ICES Journal of
Marine Science

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2021), 78(4), 1386–1397. doi:10.1093/icesjms/fsaa249

# Wrasse fishery on the Swedish West Coast: towards ecosystem-based management

Sarah J. Bourlat [1]*, Ellika Faust[2,3], Håkan Wennhage[4], Andreas Wikström[4], Kristie Rigby[2], Maria Vigo[2], Paul Kraly[2], Erik Selander[2], and Carl André[3]

[1]*Centre for Biodiversity Monitoring, Zoological Research Museum Alexander Koenig, Adenauerallee 160, Bonn 53113, Germany*
[2]*Department of Marine Sciences, University of Gothenburg, Gothenburg SE-450 30, Sweden*
[3]*Department of Marine Sciences-Tjärnö, University of Gothenburg, Strömstad SE-452 96, Sweden*
[4]*Department of Aquatic, Resources, Institute of Marine Research, Swedish University of Agricultural Sciences (SLU), Box 4, Lysekil SE-45330, Sweden*

**Corresponding author: tel: +49 228 9122 353; e-mail: s.bourlat@leibniz-zfmk.de.*

Bourlat, S. J., Faust, E., Wennhage, H., Wikström, A., Rigby, K., Vigo, M., Kraly, P., Selander, E., and André, C. Wrasse fishery on the Swedish West Coast: towards ecosystem-based management. – ICES Journal of Marine Science, 78: 1386–1397.

Received 9 September 2020; revised 15 December 2020; accepted 15 December 2020; advance access publication 10 March 2021.

Fishing and translocation of marine species for use in aquaculture is widespread. Corkwing, goldsinny, and ballan wrasse (*Symphodus melops*, *Ctenolabrus rupestris*, and *Labrus bergylta*) are fished on the Swedish west coast for use as cleaner-fish in Norwegian salmon farms. Here, we aim to provide knowledge and recommendations to support ecosystem-based management for wrasse fisheries in Sweden. We compared fished and non-fished areas to test if current fishery levels have led to stock depletion. To gain insight on the role of wrasse in the algal belt trophic chain, we analysed the gut contents of goldsinny and corkwing using metabarcoding. Finally, we analysed the trophic interactions of wrasse and potential prey in a mesocosm study. We could not detect any signs of stock depletion or altered size structure in fished areas compared to the protected control area. Gut analyses confirmed both goldsinny and corkwing as non-specialized, omnivorous opportunists and revealed, with 189 prey taxa detected, a broader spectrum of prey than previously known. Common prey items included mesoherbivores such as small gastropods and crustaceans, but also insects and algae. We conclude that there are no visible signs of stock depletion at the current removal level of wrasses by the fishery. However, this emerging fishery should be closely monitored for potential cascading effects on the algal belt ecosystem, and our study could provide a baseline for future monitoring.

**Keywords:** cleaner fish, *Ctenolabrus rupestris*, diet analysis, ecosystem-based management, mesocosm, metabarcoding, Symphodus melops, wrasse fisheries

## Introduction

Sea lice infestation is a major problem faced by the salmon aquaculture industry, and the use of wild caught cleaner-fish to control the lice is seen as the most environmentally-friendly option compared to other methods (Gonzalez and de Boer, 2017), and more effective than chemical treatments in the case of diseased or stressed salmon (Deady *et al.*, 1995). Over the last decade, the number of cleaner fish used in the Norwegian salmon production has increased from 1.7 million in 2008, to 61 million in 2019. This includes farmed lumpfish and ballan wrasse, but 37% is wild caught fish, of which wrasses constitute the largest share (92%) (Norwegian Directorate of Fisheries, 2019). Norwegian fisheries alone can no longer support the demand from the salmon industry, and approximately 1 million wild-caught wrasses are imported from the Swedish Skagerrak coast yearly since 2010 (Halvorsen *et al.*, 2017a). The Swedish wrasse fishery targets corkwing wrasse (*S. melops*), goldsinny wrasse (*C. rupestris*), and ballan wrasse (*L. bergylta).* Wrasse were not previously considered a commercial species and information on stock structure and population dynamics is scarce. There is consequently not enough data to support an ecosystem-based management plan for the wrasse fishery.

The three species of wrasse are known to have high site fidelity and narrow home ranges, which would suggest low levels of migration and the existence of local populations (Sayer, 1999; Villegas-Ríos *et al.*, 2013; Halvorsen *et al.*, 2017a). Recent studies along the Norwegian Skagerrak coast found that local wrasse populations show signs of depletion. Catches per unit effort of goldsinny wrasse were 33–65% higher in marine protected areas (MPAs) and also higher in three out of four MPAs for corkwing wrasse (−16 to +92%). In addition, corkwing wrasse above the minimum size (12 cm) were older and larger in MPAs, although this was not the case for goldsinny wrasse (Halvorsen *et al.*, 2017a). Many wrasse species have complex reproduction strategies, such as sequential hermaphroditism or sneaking behaviour, and often display large size differences between sexes and reproductive strategies. It has thus been suggested that a minimum size limit may target the alternative sexes and male strategies differently (Halvorsen *et al.*, 2016, 2017b). This can have important consequences for population productivity, especially as both ballan and corkwing wrasse have obligate male parental care and are considerably larger than their female counterparts. The Swedish wrasse fishery started in 2010, and no comparisons of fished and non-fished areas have yet been made.

Wrasses are key intermediate predators in the coastal algal belt (Skiftesvik *et al.*, 2015). Caging experiments in seagrass meadows on the Swedish Skagerrak coast show that predatory fish including wrasses reduce the numbers of mesoherbivores such as small crustaceans and gastropods, which in turn results in a several fold increase in fouling algae (Moksnes *et al.*, 2008). Thus, it is possible that wrasse fisheries may lead to structuring effects in the algal belt ecosystem that go beyond the depletion of the target wrasse species. Mesopredatory fish have generally increased, which has been attributed to the depletion of larger piscivorous fish stocks (Sieben *et al.*, 2011). Thus, removing wrasse by fishing should in theory release mesoherbivores from predation and thereby reduce fouling organisms.

Traditional gut content analyses have shown that corkwing wrasse feed extensively on small mesoherbivores. The gut contents of corkwing from Ireland and France were dominated by gastropods, amphipods, isopods, ostracods, bivalves, and polychaete worms, with crustaceans favoured by younger, smaller fish and molluscs by older, larger fish (Deady and Fives, 1995). Other prey species found included hydrozoans, cirripedes, copepods, decapods, echinoderms, oligocheates, fish eggs, insects, and algae (Deady and Fives, 1995; Sayer *et al.*, 1996). Goldsinny have been shown to feed on small invertebrates such as gastropods, bivalves, hydrozoans, cirripedes, amphipods, copepods, decapods, isopods, polychaetes, and bryozoans (Sayer *et al.*, 1996, Deady and Fives, 1995). Traditional gut content analyses are however limited to morphologically identifiable remains and the full diet and detailed position in the food web is still poorly known for wrasse.

Here we aim to gather some of the fundamental data needed to implement an ecosystem based approach to management of this new emerging fishery. We compare catch per unit effort in fished and non-fished areas in Sweden over 4 fishing seasons from 2014 until 2017. In addition, we monitor coverage of the epiphytic community on *Saccharina latissima*, a habitat building brown alga in the study area. We establish the full diet of two of the most abundant and harvested species, goldsinny and corkwing wrasse using metabarcoding methods, which combine DNA-based identification and high-throughput sequencing, allowing the simultaneous identification of a wide array of prey species, even from highly digested gut contents (Pompanon *et al.*, 2012). Metabarcoding allows the identification of many more prey taxa than visual identification, as well as higher taxonomic resolution (Jakubavičiūtė *et al.*, 2017). Accurate diet determination will provide important information on the role of wrasse as a mesopredatory fish in the algal belt and the potential cascading effects of their removal on the ecosystem. To gain a mechanistic understanding of the effects of wrasse in the algal belt, we performed a controlled mesocosm study, where wrasse presence was manipulated in a simplified community of habitat building brown algae and mesoherbivores, and fouling organisms were monitored over time.

## Material and methods

### Fish survey

To understand if local wrasse populations show signs of depletion, such as lower density or average size in fished areas, we compared a marine protected area (Kåvra: 58.33 N , 11.36E) with two adjacent fished areas (Byxeskär: 58.25 N , 11.38E and Stora Kornö: 58.29 N , 11.37E, see Figure 1). Kåvra is a 2.6 $km^2$ marine protected area in Bohuslän on the west coast of Sweden. Fishing has been prohibited in Kåvra since 1989, thus predating the start of the Swedish wrasse fishery by more than twenty years. In the process of finding fished areas to compare with the marine protected area Kåvra, a discussion was held with fishermen targeting wrasse in Lysekil. The fishermen pinpointed fishing grounds around Stora Kornö and Byxeskär. In order to estimate how much these areas were potentially being used as fishing grounds, statistics from the fishermen's mandatory extended journals were compiled. Fishermen who have been granted a licence to fish and sell wrasse are required to report their catch on a daily basis, including information on the number of individuals per species, number of gears used (fyke nets/creels), and area used as a fishing ground. The area used as a fishing ground is defined by specifying the northernmost and southernmost positions, allowing the daily geographical determination of fishing grounds. By doing this and noting if the reference areas are within the fishing grounds, a ratio of how much of these areas are potentially being used as fishing grounds for wrasse was determined for the fishing seasons 2014–2017. The total number of fishing days per season varied between 102 and 127 days for the years studied. The data originate from two fishermen active in the area (Table 1).

For the field sampling, wrasse creels (81×40×28 cm with double entrances 4×9 cm and a mesh size of 10 mm) and fyke nets (double-codend with 3 chambers and 7 hoops, the largest 30 cm, 6 m leader, mesh size 10 mm in codend and 15 mm in leader) were used. These were the same gear as those used by commercial wrasse fishermen. Sites for fyke net deployment were randomized within each area (St. Kornö, Byxeskär, and Kåvra) across three different depth intervals, 0–6, 6–10, and 10–20 m (SwAM, 2016). Wrasse cages were deployed between 0 and 7 m depth and frozen shrimp were used as bait. In commercial fishing, fyke nets are used to target ballan and corkwing wrasse, while cages (creels) are normally used to target goldsinny wrasse. A total of 108 creels

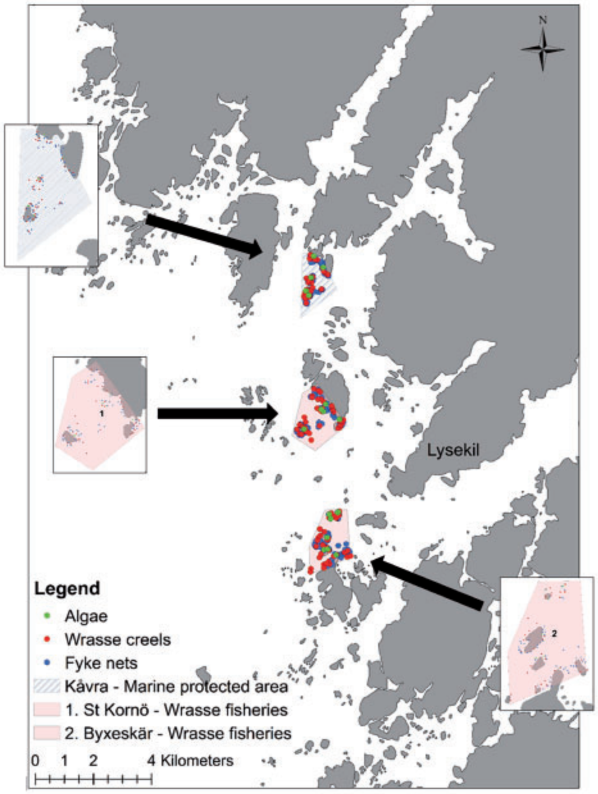

**Figure 1.** Map of the study area outside Lysekil on the Swedish Skagerrak coast. The Kåvra area (hashed area) is a marine reserve where wrasse have not been fished for the last 30 years. Both St. Kornö and Byxeskär (pink areas) have been subjected to an active wrasse fishery since 2013. The blue dots show the positions for the fyke net deployments, the red dots the wrasse creels, and the green dots represent the localities where 10 *S. latissima* algae were bag-sampled.

**Table 1.** Total number of fishing days for two local fishermen targeting wrasse during 2014–2017 and the estimated number of days (given as % of the total number of days per fishing season) spent fishing within Stora Kornö and Byxeskär.

| Year | Total number of fishing days | Area | Days fished (%) including the area |
|---|---|---|---|
| 2014 | 127 | Stora Kornö | 74.8 |
| | | Byxeskär | 58.3 |
| 2015 | 116 | Stora Kornö | 69.0 |
| | | Byxeskär | 85.3 |
| 2016 | 120 | Stora Kornö | 58.3 |
| | | Byxeskär | 69.2 |
| 2017 | 102 | Stora Kornö | 65.7 |
| | | Byxeskär | 81.4 |

There were no records of fishing in the MPA Kåvra.

and 162 fyke nets were deployed across the three different sites, 12 creels and 18 fyke nets per day over a 9-day period between 14.08.2016 until 23.08.2016 with an average soak time of 23.4 h (see Figure 1).

Organisms caught were classified to species, counted, measured, and released immediately after each haul. When larger numbers of a single species were caught, only a subsample was measured to minimize suffering and handling time. A subset of the corkwing and goldsinny wrasse from the three study areas (24 corkwing and 24 goldsinny wrasse individuals from each of the three study areas, giving a total of 144 fish) was euthanized using MS222 and kept on ice for gut content analysis. The catch was standardized to catch per gear per 24 h, defined as catch per unit effort (CPUE), enabling comparison of data between samples independent of soak time. To evaluate the difference in CPUE between the studied areas a permutational MANOVA (PERMANOVA) was used with Area as a fixed factor. Analyses were performed using the software Prime 7 version 7.0.10 (with add on PERMANOVA+). Resemblance matrices were calculated upon Bray–Curtis coefficient of similarity with data square root transformed. To test the data for homogeneity of dispersion, a PERMDISP test (Distance based test for homogeneity of multivariate dispersions) was conducted.

## Algal samples

In each fishing area (St. Kornö, Byxeskär, and Kåvra), we also hand-sampled ten individuals of the brown alga *S. latissima* together with their associated fauna in six places (Figure 1). Plastic polyethylene bags approximately 1 m×0.3 m were prepared by heat sealing polyethylene layflat tubing. The bag was threaded inside out over the arm of the diver. The diver then submerged to 2–5 m, pinched the apical tip of the first encountered *S. latissimia* through the bag, and pulled the base of the bag over the entire thallus. The hapter was snapped and the alga brought to the surface inside the bag. Water was drained through a 200 μm mesh sieve to retain organisms in the sampling bag. The algae were stored on ice at sea, and frozen at −15°C until further analysis.

## Gut content analyses

Fish for gut content analysis were kept on ice until transport to the lab, after which they were frozen whole and kept at −20°C. Prior to dissection, fish were slowly defrosted at 4°C, measured, weighed, and sexed. Stomachs were removed and contents were flushed with 95% ethanol to remove all content. The dissection tools were cleaned and rinsed with bleach and Milli-Q water between each dissection to avoid cross-contamination. Dissected stomach contents were stored at −20°C in 95% EtOH until DNA extraction. Gut content DNA was extracted from 24 corkwing and 24 goldsinny wrasse individuals from each of the three study areas, giving a total of 144 samples. Each sample was homogenized in ethanol using a Polytron PT1200c handheld homogeniser (Kinematica AG). A subsample of 0.1–0.6 ml of the homogenate was taken and transferred to an eppendorf tube. The ethanol was removed by centrifuging the sample and removing the supernatant. DNA was extracted using the DNeasy Blood & Tissue Kit (Qiagen) with optional RNAse treatment (200 mg RNAse). DNA quantity and quality (i.e. presence of contaminants, degradation etc.) were assessed using the Qubit dsDNA BR AssayKit (Invitrogen–ThermoFisher Scientific) and on a 1% agarose gel. Samples which amplified poorly during PCR were also purified with standard ethanol/isopropanol precipitation.

## Metabarcoding of gut content

Mitochondrial cytochrome oxidase 1 was amplified from the gut content DNA using metazoan primers developed by Leray *et al.* (2013), yielding a 313 bp fragment termed the "mini-barcode" (mICOIintF-dgHCO2198). The amplicon primers (mlCOIintF_MiSeq: TCGTCGGCAGCGTCAGATGTGTATAAGAGACAG**GGWACWGGWTGAACWGTWTAYCCYCC** and dgHCO2198_MiSeq: GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAG**TAAACTTCAGGGTGACCAAARAAYCA**) included illumina overhang adapter sequences (shown in regular font).

Amplicon library preparation was carried out using the dual PCR amplification method described in (Bourlat *et al.*, 2016). To avoid preferential amplification of the predominant, less degraded predator sequences, specific blocking primers were designed as described in (Leray *et al.*, 2013). These blocking primers for *S. melops* (CAAAGAATCAAAATAGATGTTGATAAAGAA-C3) and *C. rupestris* (CAAAGAATCAAAATAAGTGTTGATAAAGGA-C3) include a Spacer C3-CPG at the 3′ end to prevent elongation without affecting annealing. It is worth noting here that the blocking primer for goldsinny (*C. rupestris)* was inefficient. For each sample, three independent PCR reactions were performed and later pooled, ensuring greater coverage of prey items amplified. Amplicon PCRs were performed as 25 µl reactions with 20 pm of each primer and 100 pm of blocking primer and using Pfu proofreading DNA polymerase (Promega). Cycling conditions were as follows: 2 min at 95°C (1×); 1 min at 95°C, 45 s at 57°C, 1 min at 72°C (25×); 5 min at 72°C (1×); hold at 4°C. Amplicons were checked on a 2% agarose gel. In a second PCR step, Illumina dual index adapters were incorporated to the amplicons using a limited number of cycles before sequencing as paired-ends using Illumina MiSeq 1.8, reagent v3 (Macrogen). 108 stomach content samples were successfully sequenced producing a total of 47 129 702 raw reads of 300 bp in length. Raw sequence data for this project are deposited at the NCBI SRA under BioProject ID PRJNA655463 and BioSample accessions SAMN15735264–SAMN15735371.

## Bioinformatic processing and analysis

Raw reads were demultiplexed using bcl2fastq v2.20.0.422 (Macrogen), yielding a total of 23 563 377 paired-end reads. The 108 forward and 108 reverse demultiplexed fastq sequences were trimmed of their forward (GGWACWGGWTGAACWGTWTAYCCYCC) and reverse (TAAACTTCAGGGTGACCAAARAAYCA) primers using the following parameters (cutadapt -g GGWACWGGWTGAACWGTWTAYCCYCC -G TAAACTTCAGGGTGACCAAARAAYCA -e 0.1 -O 10 -m 150 -j 0 –discard-untrimmed) in cutadapt version 1.18 (Martin, 2011). The primer trimmed sequences were then imported in Qiime2 version 2018.11 (Bolyen *et al.*, 2019) for further processing using the denoiser DADA2, which infers amplicon sequence variants (ASVs) from Illumina amplicon data (Callahan *et al.*, 2016). Denoising removes errors introduced by amplification and sequencing, and allows the inference of biological sequences in the data without the arbitrary dissimilarity thresholds used for OTU clustering.

After quality filtering, denoising, merging, and chimera-removal steps in DADA2, a total of 2 514 227 non-chimeric reads were produced. Taxonomy assignment was carried out with the Qiime 2 feature classifier using a consensus BLAST search at 97% identity against the GenBank database downloaded on the 12th of November 2018. The classification resulted in a total of 3 933 assigned and unassigned ASVs.

The blocking primers designed to block *C. rupestris* were inefficient, resulting in this sequence dominating the gut content samples for this species. This means that the gut content data produced for our two species are not quantitative with respect to relative abundances but that presence/absence metrics can be used instead to infer frequency of occurrence. In addition, predator sequences (*C. rupestris*, *S. melops*, and *L. bergylta*) were found in most of the samples, presumably due to cross contamination from handling of the fish in the field. Therefore, all sequences derived from our species of interest (*C. rupestris*, *S. melops*, and *L. bergylta)* were removed from the dataset using the qiime script taxa filter-table. Records from mammals and birds which are derived from environmental DNA present in the field were also removed. To enable analysis independently of read counts, ASV numbers were transformed into a binary presence/absence matrix. Frequency of occurrence (FOO) of each prey item was then computed, corresponding to the percentage of individual fish in which a prey ASV was found (%FOO)(Deagle *et al.*, 2019). For the plots (Figures 5–7) we used only ASVs identified to at least family level at 97% sequence similarity and plotted the data in Excel version 16.16.8.

## Mesocosm study

From May 28–June 12, 2017, a mesocosm experiment was run at Tjärnö Marine Laboratory. A simplified assembly of habitat-building brown algae consisting of three *Fucus serratus* sitting at the bottom of the tank and three *S. latissima* hanging from the top of the tank were added to each of eight 1 m$^3$ (1.1×1.4×0.64 m) tanks. In four of the tanks, two individuals of goldsinny wrasse were added (ethical permit numbers 5.8.18-06922/2017 and Idnr 000818-2017). The remaining four were kept as fish-free controls. All tanks were enriched with small pieces of tubing at the bottom for the fish to take shelter in. Invertebrates (amphipods, isopods, gastropods) were caught in the algal belt and evenly distributed among the tanks at the start of the experiment. All tanks had a continuous supply of surface water, and drained through pipes covered with mesh to prevent loss of invertebrates. The tanks were covered by insect mesh to avoid bird predation and reduce light intensity. Temperature was recorded each morning and ranged from 15.1 to 17.5°C.

The goldsinny wrasse used in the experiments were collected with fyke nets or baited traps within 2 km of the experimental site. *Saccharina latissima* were from a nearby aquaculture facility, and *F. serratus* individuals were collected from boats in the vicinity of the lab. The invertebrates were collected by shaking algae into a bucket, as well as trawling with a meshed net at the shores of the surrounding islands. Individuals caught were evenly divided among all eight tanks. A total number of 25 individual grazers were added over the course of the experiment to each tank to simulate replacement of consumed herbivores from adjacent areas. The additions were made every fifth day, in total 25 invertebrates (20% Palemon elegans, 25% Littorina littorea, 16% Littorina obtusata, and 40% amphipods).

The experiment was terminated after 15 days. Invertebrates were collected on a 200 µm mesh and preserved in ethanol for later analysis. Each alga was photographed on a light table to monitor epibiont coverage.

## Image analysis of epibionts

Epibiont coverage on *S. latissimia* was determined using ImageJ version 2.0.0-rc-54. For *F. serratus* the epibionts grew on top of each other, meaning coverage of individual species could not be determined. Instead, epibionts were scraped off with a scapula and epibiont wet weight normalized to algal biomass ([wet weight of epibionts/wet weight of algae] × 100) was determined. The epibionts were blotted dry five times on a paper towel before measuring wet weight to standardize water content. Invertebrates were sorted under a dissecting microscope to determine species; each individual species was blotted dry as above, weighed, and the number of individuals counted.

# Results

## Fish survey

Estimates of the fishery for wrasse during 2014–2017 in the reference areas Stora Kornö and Byxeskär show that the seasonal average for Stora Kornö was 67% of the total fishing days potentially being in the study area. The corresponding value for Byxeskär was 74%, indicating that both Stora Kornö and Byxeskär are representative reference fishing grounds for wrasse compared to the marine protected area Kåvra (Table 1).

The results from the field sampling with fyke nets did not show any differences in numbers of corkwing, goldsinny, or ballan wrasse between the three different localities (Figure 2). In the fyke nets, the total abundance of wrasse caught in Kåvra was 1728 individuals, distributed among corkwing (67.7%), goldsinny (31.7%), and ballan wrasse (0.5%). At Stora Kornö, the total abundance of wrasse was 2081 individuals distributed among corkwing (71.8%), goldsinny (26.8%), and ballan wrasse (1.4%). In Byxeskär, the total abundance of wrasse was 2086 individuals distributed between corkwing (67.2%), goldsinny (31.9%), and ballan wrasse (0.8%). The distribution and ratio of the three species of wrasse were similar among the three areas. Noticeably, other wrasse species were also caught in the field sampling such as rock cook and cuckoo wrasse. However, these species are not target species for wrasse fishermen in Sweden and are therefore not presented in detail.

The size distributions of corkwing and goldsinny wrasse in Kåvra were similar to those at Stora Kornö and Byxeskär (Figure 2). The average body size of corkwing wrasse in Kåvra was 12.1 cm, in Stora Kornö 11.8 cm, and in Byxeskär 12.0 cm. The average body size for goldsinny wrasse in Kåvra was 10.0 cm, in Stora Kornö 9.8 cm, and in Byxeskär 10.2 cm. Regarding ballan wrasse, the number of fish caught in the sampling with fyke nets was too low to enable any conclusions regarding size distribution in the studied areas.

Field sampling with creels show no differences in CPUE of goldsinny wrasse and corkwing wrasse in Kåvra compared to Stora Kornö and Byxeskär (Figure 3). The size distribution for corkwing and goldsinny wrasse in Kåvra was also similar to the results from Stora Kornö and Byxeskär (Figure 3). The average body size of corkwing wrasse was 12.7 cm in Kåvra, 12.2 cm in Stora Kornö, and 12.5 cm in Byxeskär. The average body size for goldsinny wrasse was 9.0 cm in Kåvra, 9.2 cm in Stora Kornö, and 9.2 cm in Byxeskär.

## Algal samples

In line with the lack of difference in wrasse densities in the different areas, we found no difference in the fauna found on individually bag-sampled *S. latissima*. In total, 62 samples were analysed and 26 taxa were identified to species or to the nearest possible taxonomic level. The fauna was dominated by small gastropods, mainly of the genera *Lacuna* and *Rissoa*. Isopods and amphipods were the most abundant crustaceans, and polychaetes and echinoderms were commonly found but in lower numbers (full details in Supplementary Table S2). Neither biomass nor species richness differed among the three areas (ANOVA, $p = 0.42$ and 0.63 respectively). When each measurement of total epibiont biomass was compared to the nearest estimate of wrasse density however, there is a trend towards a positive relationship ($p = 0.20$, Figure 4).

When each measurement of total epibiont biomass was compared to the nearest estimate of wrasse density however, there is a trend towards a positive relationship between total epibiont biomass and wrasse density (biomass caught per unit effort, Figure 4).

## Gut content analysis

Using metabarcoding, 189 taxa were identified in the gut contents of 67 goldsinny and 30 corkwing individuals: 15 phyla, 29 classes, 65 orders, 135 families, 166 genera, and 161 species. The whole list of prey amplicon sequence variants (ASVs) found with full taxonomic lineage and frequency of occurrence is presented in Supplementary Table S1. Arthropods were the prey type most commonly found in our samples, in 69% of goldsinny and 97% of corkwing (Figure 5). Most of the arthropods found belong to the class Malacostraca (51% goldsinny and 90% corkwing) and Insecta (27% goldsinny and 63% corkwing) (Figure 6). The second most commonly found group are algae, with Rhodophyta found in 33% of goldsinny and 57% of corkwing, and Ochrophyta found in 21% of goldsinny and 53% of corkwing (Figure 5). Goldsinny have previously been observed to graze on algae off the nets of salmon cages suggesting that algae might be grazed directly by the wrasse (Deady *et al.*, 1995).

At the species level, the most frequently found taxa in the gut of goldsinny were the red alga *Bonnemaisonia hamifera* (27%), the pelagic copepod *Paracalanus parvus* (24%), the amphipods *Monocorophium insidiosum* (21%), *Aora gracilis* (19%), and *Jassa marmorata* (18%), the gastropod *Pusillina inconspicua* (18%), the amphipod *Jassa falcata* (15%), the pelagic copepod *Centropages typicus* (13%), the amphipods *Ischyrocerus anguipes* (10%) and *Dexamine spinosa* (10%), and the red alga *Delesseria sanguinea* (10%).

In corkwing, the most frequently found species in the gut contents were the red alga *Bonnemaisonia hamifera* (50%), the alga *Halidrys siliquosa* (43%), the amphipods *Ischyrocerus anguipes* (43%), *Aora gracilis* (40%), *Jassa marmorata* (40%), *Dexamine spinosa* (37%), *Ampithoe rubricata* (37%), and *Jassa falcata* (33%), the amphipod *Scopelocheirus schellenbergi* (33%) and the amphipods *Monocorophium insidiosum* (30%) and *Parajassa pelagica* (30%).

Fewer individuals were successfully amplified and sequenced in corkwing (30 individuals) due to the successful use of our blocking primer. As expected, the blocking primer resulted in fewer reads attributed to corkwing itself and more reads attributed to prey species. The blocking primer was not functional in *C. rupestris*, resulting in a higher PCR success rate (67 individuals), but with fewer reads attributed to prey species and more reads attributed to *C. rupestris* itself.

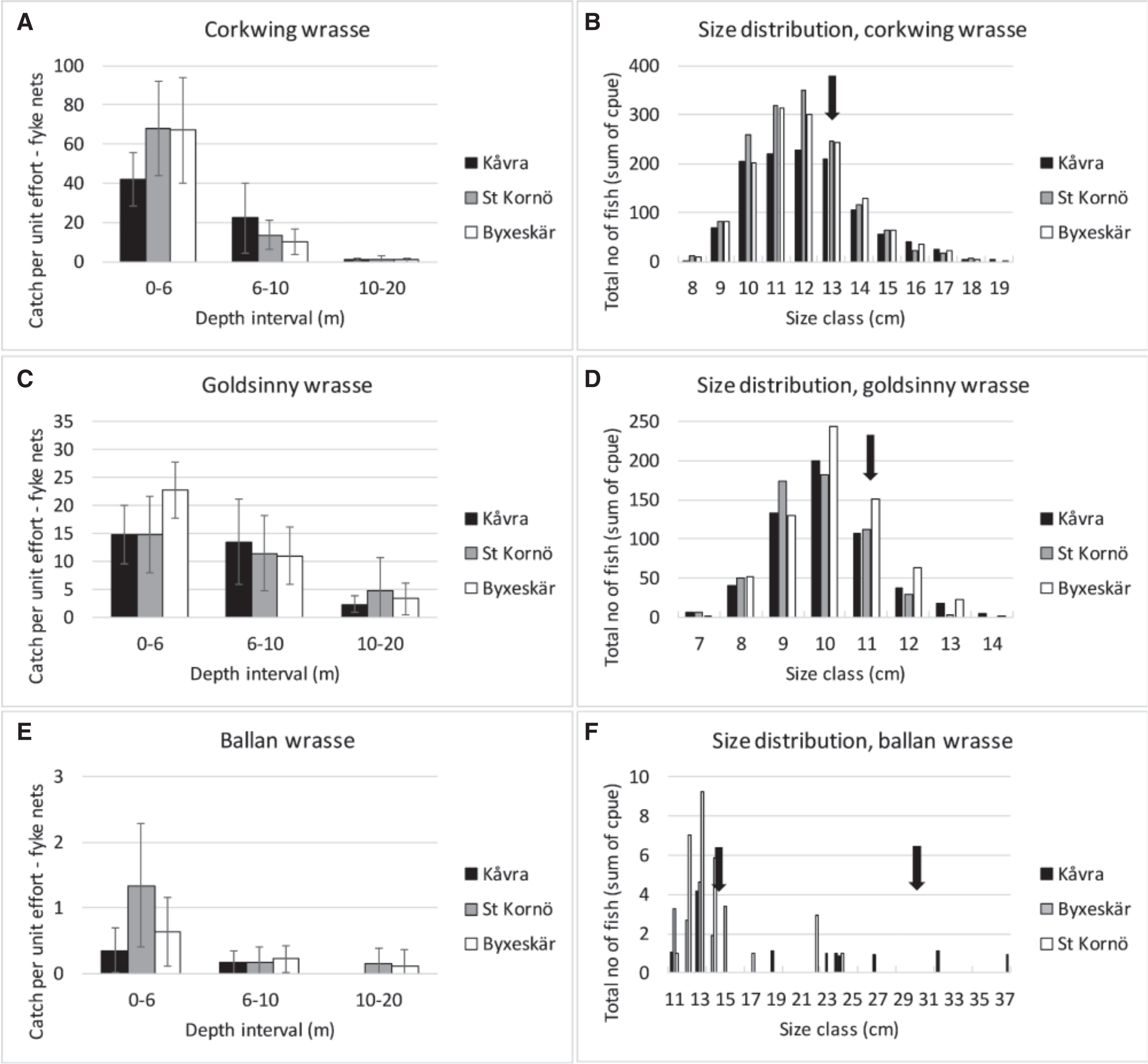

**Figure 2.** Results from field sampling with fyke nets in a marine protected area (Kåvra) and two nearby areas used as fishing grounds for commercial wrasse fishery (Stora Kornö and Byxeskär): (a and b) represent the results for corkwing wrasse; (c and d) represent the results for goldsinny wrasse and (e and f) represent the results for ballan wrasse. The panels to the left show catch per unit effort (CPUE±95% *CI*) based on 18 samples per area and depth interval. No statistical differences in fish numbers (CPUE) were documented among areas for thecorkwing wrasse (F2, 159 = 1.35546; $p > 0.05$) or goldsinny wrasse (F2, 159 = 0.62802; $p > 0.05$) three wrasse species. Only a descriptive comparison is done with the result for Ballan wrasse (e and f). The panels to the right represent size distribution for the three wrasse species in the three areas. Black arrows show minimum landing size, for ballan wrasse there is a legal size interval for landings in commercial fishery.

Prey overlap between the two species is represented in Figure 7. Out of 189 prey taxa, 130 are found in corkwing and 127 in goldsinny, with 68 taxa in common between the two species. The large number of prey species found in the gut contents of wrasse and the low level of overlap between the species suggest that they may be feeding opportunistically.

Prey species from metabarcoding were categorized according to their occurrence along the Swedish coast by using GBIF records and consultation with experts (data not shown). Of the 189 taxa, 107 species were confirmed to occur in the region. A further 67 taxa were found to occur at the family or genus level, suggesting that there may be no close match from a local species in the reference database. Only 15 taxa were categorized as not found or unlikely to exist in the studied area at family level or lower. Perhaps surprisingly, of the 173 taxa found in the area, 41 were found to be terrestrial insects (93%).

## Mesocosm study

The controlled mesocosm study confirmed that wrasse are efficient predators on mesoherbivore crustaceans and littorinid snails (Figure 8) but also on other intermediate consumers such as

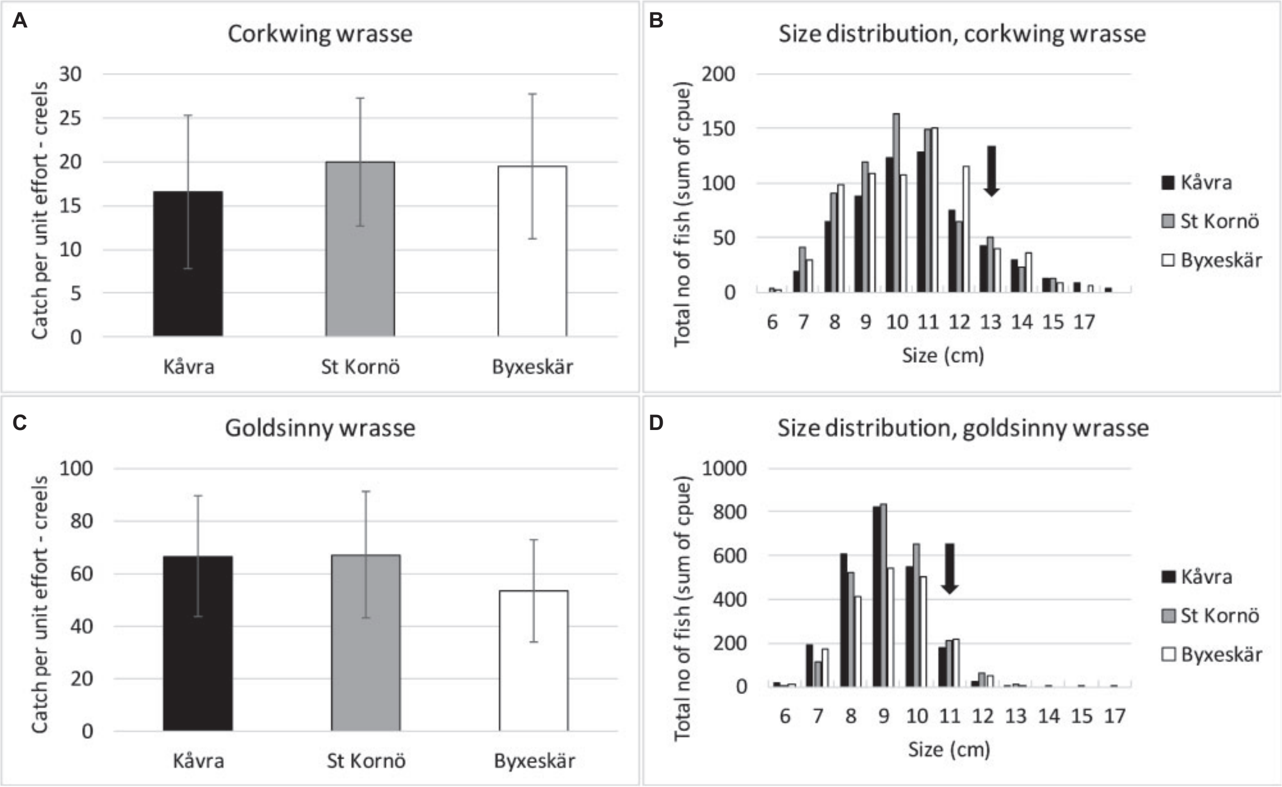

**Figure 3.** Results from field sampling with wrasse creels in the marine protected area Kåvra and two nearby areas used as fishing grounds for commercial wrasse fishery (Stora Kornö and Byxeskär): (a and b) represents the results for corkwing wrasse and (c and d) represents the results for goldsinny wrasse. The figures to the left show catch per unit effort (±95% *CI*) based on 36 samples per area. No statistical differences among areas were documented for corkwing wrasse (F2, 105 = 1.9356; $p > 0.05$) or goldsinny wrasse (F2, 105 = 0.48744; $p > 0.05$). The figures to the right represent size distribution for the wrasse species. Black arrows represent the minimum catch size for commercial fishery.

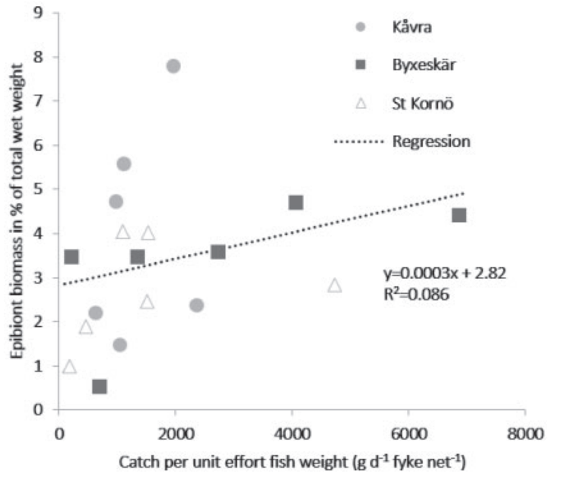

**Figure 4.** Epibiont biomass expressed as percent of wet weight of the field sampled *S. latissima* leaf it was scraped off from in relation to fish abundance ($p = 0.2$, $R^2 = 0.086$). The fish catch per unit effort comes from the nearest test fishing site.

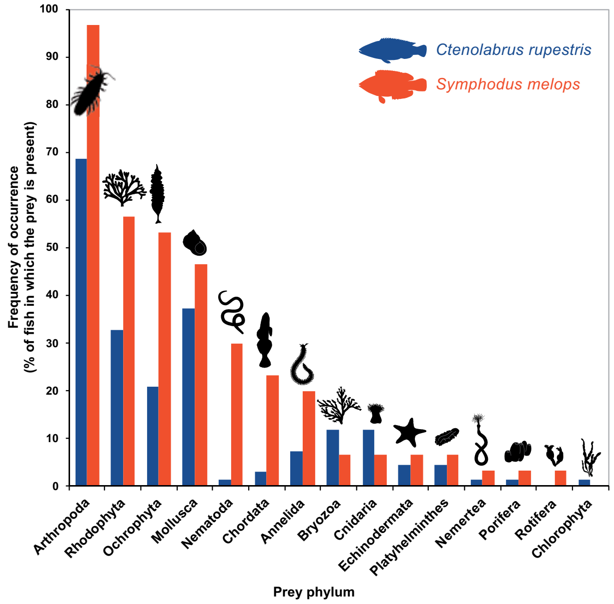

**Figure 5.** Bar chart showing frequency of occurrence [% of fish in which this amplicon sequence variant (ASV) was found] of various phyla in the gut contents of goldsinny (*C. rupestris*) and corkwing wrasse (*S. melops*).

Palaemonidae shrimps which complicates the effects of wrasse on food web dynamics. The only significant effect on the fouling community was an increased coverage of bryozoans on

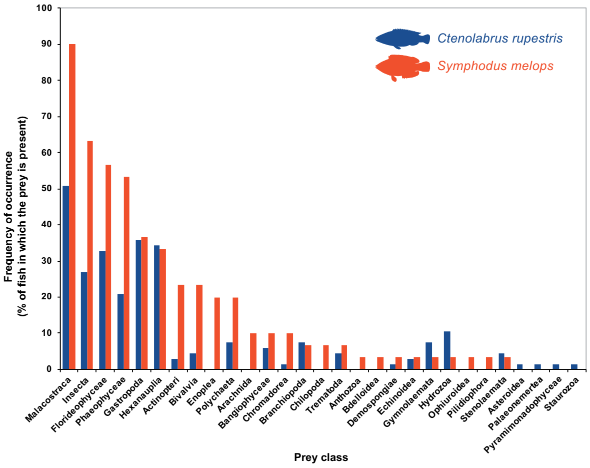

**Figure 6.** Bar chart showing frequency of occurrence [% of fish in which this amplicon sequence variant (ASV) was found] of various classes in the gut contents of goldsinny (*C. rupestris*) and corkwing wrasse (*S. melops*).

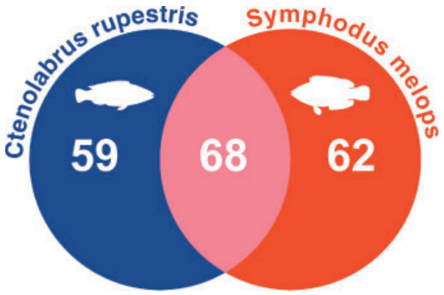

**Figure 7.** Overlap of prey species between goldsinny (*C. rupestris*) and corkwing wrasse (*S. melops*).

*S. latissima* leaves in tanks with wrasse (Figure 8b). The *F. serratus* at the bottom of the tanks were generally more fouled already at the start at the experiment, but total biomass of fouling organisms was not different between wrasse and control tanks (Figure 8c).

## Discussion

### Fish survey

The comparison between the protected area and the two fished areas did not show any differences in catch per unit effort (CPUE) or size distribution of goldsinny or corkwing wrasse that would suggest a local depletion of the wrasse populations in the fished areas. The design of the present field study was based on earlier findings indicating a decline in CPUE and a change in size structure over time in sites with a high fishing intensity (Darwall *et al.*, 1992; Sayer *et al.*, 1996; Varian *et al.*, 1996). Our findings are also in contrast to a Norwegian study showing that MPAs exhibited higher densities and larger sizes of wrasse only a few years after establishment (Halvorsen *et al.*, 2017a). The analysis of the Swedish fishing journals agreed with the suggestion by the commercial fishermen that the two fished areas are important fishing grounds. Fishing pressure may, however, be relatively low with only 14 fishermen currently allowed to fish wrasse along the Swedish west coast and with no more than 50 pieces of gear each in the water at any one time. The much larger wrasse fisheries in Norway started already in 1988, and have been going on for more than 20 years longer than the Swedish fisheries (Bjordal, 1991). On the other hand, the wrasse fishery that started in Sweden in 2010 was preceded by a larger eel fishery (in terms of fishing effort) in the same general habitats as the wrasse fishery (Lagenfelt and Svedäng, 1999). The eel fishery that was discontinued in 2012 was mainly done with fyke nets and eel-traps and had considerable mortality of bycaught wrasses (Svedäng, 1999). Consequently, the lack of difference between protected and fished areas should only be considered in the spatial context investigated here, and does not imply that the demography and densities of wrasse populations all along the Swedish west coast represent completely undisturbed populations. Ecosystem effects of

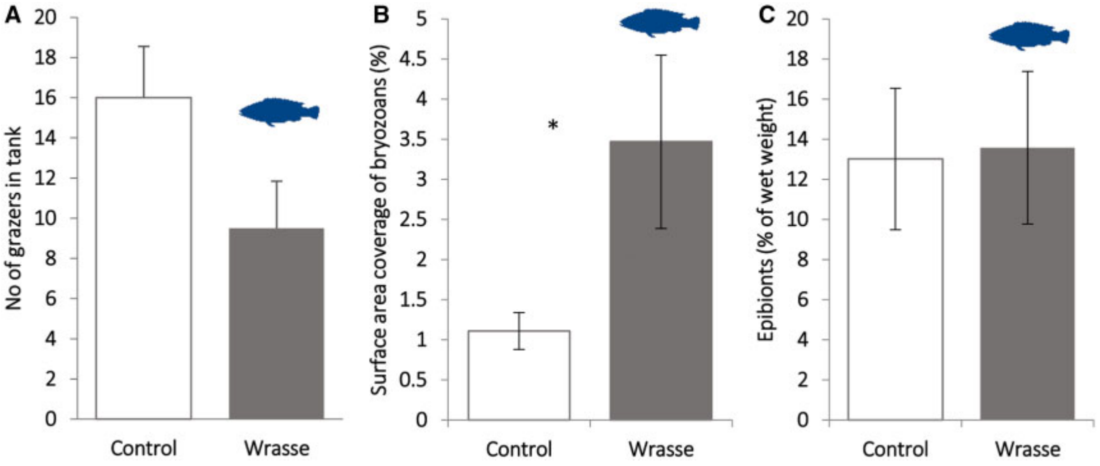

**Figure 8.** Results from mesocosms with and without wrasse. The wrasse tanks held two goldsinny wrasse in one cubic metre tanks. A. The total number of mesoherbivores was 40% less in tanks with wrasse at the end of the experiment. B. The coverage of bryozoans on *S. latissima* hanging in the tank was significantly lower in the control tanks. C. The total biomass of epibionts on the *F. serratus* algae on the bottom of the tank was not different between control and wrasse tanks.

**Figure 9.** Male corkwing wrasse engaged in nest building. Photos by Dr Paul Naylor in Devon, UK.

selectively removing wrasses through fishing on other components of the foodweb may however not be expected to occur in the area studied here.

Wrasse population structure varies along the Scandinavian coast, where Norwegian west coast populations generally show a higher degree of genetic differentiation among localities compared to what has been found within the Kattegat–Skagerrak area. This pattern is more pronounced for corkwing (E. Faust, pers. comm.) than ballan (Seljestad *et al.*, 2020) and goldsinny wrasse (Jansson *et al.*, 2017). One possible explanation is that Kattegat–Skagerrak wrasse are less geographically stationary than wrasse found on the Norwegian west coast. However it is also possible that the lack of differentiation is a result of historical connectivity and other demographic events such as bottlenecks and subsequent increases in population size, and that movement of fish between areas contributes to even out the densities (Mattingsdal *et al.*, 2020).

## Algal samples

Data on fouling organisms and associated fauna on *S. latissima* algae showed no differences between the protected area Kåvra and the two fished localities. This is expected as there were no differences in CPUE or size distribution of wrasse between the marine reserve and the fished areas. The current study, however, serves as a good baseline for follow up studies on this wrasse fishery. Should stock depletion commence, it will be possible to evaluate the effect in a before and after controlled design.

## Gut contents

Our results largely confirm previous morphological studies of gut contents from wrasse (Deady *et al.*, 1995; Sayer *et al.*, 1996) with added breadth and taxonomic information up to the species level, and show that Arthropoda (Crustacea and Insecta) are the most commonly found prey taxa. Within Crustacea, the class Malacostraca was the most commonly found group, followed by Hexanauplia and Branchiopoda. Within Malacostraca, Amphipoda dominated followed by Decapoda and Isopoda. Within Insecta, the classes Diptera, Lepidoptera, Hemiptera, and Hymenoptera were commonly found, with chironomids the most commonly found family within the Diptera (see Supplementary Table S1).

Insect larvae such as chironomids have previously been established through metabarcoding as an important food source for the three-spined stickleback (*Gasterosteus aculeatus*) (Jakubavičiūtė *et al.*, 2017). Chironomid larvae and other dipterans were previously reported in corkwing and goldsinny through morphological analysis of their gut contents (Sayer *et al.*, 1996), and were shown to be most abundant in smaller fish between 6 and 8.9 cm in length, indicating that they might constitute an important food source for young fish. Corkwing also displayed opportunism with respect to seasonal variation in prey availability, with the increased consumption of chironomid larvae during the months when they were the most abundant (Deady and Fives, 1995; Deady *et al.*, 1995). Even though insects were found in 27% of goldsinny and 63% of corkwing in our study, we cannot say in what proportion they contribute to the bulk of their diet, since our study is not quantitative. A previous study from Galway Bay, which has looked at gut food items quantitatively, suggests that insects constitute only 2.4–4.8% of food items consumed (Deady and Fives, 1995).

Algae constituted the second most commonly found food item in the gut contents of wrasse with Rhodophyta dominating, then Ochrophyta. The high frequency of occurrence of algae in the gut contents of wrasse might seem surprising given wrasse are thought to be primarily carnivorous. However, this has previously been observed in another study from Galway Bay showing that 48.6% of corkwing had ingested algae (Deady and Fives, 1995). This shows that algae might be grazed intentionally rather than accidentally from the sea bed while searching for prey. Algae even comprised the bulk of ingested food in corkwing from salmon cages (Deady and Fives, 1995; Deady *et al.*, 1995). Even though algae are frequently found in the guts of wrasse, we cannot say if they constitute a large proportion of the food ingested by wrasse as our study is not quantitative. The study from Galway Bay which has looked at gut food items quantitatively suggests that algae constitute only 3.1–3.6% of the bulk of food items consumed, but that they were found in almost half the fish, with an increasing frequency with increasing fish length (Deady and Fives, 1995).

It should be noted that male corkwing have been shown to use algae for building nests in which eggs are deposited. *Corallina officinalis* is one of the principal algal components of the nest of the male corkwing (Deady and Fives, 1995), but male corkwing have also been observed with *Halidrys siliquosa* at Tjärnö Marine Laboratory (E. Faust Pers. comm., also see Figure 9: photos of corkwing males fetching *Corallina* sp. taken in Devon, Great Britain, by Dr Paul Naylor). In contrast to corkwing wrasse, goldsinny wrasse are pelagic spawners and only use available crevices and seaweed for shelter. Although they do defend the area around their shelter, literature suggests that they are dependent on the already present algae (Hilldén, 1981), and there are no known observations of goldsinnies carrying algae for nest building.

The Mollusca (mostly Gastropoda and some Bivalvia) also constituted some of the most commonly found prey items in our study. Using molecular methods, we were able to detect 189 species belonging to 15 phyla, obtaining information from even highly digested prey. Our results suggest that wrasse feed opportunistically and according to prey availability, although there may be size and age related differences which we have not explored in this study (Deady and Fives, 1995).

## Mesocosm study

The mesocosm experiments confirm that wrasse prey efficiently on mesoherbivores. The experiment lasted 15 days and in that time period total invertebrate abundance was decimated by 61% in the wrasse tanks and by 36% in the control tanks. Wrasse, however, do not only feed on mesoherbivore snails and crustaceans, but also on intermediate consumers such as *Palemon* sp. and also primary producers, which indicates that wrasses may have multiple effects on food web dynamics. Moreover, the *Saccharina* algae in the experiments were significantly less fouled by epiphytic bryozoans in the control tanks which suggests that cascading effects may result if wrasses are decimated by fishing.

## Towards ecosystem-based management of wrasse fisheries

Currently, Sweden has adopted a precautionary approach to wrasse fishery management since no management plan exists that connects exploitation rates with the biology of any of the wrasse species. The Swedish fishery is limited by effort, and fishermen can only fish for wrasse after receiving an exemption for using gear without escape openings. Indeed, only 14 such exemptions are in place (as of 2020). In this study, we could not detect any differences in fish nor potential prey between fished and non-fished areas, but we provide a baseline for future monitoring. The continued monitoring of abundance and size structure of fish stocks is necessary for sustainable fisheries management. This is especially true for wrasse, as traits like high site fidelity, narrow home range and complex life history suggest that an increased local fishing pressure could quickly alter population demographics or even deplete local stocks. For future monitoring, both fishery-independent and fishery-dependent programs will be valuable. Catchability (affecting the estimates of abundance) and demography depend on many factors such as temperature, season, depth, or exposure, which is especially evident for passive fishing gears. Therefore, it is important to account for spatial and temporal heterogeneity in the monitoring data, while taking population structure into account.

The present fishery management—only safeguarded by a precautionary approach and without quantitative reference levels for sustainable use—raises concerns of potential future overfishing and the possible effects on local ecosystems. The use of no-take areas to infer effects on target species as well as ecosystem effects of fishing in this and earlier studies e.g. (Halvorsen *et al.*, 2017a), may contribute to a future ecosystem approach to wrasse fishery management. The county administration has implemented limits on the number of fishermen that are allowed to fish in individual Natura 2000-areas, a concept that could be extended to create "scientific reference areas". This approach would assist in disentangling the effects of the fishery on the target species and the ecosystem from other impacts such as climate change and coastal exploitation. The combination of catch data from onboard observers of the fishery with monitoring data from fished areas and no-take areas could form the basis for the biological advice needed for ecosystem-based fisheries management.

## Concerns associated with the use of cleaner fish in the aquaculture industry

In this study, we investigated the effects of wild cleaner fish targeted by fishery on the Swedish west coast. However, the 1 million wrasse caught annually in Sweden are only a small fraction of the total number of cleaner fish used in aquaculture for parasite control. In Norway, over 60 million cleaner fish were put into salmon farms in 2019, and of these, approximately 30% were wild caught wrasse. The UK applies a similar system to Norway with a mix of farmed and wild-caught cleaner fish for parasite control. Currently, an estimated 1 million wrasse are harvested in southwestern England annually for live transport to salmon farms in Scotland every year (Riley *et al.*, 2017). Other countries, e.g. Canada, do not allow the use of wild caught cleaner fish in open marine aquaculture (Boyce *et al.*, 2018). The use of cleaner fish for parasite control in other parts of the world is still relatively rare but is likely to increase as more countries have started to investigate the possibility of utilizing cleaner fish for parasite control (Sánchez *et al.*, 2018).

Besides overfishing and cascading ecological effects, there are additional concerns with the current use of cleaner fish in the aquaculture industry. Cleaner fish are often transported long distances to be used in areas far away from where they were caught. Translocated cleaner fish may act as vectors of disease, being asymptomatic carriers of bacterial, viral, and parasitic disease agents (Korsnes *et al.*, 2017). These diseases may pose a risk to farmed Atlantic salmon that have not developed the same natural resistance. The risks are however not restricted to farmed fish, but as cleaner fish have been shown to escape (Faust *et al.*, 2018), they also pose a threat to other local species and populations. In addition to spreading disease, escaping translocated wrasse may also affect the genetic makeup of local populations by introducing new genetic material or even establishing new populations outside their original distribution range. Previous studies have shown that transported fish are able to escape and hybridize with local populations and have also contributed to newly established populations (Jansson *et al.*, 2017; Faust *et al.*, 2018; Seljestad *et al.*, 2020). Introduced individuals can also have ecological impacts on their new environment. Even if a species is already present in an ecosystem, introduced individuals of the same species may not be ecologically equivalent. Translocated organisms can vary strongly in their ecological impacts compared to the pre-existing population, for example through differences in prey consumption (Evangelista *et al.*, 2019). Finally, an annual use of approximately 60 million fish with the only purpose of de-lousing another aquaculture species raises ethical concerns. Many cleaner fish are killed during handling and transportation (up to 40%) or during other salmon delousing procedures. At present, the loss of approximately 20% of farmed salmonids is considered unacceptable, while it has been suggested that a mortality rate of near 100% in a production cycle is normal for cleaner fish (Hjeltnes *et al*., 2019). Thus, more work is needed to increase cleaner fish welfare and to minimize the risks associated with the increasing use and translocation of cleaner fish for salmon lice control.

## Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

## Acknowledgements

We are grateful to Dr Paul Naylor for providing the beautiful diving photos of male corkwing wrasse engaged in nest building. We also wish to thank Jan Heuschele for help with graphics. Funding was provided by the Swedish Research Council FORMAS and the EU Interreg project MarGen II.

## Data availability

The data underlying this article are available in the NCBI SRA archive at https://www.ncbi.nlm.nih.gov/sra, and can be accessed under BioProject ID PRJNA655463 and BioSample accessions SAMN15735264 to SAMN15735371.

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*Handling editor: Mark Gibbs*