^{3-} in the entire study area during this period was $0.13 \mu\text{mol L}^{-1}$ at 25 m. All of these stations were either close to ($<260 \text{ m}$) or down-current from the fish farm.

4. Discussion

4.1. Extent of water quality impacts from the fish farm

Several water column variables (bacterial abundance, Chl-*a*, and DIN:SRP ratio) were consistent indicators of changes to sea water down-current from the fish farm across all sampling months. A difference in characteristics of water up- and down-current from the farm was also seen during a fish feeding event in the form of elevated dissolved and particulate nutrients as well as Chl-*a*. Both principal components analysis and linear discriminant analysis showed that water collected in this fish feeding event differed based on location, with down-current stations and stations located nearby (within 260 m) the farm showing separations in quality and signs of higher PON and POC, Chl-*a*, and PO_4^{3-} . These patterns indicate that the fish farm is altering water quality in this typically low-nutrient environment.

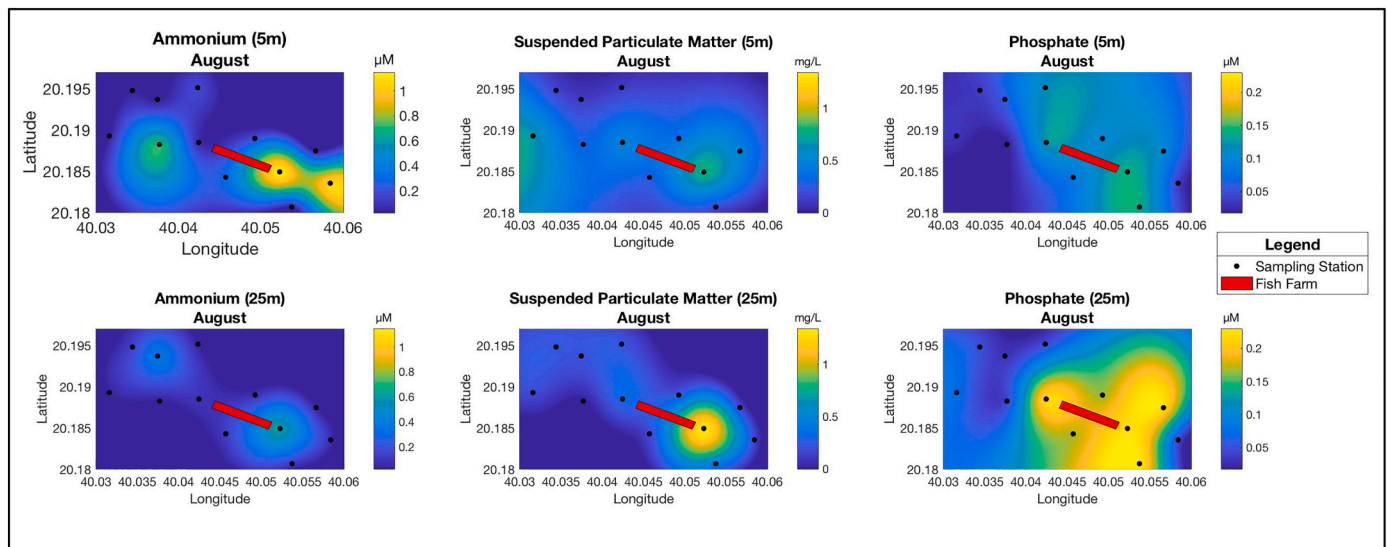


Fig. 6. Heat map of ammonium, suspended particulate matter, and phosphate concentrations in August at 5 m depth and 25 m depth. Black dots are the locations of the sampling stations, and the red rectangle is perimeter of the fish farm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Changes in the dissolved inorganic nutrient composition of water associated with the farm are indications of the farm's effect on the surrounding environment. The mean DIN:SRP ratio of water up-current from the farm was 16.0 across all sampling seasons, which matches exactly the corresponding Redfield Ratio (Redfield, 1958), while water down-current had a mean DIN:SRP ratio of 9.8 across all sampling seasons. In August, PO_4^{3-} concentrations were also elevated in water nearby and down-current from the farm. This decreased DIN:SRP ratio over all sampling months and increased level of phosphate in August down-current from the farm suggests signs of phosphorus enrichment associated with fish production and fish farm waste. Elevated PO_4^{3-} concentrations in water and sediment associated with aquaculture have been reported in studies of other fish farms (Morata et al., 2015; Farmaki et al., 2014; Apostolaki et al., 2007; la Rosa et al., 2002), including another barramundi cage culture in Australia (McKinnon et al., 2010). The excess supply of PO_4^{3-} from the fish farms will likely have an impact in the microbial biota of phosphorus limited waters such as the Red Sea (Fahmy, 2003; Mackey et al., 2007). The observed phosphorus enrichment around the fish farm is likely due to fish waste and uneaten fish feed being lost to the surrounding environment. While we did not have information from the fish farm operators about the type of feed used at this facility, aquaculture fish feed often contains phosphorus as it is an essential element in fish diets (Storebakken et al., 1998; Kaushik et al., 2004).

Elevated levels of NH_4^+ and SPM were also detected around the farm in August, and are likely due to fish waste and excess fish food. NH_4^+ is a waste product of fish metabolism (Shpigel et al., 2019; Morii et al., 1978), and is likely being discharged by fish inside of the cages and entrained into the ambient flow field. NH_4^+ can, in high concentrations, cause eutrophication that stimulates algal growth (Leoni et al., 2018; Vieira et al., 2009), which could affect the planktonic community in the Red Sea and other tropical areas. Signs of farm waste were also detected in the higher SPM concentrations found deeper in the water column close to and down-current from the fish farm. This indicates a flux of particulate matter settling quickly after being emitted from the farm. Fish feces and uneaten food particles have been known to rain down on the seafloor under finfish cages (Holmer et al., 2008), so the spike in SPM concentration at this location and depth is likely the result of these organic particles being advected out of the fish farm cages and settling toward the bottom. Chlorophyll-*a*, the widespread proxy for algal biomass, was also more than 30% higher in down-current water

compared to background levels across sampling months and is a possible and direct biological response to nutrient enrichment from the fish farm. Average concentrations of chlorophyll-*a* in the southern-central Red Sea basin are typically less than $0.4 \mu\text{g L}^{-1}$ through much of the spring, summer, and fall (Raitsos et al., 2013). Water down-current from the fish farms exceeded that value in several sampling months, including in August when background concentrations are particularly low in this region (Raitsos et al., 2013) and in water sampled up-current of the farm (down-current average of $0.43 \pm 0.05 \mu\text{g L}^{-1}$ in August and $0.45 \pm 0.05 \mu\text{g L}^{-1}$ in December) (Table S1).

Another biological response due to organic and inorganic enrichment associated with fish feeding and production was the greater heterotrophic bacterial abundance observed in down-current water. Increased bacterial abundance or changes in microbial community structure have been observed down-current of or in the effluent from large aquaculture facilities (Kamjunke et al., 2017; Becker et al., 2017) and as a result of elevated nutrient inputs in the environment (Olsen et al., 2017). Heterotrophic bacteria have been recently suggested to be phosphorus limited in coastal waters of the central Red Sea (Silva et al., 2019). Thus, the increased bacterial abundance observed in water down-current from the fish farm could have been triggered by an excess of nutrients (particularly PO_4^{3-}) and lower DIN:SRP ratios leaving the farm. Since inorganic nutrients are largely processed first by phytoplankton, the longer period before freshly produced DOM is made available (and a given amount dispersed) to heterotrophic bacteria would diminish the enrichment effect on this planktonic group. Also, the low bacterial growth efficiencies (BGE, typically below 10%) in the Red Sea (Silva et al., 2019) would also contribute to lower impact on heterotrophic bacterioplankton. However, Navarro et al., 2008 found that heterotrophic microbial communities were more responsive than phytoplankton communities to the nutrient inputs from aquaculture and are likely a strong indicator of local ecological effects of fish farms. Other measurements of heterotrophic bacterial abundances in surface and coastal waters of the central Red Sea range from $1.46\text{--}4.97 \times 10^5 \text{ cells L}^{-1}$ (Al-Otaibi et al., 2020; Sabbagh et al., 2020; Silva et al., 2019), and while bacterial abundances measured down-current from the fish farm fall within this range, they are higher than up-current water and represent an increase in the bacterial community above background levels at the site.

The response of the bacterial community may play an important role in the level of impact that aquaculture production has on this warm,

oligotrophic system, as microbial communities are known to rapidly recycle organic matter in tropical ecosystems (Alongi, 1994) and organic carbon degradation rates in mesopelagic waters have been shown to increase with warmer temperatures (Kheireddine et al., 2020). Metabolic rates and biological activity are known to increase with temperature (Brown et al., 2004), and given the high water temperatures of this area (up to 31.7 °C in this study) and many other parts of the Red Sea, it is likely that microbes will respond rapidly to new inputs of nutrients and organic matter and degrade them quickly. The increase in bacterial abundance, even with overall low BGE values, could mean that the microbial community responds to local enrichment and speedily takes up excess nutrients and organic matter in this system.

The detection and spatial extent of an organic enrichment signal in the water column near the fish farm observed here is atypical when compared to other offshore aquaculture case studies. Some studies have detected differences in dissolved nutrients or organic carbon between areas with fish farms and areas with no fish farms (la Rosa et al., 2002; Pitta et al., 2005; Morata et al., 2015), but few detected a plume or resolved the spatial extent to which fish farm effluent is traceable in the water column. A study in Brazil (Chaves et al., 2021) also investigated the spatial extent of Nile tilapia aquaculture outflows in a tropical reservoir, finding effects on the characteristics of dissolved organic matter in water up to 100 m from the farm. Signs of fish farm effluent in our study were detected during one sampling month (August) at greater distances from the farm, with elevated values of NH_4^+ and PO_4^{3-} detected in surface waters up to approximately 800 m and 650 m away from the edge of the fish farm cages, respectively. This may point to dissimilar impacts by different aquaculture species and facilities in different regions.

A review by Ticina et al. (2020) found that the impacts of fish farms on the biotic environment were more evident over the seafloor than in the water column. Most often, impacts of aquaculture are seen in underlying sediments or benthic communities (Basaran et al., 2010; Cao et al., 2007; Holmer et al., 2002; Mayor et al., 2017), as the sediments tend to be an integration of the material emitted from fish farms. As benthic impacts of aquaculture are typically easier to detect than impacts on the water column, it is likely that, given the measurable influences on the water column around the fish farm in this study, effects on the benthos at this site would also have been significant and possibly greater than what was measured in the pelagic environment.

The difference in results between this study and those previously mentioned may be due to the sampling design. In this study we took samples in a grid around the fish farm, with multiple cross-shelf transects both up and down-current from the farm cages. In many studies of aquaculture impacts, samples are taken inside of or near to the farm and compared to control site away from the farm (usually more than 1 km away), determining a difference between the two sites but not the spatial extent of such differences or the way in which waste is transported from the cages. Here we applied a sampling design with a wide array of stations located around the fish farm up- and down-current in order to take into account the direction of water movement. This study also sampled across several seasons, covering months that annually show seasonal differences in sea surface temperature, chlorophyll-*a*, and bacterial abundance in the Red Sea (Raitsos et al., 2013; Silva et al., 2019). We believe that this approach enhances the opportunities of detecting and measuring the spatial extent of organic and inorganic enrichment in the water column associated with fish farm.

4.2. Ecological and management implications

Excess nutrients and particulate matter from this or other fish farms in tropical areas could impact these typically low-nutrient environments, both in the pelagic and benthic habitats. Phosphorus is often a limiting nutrient in the marine environment and sometimes in the Red Sea (Kürten et al., 2019; Silva et al., 2019), and phosphorus enrichment has been shown to stimulate photosynthetic production (Elser et al.,

2007), which can lead to a suite of repercussions resulting from enhanced phytoplankton growth, such as decreases in water column transparency, and eventually depletion of subsurface water oxygen (Smith, 2003). Like others in tropical regions, this farm is located in an area with many coral reefs, seagrasses, and mangroves, and both nutrient loading and particulate organic matter sedimentation can cause disturbances in these habitats. Phosphorus enrichment has been linked with reductions in coral skeletal density, reduction in coral population size, and reef-wide shifts from calcifying reef building organisms to macroalgae and rubble (Koop et al., 2001; Smith, 2003; Martinez-Escobar and Mallela, 2019). Excess nitrogen has been shown to promote the growth of N-limited turf algae on Red Sea coral reefs (Karcher et al., 2020), and nutrient enrichment has been shown to exacerbate the effects of heat stress to spark mass coral bleaching in the Red Sea (Decarlo et al., 2020). Nutrient enrichment can decrease the resilience of mangroves and increase their mortality during drought (Lovelock et al., 2009), and sedimentation and nutrient loading can interact to decrease seagrass survival (Ceccherelli et al., 2018).

Monitoring and mitigation of excess inorganic nutrients and organic matter loading from fish farms will be important for protecting these typically nutrient-poor ecosystems, particularly as aquaculture continues to develop in tropical coastal waters around the globe. In this study, the clearest signals of nutrient and particulate matter enrichment from the farms were seen around the time of a feeding event, suggesting that excess feed escaping the cages could be contributing the farm's effluent. Feed wastage has been flagged as a major contributor to organic and nutrient loadings from aquaculture facilities (Cao et al., 2007), and the management of feed has been suggested as a primary solution for mitigating the environmental impacts of aquaculture (Dauda et al., 2019). Overfeeding should be avoided and feeds with more bioavailable nutrients (which are incorporated into fish biomass rather than excreted undigested) can be selected to limit the waste from feeding activities. Water quality monitoring by farm operators can help track the efficiency or wastage of different feeding strategies.

Site selection is also an important factor in fish farm operation. The farm in this study was built in a relatively open, well-flushed part of the coastline rather than an embayment with little water exchange. The water movement around the farm likely dispersed nutrients and particulate matter and limited the accumulation of these pollutants more than if it had been in a protected, less hydrodynamically active area. The hydrodynamics and water residence times should be considered in the selection of future fish farm sites. Other management techniques, such as reducing density of farms, avoiding areas with sensitive benthic habitats, and using integrated multitrophic aquaculture (culturing organisms of different trophic levels in the same area to reduce nutrient concentrations) have also been suggested as ways to reduce the environmental impacts of fish farm waste pollution (Gentry et al., 2017b; Klinger and Naylor, 2012).

5. Conclusion

As aquaculture production rates increase to feed our growing demand for seafood, and coastal countries develop more fish farming in tropical regions, this study provides an example of the nutrient enrichment that can result from aquaculture facilities in warm, oligotrophic waters. The changes in water quality associated with the location of the fish farm over the study period indicate that this Red Sea fish farm causes local organic and inorganic enrichment. The increased levels of nutrients emitted is a deviation from the natural condition of this and other tropical seas. Overall, patterns of enrichment associated with the fish farm were fairly local in spatial extent. Elevated levels of nutrients and particulate matter were generally limited to the sampling stations closest to the farm, with strong signals of these variables being detected less than 1 km away from the fish farm boundaries and rarely showing elevated concentrations beyond this distance, although delayed impacts further down-current are possible and may not have been detected

within our radius of sampling. The extent of measurable changes to water column chemistry were typically detectable within several hundred meters of the fish farm, which provides an example of how this system reacts to organic loading and dissipates waste from offshore aquaculture. This radius of impact coupled with measurable down-current effects suggests managers should not only take into consideration the main currents around aquaculture facilities, but also to keep a safe distance from sensitive habitats like coral reefs and mangroves to minimize potential negative impacts. The outputs that this and other fish farms emit should be considered as coastal regions expand sizes and production rates of offshore aquaculture, thereby magnifying the impact. If fish farms are developed more widely along tropical coastlines, particularly in semi-enclosed basins like the Red Sea which have restricted water inflow and outflow, the possibility of affecting larger areas of the basin should be considered in planning.

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CRediT authorship contribution statement

Aislinn Dunne: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Susana Carvalho:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Xosé Anxelu G. Morán:** Conceptualization, Resources, Writing – review & editing, Supervision. **Maria Ll. Calleja:** Methodology, Investigation, Writing – review & editing. **Burton Jones:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2021.112732>.

References

- Al-Otaibi, N., Huete-Stauffer, T.M., Calle, M.L., Irigoien, X., Moran, X.A.G., 2020. Seasonal variability and vertical distribution of autotrophic and heterotrophic picoplankton in the Central Red Sea. *PeerJ* 8, 25.
- Alongi, D.M., 1994. The role of bacteria in nutrient recycling in tropical mangrove and other coastal benthic ecosystems. In: *Ecology and Conservation of Southeast Asian Marine and Freshwater Environments Including Wetlands*. Springer.
- Apostolaki, E.T., Tsagaraki, T., Tsapakis, M., Karakassis, I., 2007. Fish farming impact on sediments and macrofauna associated with seagrass meadows in the Mediterranean. *Estuar. Coast. Shelf Sci.* 75, 408–416.
- Basaran, A.K., Aksu, M., Egemem, O., 2010. Impacts of the fish farms on the water column nutrient concentrations and accumulation of heavy metals in the sediments in the eastern Aegean Sea (Turkey). *Environ. Monit. Assess.* 162, 439–451.
- Becker, C., Hughen, K., Mincer, T.J., Ossolinski, J., Weber, L., Apprill, A., 2017. Impact of prawn farming effluent on coral reef water nutrients and microorganisms. *Aquac. Environ. Interact.* 9, 331–346.
- Birkicht, M., 2012. Standard Operation Procedure: Fluorometric Ammonium Determination. Leibniz ZMT.
- Bongiorni, L., Shafir, S., Rinkevich, B., 2003. Effects of particulate matter released by a fish farm (Eilat, Red Sea) on survival and growth of *Stylophora pistillata* coral nubbins. *Mar. Pollut. Bull.* 46, 1120–1124.
- Bostock, J., McAndrew, B., Richards, R., Jauncey, K., Telfer, T., Lorenzen, K., Little, D., Ross, L., Handisyde, N., Gatward, I., 2010. Aquaculture: global status and trends. *Philos. Trans. R. Soc. Lond. B* 365, 2897–2912.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789.
- Calleja, M.L., Al-Otaibi, N., Morán, X.A.G., 2019. Dissolved organic carbon contribution to oxygen respiration in the Central Red Sea. *Sci. Rep.* 9, 1–12.
- Calvo-Díaz, A., Morán, X.A.G., 2006. Seasonal dynamics of picoplankton in shelf waters of the southern Bay of Biscay. *Aquat. Microb. Ecol.* 42, 159–174.
- Cao, L., Wang, W., Yang, Y., Yang, C., Yuan, Z., Xiong, S., Diana, J., 2007. Environmental impact of aquaculture and countermeasures to aquaculture pollution in China. *Environ. Sci. Pollut. Res. Int.* 14, 452–462.
- Castine, S.A., Bourne, D.G., Trott, L.A., McKinnon, D.A., 2009. Sediment microbial community analysis: establishing impacts of aquaculture on a tropical mangrove ecosystem. *Aquaculture* 297, 91–98.
- Ceccherelli, G., Oliva, S., Pinna, S., Piazzoli, L., Procaccini, G., Marin-Guirao, L., Dattolo, E., Gallia, R., la Manna, G., Gennaro, P., Costa, M.M., Barrote, I., Silva, J., Bulleri, F., 2018. Seagrass collapse due to synergistic stressors is not anticipated by phenological changes. *Oecologia* 186, 1137–1152.
- Chaves, R.C., Figueredo, C.C., Boëchat, I.G., Gücker, B., 2021. Impacts of fish farming on elemental stoichiometry, fluorescence components, and stable isotopes of dissolved organic matter in a tropical reservoir. *Environ. Pollut.* 268, 115704.
- Dauda, A.B., Ajadi, A., Tola-Fabunmi, A.S., Akinwole, A.O., 2019. Waste production in aquaculture: sources, components and managements in different culture systems. *Aquac. Fish.* 4, 81–88.
- Decarlo, T.M., Gajdzik, L., Ellis, J., Coker, D.J., Roberts, M.B., Hammerman, N.M., Pandolfi, J.M., Monroe, A.A., Berumen, M.L., 2020. Nutrient-Supplying Ocean currents modulate coral bleaching susceptibility. *Sci. Adv.* 6, eabc5493.
- Delgado, O., Grau, A., Pou, S., Riera, F., Massuti, C., Zabala, M., Ballesteros, E., 1997. Seagrass regression caused by fish cultures in Fornells Bay (Menorca, Western Mediterranean). *Oceanol. Acta* 20, 557–563.
- Elser, J.J., Bracken, M.E., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B., Smith, J.E., 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* 10, 1135–1142.
- Fahmy, M., 2003. Water quality in the Red Sea coastal waters (Egypt): analysis of spatial and temporal variability. *Chem. Ecology* 19, 67–77.
- FAO, 2020. The State of World Fisheries and Aquaculture 2020. Sustainability in Action. The State of World Fisheries and Aquaculture. Food and Agriculture Organization of the United Nations, Rome.
- Farmaki, E.G., Thomaidis, N.S., Pasias, I.N., Baulard, C., Papaharisis, L., Efsthathiou, C.E., 2014. Environmental impact of intensive aquaculture: investigation on the accumulation of metals and nutrients in marine sediments of Greece. *Sci. Total Environ.* 485, 554–562.
- Gasol, J.M., Moran, X.A.G., 2015. Flow cytometric determination of microbial abundances and its use to obtain indices of community structure and relative activity. In: *Hydrocarbon and Lipid Microbiology Protocols*. Springer.
- Gentry, R.R., Froehlich, H.E., Grimm, D., Kareiva, P., Parke, M., Rust, M., Gaines, S.D., Halpern, B.S., 2017a. Mapping the global potential for marine aquaculture. *Nat. Ecol. Evol.* 1, 1317.
- Gentry, R.R., Lester, S.E., Kappel, C.V., White, C., Bell, T.W., Stevens, J., Gaines, S.D., 2017b. Offshore aquaculture: spatial planning principles for sustainable development. *Ecol. Evol.* 7, 733–743.
- Gundersen, K., Heldal, M., Norland, S., Purdie, D.A., Knap, A.H., 2002. Elemental C, N, and P cell content of individual bacteria collected at the Bermuda Atlantic time-series study (BATS) site. *Limnol. Oceanogr.* 47, 1525–1530.
- Holm-Hansen, O., Lorenzen, C.J., Holmes, R.W., Strickland, J.D.H., 1965. Fluorometric determination of chlorophyll. *ICES J. Mar. Sci.* 30, 3–15.
- Holmer, M., Hansen, P.K., Karakassis, I., Borg, J.A., Schembri, P.J., 2008. Monitoring of Environmental Impacts of Marine Aquaculture. *Aquaculture in the Ecosystem*. Springer Netherlands, Dordrecht.
- Holmer, M., Marba, N., Terrados, J., Duarte, C.M., Fortes, M.D., 2002. Impacts of milkfish (*Chanos chanos*) aquaculture on carbon and nutrient fluxes in the bolinao area, Philippines. *Mar. Pollut. Bull.* 44, 685–696.
- Hozumi, A., Hong, P.-Y., Kaartvedt, S., Røstad, A., Jones, B.H., 2018. Water quality, seasonality, and trajectory of an aquaculture-wastewater plume in the Red Sea. *Aquac. Environ. Interact.* 10, 61–77.
- Kamjunke, N., Nimptsch, J., Harir, M., Herzsprung, P., Schmitt-Kopplin, P., Neu, T.R., Graeber, D., Osorio, S., Valenzuela, J., Reyes, J.C., 2017. Land-based salmon aquacultures change the quality and bacterial degradation of riverine dissolved organic matter. *Sci. Rep.* 7, 43739.
- Karcher, D.B., Roth, F., Carvalho, S., El-Khaled, Y.C., Tilstra, A., Kürten, B., Struck, U., Jones, B.H., Wild, C., 2020. Nitrogen eutrophication particularly promotes turf algae in coral reefs of the Central Red Sea. *PeerJ* 8, e8737.
- Karner, M.B., Delong, E.F., Karl, D.M., 2001. Archaeal dominance in the mesopelagic zone of the Pacific Ocean. *Nature* 409, 507–510.
- Kaushik, S., Coves, D., Dutto, G., Blanc, D., 2004. Almost total replacement of fish meal by plant protein sources in the diet of a marine teleost, the European seabass, *Dicentrarchus labrax*. *Aquaculture* 230, 391–404.
- Kheireddine, M., Dall'Olmo, G., Ouhssain, M., Krokos, G., Claustre, H., Schmechtig, C., Poteau, A., Zhan, P., Hoteit, I., Hossain, B.H., 2020. Organic carbon export and loss rates in the Red Sea. *Glob. Biogeochem. Cycles* 34, e2020GB006650.
- Klinger, D., Naylor, R., 2012. Searching for solutions in aquaculture: charting a sustainable course. *Annu. Rev. Environ. Resour.* 37, 247–276.
- Koop, K., Booth, D., Broadbent, A., Brodie, J., Bucher, D., Capone, D., Coll, J., Dennison, W., Erdmann, M., Harrison, P., 2001. ENCORE: the effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. *Mar. Pollut. Bull.* 42, 91–120.

- Kürten, B., Zarokanellos, N.D., Devassy, R.P., El-Sherbiny, M.M., Struck, U., Capone, D. G., Schulz, I.K., Al-Aidaros, A.M., Irigoien, X., Jones, B.H., 2019. Seasonal modulation of mesoscale processes alters nutrient availability and plankton communities in the Red Sea. *Prog. Oceanogr.* 173, 238–255.
- la Rosa, T., Mirto, S., Favaloro, E., Savona, B., Sarà, G., Danovaro, R., Mazzola, A., 2002. Impact on the water column biogeochemistry of a Mediterranean mussel and fish farm. *Water Res.* 36, 713–721.
- Leoni, B., Patelli, M., Soler, V., Nava, V., 2018. Ammonium transformation in 14 lakes along a trophic gradient. *Water* 10, 265.
- Link, J.S., Watson, R.A., 2019. Global ecosystem overfishing: clear delineation within real limits to production. *Sci. Adv.* 5, 11.
- Lovelock, C.E., Ball, M.C., Martin, K.C., Feller, I.C., 2009. Nutrient enrichment increases mortality of mangroves. *Plos One* 4, 4.
- Mackey, K.R., Labiosa, R.G., Calhoun, M., Street, J.H., Post, A.F., Paytan, A., 2007. Phosphorus availability, phytoplankton community dynamics, and taxon-specific phosphorus status in the Gulf of Aqaba, Red Sea. *Limnol. Oceanogr.* 52, 873–885.
- Martinez-Escobar, D.F., Mallela, J., 2019. Assessing the impacts of phosphate mining on coral reef communities and reef development. *Sci. Total Environ.* 692, 1257–1266.
- Mayor, D.J., Gray, N.B., Hattich, G.S., Thornton, B., 2017. Detecting the presence of fish farm-derived organic matter at the seafloor using stable isotope analysis of phospholipid fatty acids. *Sci. Rep.* 7, 5146.
- McKinnon, A.D., Trott, L.A., Brinkman, R., Duggan, S., Castine, S., O’Leary, R.A., Alongi, D.M., 2010. Seacage aquaculture in a world heritage area: the environmental footprint of a barramundi farm in tropical Australia. *Mar. Pollut. Bull.* 60, 1489–1501.
- Morata, T., Falco, S., Gadea, I., Sospedra, J., Rodilla, M., 2015. Environmental effects of a marine fish farm of gilthead seabream (*Sparus aurata*) in the NW Mediterranean Sea on water column and sediment. *Aquac. Res.* 46, 59–74.
- Morii, H., Nishikata, K., Tamura, O., 1978. Nitrogen excretion of mudskipper fish *Periophthalmus cantonensis* and *Boleophthalmus boddarti* in water and on land. *Comp. Biochem. Physiol. A Physiol.* 60, 189–193.
- Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280.
- Navarro, N., Leakey, R.J.G., Black, K.D., 2008. Effect of salmon cage aquaculture on the pelagic environment of temperate coastal waters: seasonal changes in nutrients and microbial community. *Mar. Ecol. Prog. Ser.* 361, 47–58.
- Nugues, M.M., Roberts, C.M., 2003. Coral mortality and interaction with algae in relation to sedimentation. *Coral Reefs* 22, 507–516.
- Olsen, L.M., Hernández, K.L., van Ardelan, M., Iriarte, J.L., Bizsel, K.C., Olsen, Y., 2017. Responses in bacterial community structure to waste nutrients from aquaculture: an in situ microcosm experiment in a Chilean fjord. *Aquac. Environ. Interact.* 9, 21–32.
- Pauly, D., Watson, R., Alder, J., 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. *Philos. Trans. R. Soc. B* 360, 5–12.
- Pitta, P., Apostolaki, E., Giannoulaki, M., Karakassis, I., 2005. Mesoscale changes in the water column in response to fish farming zones in three coastal areas in the eastern Mediterranean Sea. *Estuar. Coast. Shelf Sci.* 65, 501–512.
- R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>.**
- Raitsos, D.E., Pradhan, Y., Brewin, R.J.W., Stenchikov, G., Hoteit, I., 2013. Remote sensing the phytoplankton seasonal succession of the Red Sea. *Plos One* 8, 9.
- Redfield, A.C., 1958. The biological control of chemical factors in the environment. *Am. Sci.* 46, 230A–221.
- Regaudie-De-gioux, A., Duarte, C.M., 2012. Temperature dependence of planktonic metabolism in the ocean. *Glob. Biogeochem. Cycles* 26.
- Sabbagh, E.I., Huete-Stauffner, T.M., Calleja, M.L.L., Silva, L., Viegas, M., Moran, X.A.G., 2020. Weekly variations of viruses and heterotrophic nanoflagellates and their potential impact on bacterioplankton in shallow waters of the Central Red Sea. *FEMS Microbiol. Ecol.* 96, 16.
- Shpigel, M., Guttman, L., Ben-Ezra, D., Yu, J., Chen, S., 2019. Is *ulva* sp. able to be an efficient biofilter for mariculture effluents? *J. Appl. Phycol.* 1–11.
- Silva, L., Calleja, M.L., Huete-Stauffner, T.M., Ivetic, S., Ansari, M.I., Viegas, M., Morán, X. A.G., 2019. Low abundances but high growth rates of coastal heterotrophic bacteria in the Red Sea. *Front. Microbiol.* 9, 3244.
- Smith, V.H., 2003. Eutrophication of freshwater and coastal marine ecosystems - a global problem. *Environ. Sci. Pollut. Res.* 10, 126–139.
- Storebakken, T., Shearer, K., Roem, A., 1998. Availability of protein, phosphorus and other elements in fish meal, soy-protein concentrate and phytase-treated soy-protein-concentrate-based diets to Atlantic salmon, *Salmo Salar*. *Aquaculture* 161, 365–379.
- Ticina, V., Katavic, I., Grubišić, L., 2020. Marine aquaculture impacts on marine biota in oligotrophic environments of the Mediterranean Sea – a review. In: *Front. Mar. Sci.*
- Vieira, A.R., Gonzalez, C., Martins-Loução, M.A., Branquinho, C., 2009. Intracellular and extracellular ammonium (NH₄⁺) uptake and its toxic effects on the aquatic biomonitor *Fontinalis antipyretica*. *Ecotoxicology* 18, 1087–1094.
- Villanueva, R.D., Yap, H.T., Montañó, M.N.E., 2005. Survivorship of coral juveniles in a fish farm environment. *Mar. Pollut. Bull.* 51, 580–589.