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Adding fish waste to the diet of Iceland scallop *Chlamys islandica*: effects on feeding and reproductive ability

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ABSTRACT: Organic enrichment from fish farming may impact benthic species and habitats in adjacent areas. Norwegian salmon farming is continuously growing, but, due to area conflicts and severe sea-lice problems in the western areas, growth of the industry is focused in the northern areas. Knowledge is scarce on how an increase in fish farming will impact Arctic and subarctic species and habitats. One such species is the Iceland scallop *Chlamys islandica*, distributed from the Lofoten Islands in Nordland County to the Varangerfjord in Troms and Finnmark County. To study the impact of fine-particle fish faeces on feeding and reproductive ability in adult Iceland scallop, particles <41 µm of finfish waste were added to the diet. Effects were tested via short-term (weeks) feeding studies using 2 diets, 100% cultured algal species and a 50% mix of algae and fish waste. In addition, a 100% fish waste diet was used to study longer-term effects on reproductive ability (months). Feeding (% particle clearance and feeding rate) on the microalgae diet tended to be higher than that on the diet containing fish waste, but the difference was significant only in 2 out of 4 cases. We did not find any effect of diets on reproductive ability (gonad development and fatty acid profiles) of scallops. Lack of knowledge on sufficient food levels for gonad maturation in this species may have affected the results. We suggest that future work includes the transplant of scallops from a reference site to fish production sites and that investigations begin immediately after spawning early in scallop gonad development.

KEY WORDS: *Chlamys islandica* · Diet · Environmental impact · Salmon waste · Feeding · Reproduction

1. INTRODUCTION

The Norwegian salmon farming industry is predicted to have the greatest expansion in the northernmost areas (Nordland, and Troms and Finnmark County) in the next decade (Breimo et al. 2018) due to increased area conflicts and environmental challenges in the mid- and southwestern regions of the country (Hersoug 2013, Sommerset et al. 2020, Johnsen et al. 2021, Sandvik et al. 2021, Grefsrud et al. 2023). The environmental impact of salmon farming is well known and well described (e.g. Taranger et al. 2015 and references therein), including emissions of organic waste particles from fish farming (faeces and excess feed). Organic enrichment is considered to be the major source of impact on benthic communities close to the farms (100–150 m) depending on the local hydrodynamics (Hansen et al. 1990, Kutti et al. 2007, Keeley et al. 2013), and concerns have been expressed about possible negative effects on sensitive habitats and species in adjacent areas (Wilding 2011, Skaala et al. 2014, Keeley et al. 2019,

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Legrand et al. 2021). The use of terrestrial plant oils such as soybean oil has increased in commercial salmon feed (Turchini et al. 2009) due to limited fish oil resources, and the levels of terrestrial fatty acids (FAs) such as oleic acid (18:1n-9), linoleic acid (18:2 n-6) and α-linolenic acid (18:3n-3) have increased substantially. Concerns have been made on how the elevated levels of terrestrial FAs may affect marine organisms consuming organic particles from fish farming (White et al. 2016).

Although the distribution and sedimentation of larger particles (>10 mm) is well studied and described (e.g. Cromey et al. 2002, Bannister et al. 2016), less is known about dispersion of smaller-sized (2.5–500 µm) particles (Law et al. 2014). Small particles stay suspended in the water column for a longer time and are potentially distributed to a larger area. Model predictions have shown that organic particles from fish farming can be transported up to 2 km away (Broch et al. 2017), and elevated levels of terrestrial FAs have been found in mobile epifauna as far as 1100 m away (Woodcock et al. 2019). These particles may form part of the diet of filter-feeding organisms in the area, either directly through uptake or secondarily through prey organisms that have foraged on waste particles (Woodcock et al. 2017, 2018), and may have a long-term impact on physiology in organisms due to non-lethal exposure levels over time, since they change the quality of the diet.

The terrestrial FAs in salmon feed have been successfully used as biomarkers in different invertebrates to identify whether organic particles from fish waste are digested and absorbed by the organism (Handå et al. 2012, Irisarri et al. 2015, White et al. 2019, Woodcock et al. 2019).

Both blue mussel *Mytilus edulis* (Handå et al. 2012, Irisarri et al. 2015) and great scallop *Pecten maximus* (Bergvik et al. 2018) have been reported to capture and absorb particles originating from salmon farms, although other investigations showed that this may not be the case *in situ* and depends on the available amount of seston (Navarrete-Mier et al. 2010, Sanz-Lazaro & Sanchez-Jerez 2017). The *in situ* studies (Handå et al. 2012, Irisarri et al. 2015, Sanz-Lazaro & Sanchez-Jerez 2017) were carried out in the near vicinity of fish farms and the bivalves used were exposed to particle sizes, concentrations and quality very different to what natural populations are expected to be exposed to at longer distances from the farms.

In northern Norway, the subarctic bivalve Iceland scallop *Chlamys islandica* is distributed along the coast from the Lofoten Islands in Nordland County to the Varangerfjord in Troms and Finnmark County (Wiborg 1963). It occurs in dense scallop beds in a few locations (Wiborg 1963) but is found throughout the area at low densities (E. S. Grefsrud pers. obs.). The Iceland scallop is a filter feeder that prefers high-current areas (Vahl 1973), making it a possible candidate for feeding on suspended fish-farm waste. It was therefore used in our study to investigate the effects of organic waste particles from salmon farming on bivalve populations in northern Norway. However, we did not find any literature on laboratory rearing of Iceland scallop broodstock, thus we adapted the procedures used for the local temperate species, *P. maximus*.

Investigation of feeding in bivalves can be used to show an early response to a changing environment, such as changes in diet quality and quantity (i.e. Tenore & Dunstan 1973, Strohmeier et al. 2009, 2012, Zhang et al. 2010). Also, studies have shown that the diet quality and quantity can affect development of the gonads and spawning success in scallops and, hence, their ability to reproduce (Devauchelle & Mingant 1991, Utting & Millican 1997, 1998, Andersen & Ringvold 2000). FA composition of gonads is affected by different diets (Caers et al. 2003, Sühnel et al. 2012) and varies during gametogenesis in scallops (Palacios et al. 2005, 2007). High content of essential FAs, such as arachidonic acid (20:4n-6), eicosapentaenoic acid (20:5n-3) and docosahexaenoic acid (22:6n-3), is important for the development of the gonads and hence for the reproductive ability (Utting & Millican 1998).

In this study, Iceland scallop was fed different diets with cultured microalgae and fish waste particles, with the aim of studying how waste particles from salmon farming may impact feeding and reproductive ability in adult Iceland scallops.

2. MATERIALS AND METHODS

2.1. Scallops

Iceland scallops *Chlamys islandica* were collected from scallop beds at Berg in the northernmost part of Balsfjord (Wiborg & Bøhle 1968), Troms and Finnmark County (Fig. 1). In 2017, SCUBA divers collected 250 scallops on 15 May at a depth of 11 m and a seawater temperature of 5–6°C (estimated, based on a temperature of 4.9°C at 2 m depth). Mean ± SD shell height (n = 99) was 82 ± 5 mm. Mean ± SD gonado-somatic index (GSI) measured in August and November (n = 66) was 26.8 ± 13.8%. In 2018, a 70 l triangular dredge was used to collect 206 scallops on

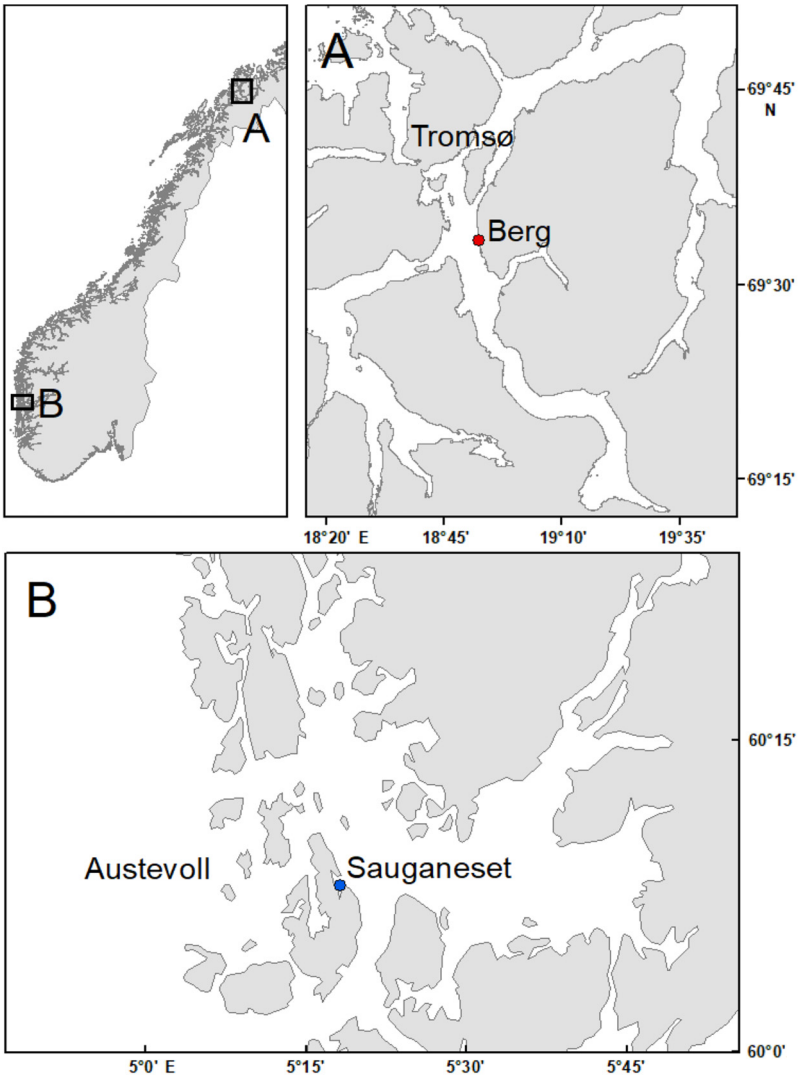

Fig. 1. Norway (top left), showing (A) the location of scallop collection at Berg in Balsfjord, Troms and Finnmark County (red dot) and (B) the location of our laboratory at Sauganeset at the Institute of Marine Research's station at Austevoll, Vestland County (blue dot)

5 April at 20 m depth and a temperature of 2.7°C; the mean ± SD (n = 30) shell height was 71 ± 6 mm and GSI was 15.9 ± 9.5%. The scallops were wrapped in wet paper, placed on top of cooling elements in boxes and transported to Sauganeset at the Institute of Marine Research, Austevoll Research Station, Vestland County (Fig. 1). It took <12 h from packing to submersion in storage tanks with a flow-through of seawater.

Scallops were evenly immersed in three 939 l (111 × 141 × 60 cm, width × length × depth) storage tanks filled with approximately 800 l seawater. A false bottom made of polypropylene net with mesh size 37 × 37 mm was placed above the bottom at a depth of 34 cm to allow faeces from the scallops to pass through. The water volume above the net bottom was approximately 532 l.

Storage tanks were supplied with either temperature-controlled seawater set at 6°C or ambient seawater at around 8°C, or a mixture, at a flow rate per tank set to 402 l h^{-1} running in a circular downwelling motion. Both seawater qualities (6 and 8°C), with a salinity of 34.8–35.0 mg l^{-1} and pH_{NBS} of 7.98, was pumped from a depth of 160 m and filtered through a sand filter (Andersen et al. 2013). The scallops were exposed to continuous light from 2 fluorescent tubes 3–4 m above the tanks, mimicking summer day length in the north.

Over a period of 15–16 d after immersion, the seawater temperature in storage tanks was increased from 6.0–6.1°C to 8.5–8.9°C, equivalent to a warm summer situation in the north (Eilertsen & Skarðhamar 2006). Storage tanks continuously received 2.3–3.5 × 10^8 particles (mean volume of 56 μm^3) d^{-1} $ind.^{-1}$ of a standard algae diet (Algae), described in detail in Section 2.2. Initially, storage tanks were set to receive a concentration of 500 particles ml^{-1} when temperatures were low, increasing with temperature up to 2000–3000 particles ml^{-1}.

In 2017, mortality in the storage tanks was 11% at Day 60. In 2018, mortality was 6% after 4 wk and 17% after 37 d in storage tanks. The shells were clean on scallops collected in 2017, but fouling had to be removed from the shells in 2018.

2.2. Diets

Diets used were a 100% mixture of 3 micro-algal species (Algae), 100% fish waste (Waste, in 2018 only) and a mixture of 50% Algae and 50% Waste (A+W).

The Algae diet used in both the storage tanks and the experiments was a standard diet composed of 3 micro-algal species commonly used for broodstock in

great scallop (*Pecten maximus*) hatcheries (Andersen et al. 2011): a 1:1:2 ratio of *Isochrysis galbana* (Tahitian strain, now *Tisochrysis lutea*; Bendif et al. 2013), *Pavlova lutheri* and *Chaetoceros muelleri*, respectively. The diet ratio of the algal species was based on a standardised total particle volume (TPV, μm^3 ml^{-1}), dividing the mean particle volume measured by a Coulter Z2 counter (Electrical Sensing Zone method, Beckman) by a standard cell volume of 50 μm^3.

Algae were grown in 80 l plastic bags, each in front of 4 fluorescent tubes and harvested twice in the early stationary phase. They were grown using a commercial fertiliser, SuperbaTM NPK 14-4-21 (Nordic Garden), bubbled with CO_2 in air (1% v/v), under a 24 h light cycle at average light intensities of 100 mE m^{-2} s^{-2} (Runge et al. 2016); silicate (Krystazil 40, BIM Norway) was added to the *C. muelleri* cultures.

Fish waste was collected from a sedimentation tank containing feed residue and faeces in low-salinity water from Lerøy in Sagen, Vestland County. In this facility, post-smolt *Salmo salar* up to minimum 0.5–1 kg are produced in a closed-containment floating facility (Preline Fishfarming System) that has mud traps to collect fish waste. The fish waste was washed into a storage tank that was emptied every 4–8 wk. The fish waste was sieved through several plankton nets with a final mesh size of 41 µm either before or after the 2–3 h transport to Austevoll Research Station. The fish waste was sieved to avoid large particles that may sediment in the tanks and clog analytical instruments. Fish waste was then stored in 2.5 or 10 l plastic containers at −20°C for up to 4 mo and thawed before use. One batch of fish waste was used in 2017 and 4 batches were used in 2018.

The combined A+W diet was made of equal TPV (μm^3 ml^{-1}) from each source (Algae and Waste), with a TPV similar to the other diet/diets.

Mean particle concentration, volume and TPV for Algae as analysed by the Coulter Z2 were around 15×10^6 particles ml^{-1}, 53 and 58 μm^3 and 873 and 918×10^6 μm^3 ml^{-1} in 2017 and 2018, respectively (Table 1). The concentration range of the 5 concentrated batches of Waste in 2017 and 2018 was $0.6–1.1 \times 10^6$ particles ml^{-1}, the volume range was 49–64 μm^3 and TPV was then $46–90 \times 10^6$ μm^3 ml^{-1} (Table 1). TPV of the diets was always calculated based on measurements by Coulter Z2 as a standard procedure in our lab. The diet volume used was calculated based on TPV (μm^3 ml^{-1}) for Algae and Waste, the set value for food concentration (2000 cells ml^{-1}) in the seawater running into the tanks and the flow rate of seawater. Information on feeding volumes for *C. islandica* was not found in the literature. We did not aim to feed to satiation, as the effect of fish waste may be dependent on food level. Instead, we aimed to keep the food concentration within natural limits. In Balsfjord, Eilertsen & Taasen (1981) reported concentrations of 40–5900 cells ml^{-1} during the summer season (April–August), which is a quite wide range. Due to a limitation in the supply of fish waste (for 500 l tanks), we could only feed at the lower fraction of the natural range (128–828 cells ml^{-1}) and at the same time ensure that the number was high enough for detection with the Coulter and PAMAS (see next paragraph) counters.

To investigate the size distribution of diet particles, samples were measured with a PAMAS single-particle laser counter (PAMAS S-4031 GO; PAMAS Partikelmess- und Analysesysteme) as described in Section 2.4. All diets showed a rapid decrease in particle numbers with diameters >8 µm, referring to particle volumes >268 μm^3 (Fig. 2). However, TPV was significant up to 40 µm. There was a higher percentage of particles >5.0–5.5 µm in A+W than in Algae in both years (Fig. 2), probably caused by the difference in particles >5.0–5.5 µm between Waste and Algae (shown in 2018). Due to the feeding experiments, measurements of particles had a higher resolution in 2017 than in 2018.

Table 1. Mean ± SD particle concentration, volume and total particle volume (TPV) for the diets Algae and Waste in 2017 (particle diameters: 3.0–8.0 µm) and 2018 (3.4–8.0 µm)

Year	Diet		Particle conc. ($\times 10^6$ particles ml^{-1})	Volume (μm^3)	TPV ($\times 10^6$ μm^3 ml^{-1})	n
2017	Algae		15.1 ± 4.1	52.7 ± 3.4	873 ± 275	10
	Waste	Batch 1	0.95 ± 0.19	48.6 ± 5.8	46.1 ± 10.2	16
2018	Algae		15.5 ± 4.0	58.1 ± 5.8	918 ± 307	14
	Waste	Batch 2	0.84 ± 0.24	61.6 ± 3.7	52 ± 16	7
		Batch 3	0.62 ± 0.28	64.1 ± 3.0	40 ± 18	22
		Batch 4	1.44 ± 0.26	62.0 ± 1.5	90 ± 17	9
		Batch 5	1.11 ± 0.10	56.7 ± 1.7	63 ± 6	3

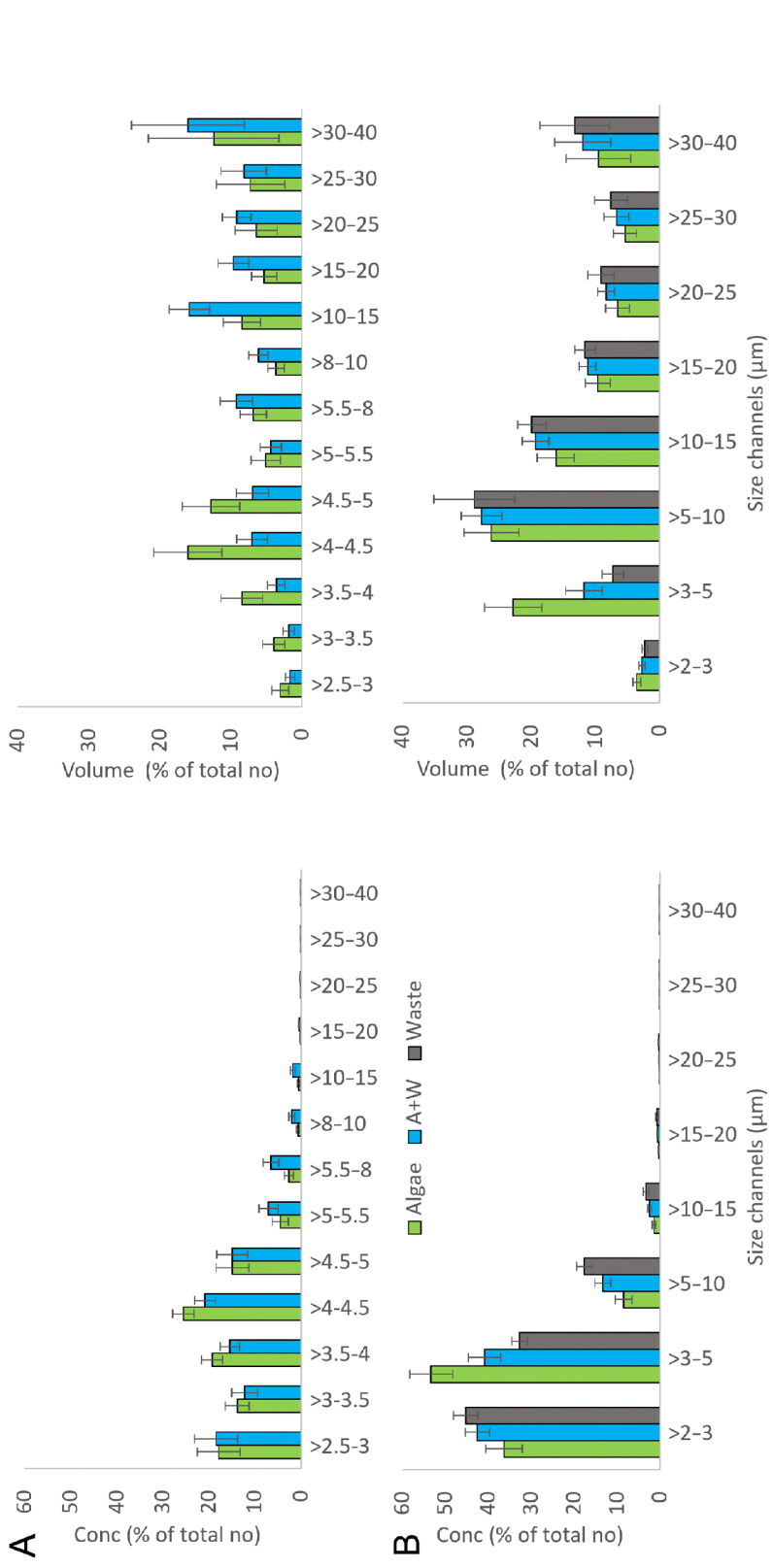

Fig. 2. Mean ± SD particle concentration in particles ml^{-1} (left) and total particle volume in μm^3 ml^{-1} (right) (% of total) for particles with diameter 2.0 or 2.5 to 40 µm from the diets Algae, A+W and Waste (2018 only) as measured with a PAMAS counter when entering the exposure tanks, for (A) 2017 (n = 33) and (B) 2018 (n = 28–30) Tanks and dates are pooled

To analyse particulate inorganic and organic matter (PIM and POM) in the diets, triplicates of 10 ml concentrated Algae or Waste were filtered onto pre-combusted and pre-weighed 24 mm GF/C (1.2 µm nominal pore size) Whatman filters. Salt was rinsed off with 3 × 2 ml isotonic ammonium formate (Strohmeier et al. 2009). Particle-free seawater (<0.2 µm) was used as control (blank). Filters were dried at 60°C for 2–4 d until a stable weight was reached. They were then combusted at 450°C for 3 h overnight to determine the weight of PIM and POM.

To analyse FAs in the diets, 300 ml samples in triplet were collected. In 2017, samples of the Algae diet from the feed mixing tanks were filtered. In 2018, the concentrated Algae was centrifuged, and in both years, concentrated Waste was centrifuged. Pre-combusted and pre-weighed 24 mm GF/C Whatman filters were used for filtration. Salt was rinsed off with 2–3 × 2 ml isotonic ammonium formate (Strohmeier et al. 2009) or distilled water. Particle-free seawater (<0.2 µm) was used as control (blank). In 2018, samples of 150 ml concentrated Algae or Waste in each of 6 tubes were centrifuged at 4000 rpm (11.5 × *g*) and 4°C for 15 min (Eppendorf 5810R). The pellet was dissolved in 2 × 50 ml isotonic ammonium formate and then in 50 ml distilled water to remove salt. Centrifugation in between rinsing was always at 4000 rpm and 4°C for 15 min. Pellets from 2 and 2 tubes respectively were pooled to give triplet samples. The pellets were transferred to pre-combusted and weighed filters and/or to lipid-free glass tubes. All samples were stored at –80°C until analysis.

The FA concentrations in samples were quantified by gas chromatography as described by Meier et al. (2006). Subsamples of 50–100 mg were weighed into 16 ml glass tubes. All samples were methylated and the respective fatty acid methyl esters (FAME) were analysed on an HP-7890A gas chromatograph (Agilent) with a flame ionisation detector (GC-FID) with the FA 19:0 (100 µg) added as an internal standard. The methylation reagent was 2.5 M dry HCl in methanol, and the FAMEs were extracted using 2 × 2 ml of hexane. One µl of the hexane extract was injected into the GC by splitless injection (the split was opened after 2 min) with the injection temperature set to 270°C. The column was a 25 m × 0.25 mm fused silica capillary, coated with a polyethyleneglycol film of 0.25 µm thickness (CP-Wax 52 CB, Varian-Chrompack). Helium (99.9999%) was used as mobile phase at 1 ml min^{-1} and the temperature of the FID was set at 300°C. The oven temperature was programmed to hold at 90°C for 2 min, then from 90 to 165°C at 30°C min^{-1} and then to 225°C at 2.5°C min^{-1} and held there for 20 min, for a total analysis time of 48.5 min. The chromatograms were integrated using EZChrom Elite software (Agilent Technologies).

FAs (as 69 FAMEs) were identified by comparing retention times with a FAME standard (GLC-463 from Nu-Chek Prep), retention index maps and mass spectral libraries (GC-MS; https://www.chrombox.org/data/) performed under the same chromatographic conditions as the GC-FID (Wasta & Mjøs 2013).

2.3. Diet mixing tanks

The concentrated diets were added to 2 (in 2017) or 3 (in 2018) diet mixing tanks and diluted with seawater to total volumes of 100 l (on Mondays and Wednesdays) or 150 l (on Fridays). One diet mixing tank supplied 3 replicate exposure tanks. The flow of the diluted diets into each exposure tank was 14–16 l d^{-1}. The diluted diets were pumped continuously by Iwaki dosage pumps into the seawater supply of the exposure tanks (Fig. 3), with a short break of maximum 1 h when the diet mixing tanks were rinsed and re-filled 3 times a week. The diluted diets were composed as identically as possible based on TPV (µm^3 ml^{-1}); hence, if mean particle volumes differed between diets, the diet volume added to the mixing tanks was adjusted accordingly.

2.4. Particle sampling and analyses

To measure particle number and volume in the concentrated Algae and Waste diets, they were diluted ×100 and ×10, respectively, using particle-free seawater (particles <0.2 µm) before being analysed by Coulter Z2 or PAMAS. Coulter Z2 analysed triplets of 0.5 ml from a sample of 20 ml, while PAMAS was set to analyse triplets of 5 ml from Algae and Waste samples of 100 ml.

To investigate feeding, samples of 150–200 ml were collected from the inlets and outlets of the exposure tanks, and PAMAS was set to analyse particle concentration and volume in triplets of 5 ml (2017) or 10 ml (2018) from the inlet and outlet samples. C is concentration (particles ml^{-1}) or TPV (µm^3 ml^{-1}).

The particle volume was calculated by the Coulter Z2 as the mean spherical particle volume (µm^3) of all particles 3.0–8.0 µm in 128 size channels. The mean spherical particle volume for PAMAS data was calculated based on the mean of minimum and maximum volume and the number of particles for each of 32 size channels, and the total volume for the size windows was then the sum of mean particle volumes for the chosen 32 size channels.

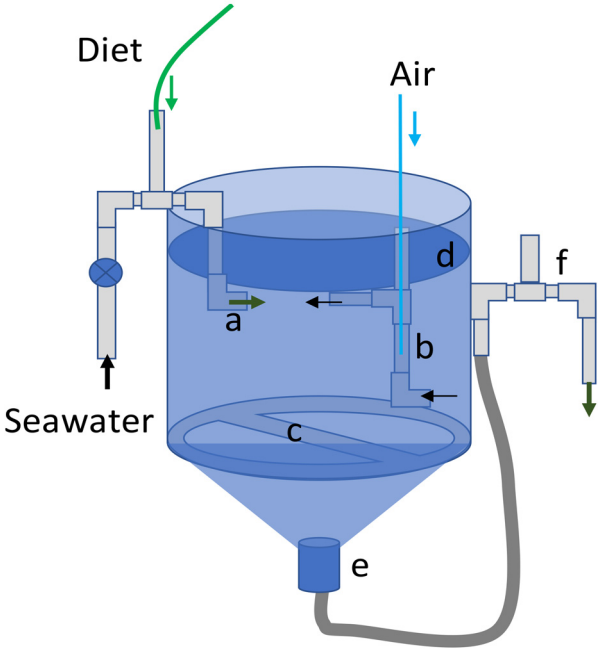

Fig. 3. Schematic drawing of circular exposure tank with a conical bottom and a circular down-welling flow-through. The inlet (a) supplied the tank with both seawater and diet particles. Internal circulation (arrows) was set by an airlift (b). Scallops were placed on a false net bottom on a frame (c). The water level (d) was set by adjusting the vertical position of the T-shaped connection (f). Samples of the outflow water (e) were collected after the T-shaped connection (f)

To find which particle sizes the scallops retained efficiently, retention efficiency (RE) was calculated using samples from the scallop feeding studies. C_{in} and C_{out} samples (µm^3 ml^{-1}) were analysed in the following PAMAS size channels: 2.5–3.0, 3.0–3.5, 3.5–4.0, 4.0–4.5, 4.5–5.0, 5.0–5.5, 5.5–8.0, 8.0–10, 10–15, 15–20, 20–25, 25–30, 30–40, 40–50, 50–70 and 70–200 µm. RE for each size channel was calculated as (Stenton-Dozey & Brown 1992, Strohmeier et al. 2012):

$$RE = 1 - (C_{out}/C_{in}) \quad (1)$$

given that $C_{out} = C_{in}$ for tanks without scallops (no sedimentation of particles, as described in Section 2.6).

2.5. Shell height, wet weight and GSI

Shell height was measured to the nearest mm using a Vernier calliper. Wet weight (ww) of soft tissue and gonads was measured to the nearest 0.1 g on an Acculab or a Scaltec SPO50 scale (Scaltec Instruments). The scallop was tilted sideways to drain water inside before it was opened and the soft tissue including liquids from the tissue was collected in a pre-weighted plastic dish before weighing. The gonad was cut away from the soft tissue including the foot and weighed in another pre-weighed dish. GSI was calculated as a percentage based on ww of the somatic tissue (MacDonald & Bourne 1987):

$$\% \text{ GSI} = \text{gonad} \times 100/\text{somatic tissue} \quad (2)$$

2.6. Experimental tanks

Exposure tanks for both feeding and reproductive experiments were circular polyethene tanks (Plastinvent) with a conical bottom (Fig. 3), a circular downwelling flow-through of seawater and modified with a false net bottom. The outlet was in the bottom centre and through a flexible pipe adjusted to set the water level in the tank (Fig. 3). Flow rate of seawater was checked by visual readings of flowmeters daily in addition to actual flow measurements. Seawater quality and light setting were the same in experiments as described in Section 2.1.

2.7. Feeding experiments, 2017

Six experimental tanks with an outer diameter of 50 cm and height of 100 cm were filled with 77–80 l seawater and the false net bottom was mounted 23–24 cm below the water surface. The temperature range during all measurements was 6.9–7.4°C in June–July and 8.4–9.0°C (ambient) in October–November. Measurements were run at 2 flow rates, (mean ± SD): Flow 1 = 1000 ± 100 ml min^{-1} tank^{-1} (n = 15) (=333 ml min^{-1} ind.$^{-1}$) and Flow 2 = 1590 ± 300 ml min^{-1} tank^{-1} (n = 18) (=530 ml min^{-1} ind.$^{-1}$). Based on studies with mussels and scallops (Filgueira et al. 2006, Strohmeier et al. 2009), Flow 2 was chosen for the feeding studies. However, due to a shortage of fish waste supply and to keep food particle concentration above detectable limits, Flow 1 was chosen for experiments in 500 l tanks with 20 individuals (reproductive ability) and was for the same reason also used in the feeding experiment. Daily means for C_{in} were 574–3974 particles ml^{-1} or 27–184 × 10^3 µm^3 ml^{-1} for all feeding experiments. The seawater had a low background particle concentration of 94 ± 24 particles ml^{-1} and a TPV of 6633 ± 1667 µm^3 ml^{-1} (mean ± SD; n = 12). Particle sizes of 3.0–8.0 µm were used to calculate all feeding results based on RE assessment and particle size distribution of the diets.

Sedimentation of particles in the tanks was measured on several occasions in 2 (June) or 3 (June–December) replicate tanks as a comparison between C_{in} and C_{out} values in the absence of scallops. C_{in} varied between 27 × 10^3 µm^3 ml^{-1} in October and 197 × 10^3 µm^3 ml^{-1} in June, and measurements were conducted at both Flow 1 (on 5 occasions) and Flow 2 (on 2 occasions) for both diets. No significant differences were found between C_{in} and C_{out} given as TPV. Sedimentation was therefore assumed to be insignificant when feeding was estimated.

Feeding is given as feeding rate (FR) and % particles cleared (Filgueira et al. 2006, % particle reduction, Pascoe et al. 2009). FR per tank with 3 individuals was estimated as:

$$FR = (C_{in} - C_{out}) \times Flr \quad (3)$$

based on the assumption that sedimentation of particles was insignificant. C_{in} and C_{out} were the TPV (µm^3 ml^{-1}) of 3–8 µm particles measured at the tank inlet and outlet, respectively, and Flr is the flow rate of seawater with diets (ml min^{-1} tank^{-1}). Percentage particles cleared per tank was calculated for 3–8 µm particles as:

$$\% \text{ particles cleared} = (C_{in} - C_{out}) \times 100/C_{in} \quad (4)$$

Optimum stocking density for the feeding experiments is assumed to be when scallops remove maxi-

mum 25–30% of C_{in} particles (Filgueira et al. 2006, Strohmeier et al. 2009), as higher retention will indicate re-filtering of water. In our pre-measurements using a stocking density of 2, 4 and 6 scallops tank^{-1}, a theoretical stocking density of 2–3 individuals was suggested to reach a retention of 30% for the 2 diets. A stocking density of 3 scallops tank^{-1} was chosen for the feeding studies.

On 30 October (24 wk after collection of scallops), 18 scallops were transferred from the storage tanks to 6 different experimental tanks (triplicate tanks for each diet) with a continuous food supply throughout the experimental period. Particles were measured at Flow 1 on 5 dates between 31 October and 9 November. Daily mean C_{in} values for both diets ranged within 53–89 × 10^3 µm^3 ml^{-1}. On 13 November (26 wk after collection), the flow rate was increased to Flow 2 and particles were measured on 4 dates during 14–25 November. Daily mean C_{in} at Flow 2 for both diets ranged within 38–60 × 10^3 µm^3 ml^{-1}. Since the theoretical particle concentration and TPV in the diet mixing tanks were the same for Flow 1 and Flow 2, the theoretical values of particles entering the exposure tanks per minute, the food flow rate (µm^3 min^{-1}), were the same. Hence, when flow rate increased from Flow 1 to Flow 2, C_{in} was reduced accordingly.

Shell height was measured and GSI assessed on 15 scallops from storage tanks on 17 October at the start of the experiment. GSI was analysed also at the end, as the reproductive status may affect non-reproductive performance (Guderley & Tremblay 2013), and to detect if spawning had taken place. GSI did not change from start to end; mean ± SD shell height and GSI were 84.2 ± 5.7 mm (n = 15) and 31 ± 16% (n = 33), respectively. A visual check showed the gonads in general to be large and seemed to cover >30% and up to 50% of the interior soft tissue space during this period. The gonads for this group, however, were not investigated further, as feeding was the focus of the experiments.

2.8. Reproductive ability, 2018

The experiment was conducted over a 96 d period in 2018 (start: 24 May, end: 28 August), starting 7 wk after the collection of scallops. Nine tanks with an inner diameter of 97 cm and height 60 cm from top to the beginning of a conical bottom were filled with around 400 l seawater (water depth to the beginning of conical bottom was 53 cm) and stocked with 20 scallops each. The net bottom was a thin, high-density polyethylene (HDPE) net bottom with mesh size 19 × 19 mm (Jula Norway), mounted at a water depth of 30 cm. The height of the conical tank bottom was 4 cm.

Temperature was measured daily with a digital thermometer (Durac, H-B Instrument, SP Scienceware) in 1 tank and the temperature range was 7.8–8.6°C. The C_{in} ranges were 24–55, 17–42 and 15–4 × 10^3 µm^3 ml^{-1} for the diets Algae, A+W and Waste, respectively, referring to an overall range of 128–828 particles (size 3–10 µm) ml^{-1}. Variation between tanks in C_{in} for all diets was low, but there was a difference in C_{in} between dates. The difference between some dates can be explained by the problem of keeping diet TPV constant over time, given a variation in both particle volume and concentration of the concentrated diets. Also, a decrease in particle concentration and increase in particle volume of the Waste diet in the feed mixing tank (S. Andersen pers. obs.) indicated an aggregation of particles that was not reversed by the peristaltic pumps.

In addition to a visual check of the flow meter on each tank daily, the flow of seawater with the diets was measured at the 9 tank inlets once a week and was adjusted if it was outside the range 6.9–7.1 l min^{-1}. The overall mean and SD flow rate per tank were 7.0 ± 0.2 l min^{-1} (n = 138). Specific flow rate was 333–350 ml min^{-1} ind.$^{-1}$, like Flow 1 in the feeding experiments (333 ml min^{-1} ind.$^{-1}$). Eleven days after initiation of the experiment, bacterial growth was observed on surfaces inside the tanks supplied with waste. All tanks were emptied, cleaned and refilled. A new batch of fish waste was used to continue the experiment. The bacterial growth was probably caused by a rather 'old' waste batch (4 wk); thus, the next waste batches were collected when they were around 2 wk old, and no bacterial growth was observed later.

Thirty scallops were collected at the start and from each diet at the end of the experiment, to register scallop shell height and weights, and to analyse gonad FAs and female gonad histology (oocyte development and size).

FA analyses of both female and male gonads were carried out to see if the diets affected their FA composition. Approximately 0.2–0.6 g tissue (testis and ovary) was cut out with a scalpel after measuring ww and placed in a pre-combusted glass tube and kept at −80°C until analysis as described in Section 2.2.

Histological samples were analysed to assess the developmental stages of the oocytes. Samples of female gonad tissue closer to the tip than to the base of the gonad were cut with a scalpel and placed in a

plastic grid before being submerged in Davidson's fixative and stored in 70% ethanol until further preparation. The tissue samples were then dehydrated in ethanol, cleared in xylene and embedded in paraffin. The paraffin-embedded tissue samples were sectioned at 3 µm thickness using a microtome HM 355S with section transfer system. Tissue sections were stained with haematoxylin, erythrosine and saffron (HES) and scanned using a NanoZoomer S60 digital slide scanner using 40× magnification. The digital images were checked and adjusted using NDP.view2 software. Gonad stages for specimens were determined by qualitative histological analysis. Six stages as described in Navarte & Kroeck (2002) (modification of Lasta & Calvo 1978) were used: early maturation, mid-maturation, ripe, partial spawn, spawn and recovery, and spent.

Oocyte area was also measured, as it shows a positive correlation with the level of gonad maturation (Navarte & Kroeck 2002). For quantitative analysis, 50 oocyte areas were measured using ImageJ software instead of oocyte diameters, as oocyte diameters can be influenced by sectioning techniques (Dukeman et al. 2005). Oocyte area (ar) was then converted to mean diameter (d) by the standard formulas for spherical shapes (where r is radius):

$$\mathrm{ar} = \pi \times r^2 \text{ and } d = 2r \quad (5)$$

To ensure sectioning through the centre of the oocytes, only oocytes in which the nucleolus was clearly visible were measured (Dukeman et al. 2005).

2.9. Statistics

Statistica (TIBCO Software, version 13.4.0.14) was used for the statistical analyses. Normality was checked using a Shapiro-Wilk normality test, and homogeneity using Levene's test for equality of variances. If assumptions were not met for parametrical tests, non-parametrical tests were used. Percentages (particles cleared and GSI) were arcsine-transformed to normalise data prior to testing. Significance was assigned at $p < 0.05$.

One-way ANOVA or Kruskal-Wallis ANOVA by ranks was used to assess the effects of tanks or dates on all variables. A non-parametric Sign test for all dates, or Mann-Whitney U-test for each date, was used to test if C_{in} and C_{out} were significantly different when assessing sedimentation in 2017. Differences between diets in C_{in} and FR (Flow 1) in 2017 was tested for each date using a t-test or a Mann-Whitney U-test. The difference between the 3 diets in C_{in} in 2018 was tested for each date by Kruskal-Wallis ANOVA. When tanks and dates were pooled, a t-test was performed to assess differences between diets in FR and % particles cleared. t-tests were also used to find if there were differences in gonad ww and GSI between genders (diets pooled) and start–end values (diets or genders pooled or not). One-way ANOVA was used to find if there were differences between diets at the end (genders pooled or not).

Statistical differences between the FAs in the gonads of the different diet groups were examined with 1-way ANOVA and Tukey-Kramer multiple comparison post hoc tests using XLSTAT software (Addinsoft). Principal component analysis (PCA) was executed in the software SIRIUS 11.5 (Pattern Recognition Systems). FA values were standardised by dividing the value of the FA by the mean value of the group. This transformation method levels out the quantitative differences among FAs and ensures that the variation in the minor FAs counts as much as the dominating FAs. The results of the PCA are shown in Figs. S1 & S2 (in the Supplement at www.int-res.com/articles/suppl/q015p195_supp.pdf). Fisher's exact probability test was used to compare the number of scallops in the different developmental stages of oocytes for each diet.

3. RESULTS

3.1. Diet quality

Both the mean dry weight (mg l^{-1}) and mean organic weight (% POM of dry weight) of particles in the Algae and Waste diets were similar for the 2 years (Table 2), but showed variation between dates and waste batches. Mean dry weight (mg) of Waste was almost half that of Algae, but % POM was similar for the 2 diets. Algae and Waste showed large differences in content of essential long-chain polyunsaturated FAs (PUFAs). Algae had much higher levels of 20:4n-6 (9–19 times higher), 20:5n-3 (5–9 times higher) and 22:6n-3 (2 times higher) than Waste did (Table 2). More details of the FA data are given in Section 3.4.2.

3.2. RE

There were only small differences in RE between diets for particle sizes 2.5–5.5 µm and between Flow 1 and 2 (Fig. 4). RE peaked for particle sizes between

Table 2. Diet quality (mean ± SD, n = 3/5) of particle dry weight (DW), particulate organic matter (POM), and essential fatty acids (FAs) (% of total FAs) for 2017 and 2018

	2017		2018	
	Algae	Waste	Algae	Waste
DW (mg l^{-1})	257 ± 23	148 ± 28	321 ± 54	174 ± 53
POM (% of DW)	89 ± 25	93 ± 6	92 ± 9	86 ± 7
Diatom FA 16:1n-7	8.8 ± 0.5	3.40 ± 0.03	18.4 ± 2.1	3.1 ± 0.9
Terrestrial FA 18:1n-9	2.7 ± 0.3	10.4 ± 0.2	4.1 ± 0.4	11.1 ± 2.0
Essential FAs				
FA 20:4n-6	1.7 ± 0.1	0.18 ± 0.04	3.3 ± 0.3	0.17 ± 0.06
FA 20:5n-3	11.8 ± 1.1	2.2 ± 0.03	13.6 ± 1.3	1.6 ± 0.3
FA 22:6n-3	7.0 ± 0.6	2.9 ± 0.04	5.6 ± 0.7	2.5 ± 0.7

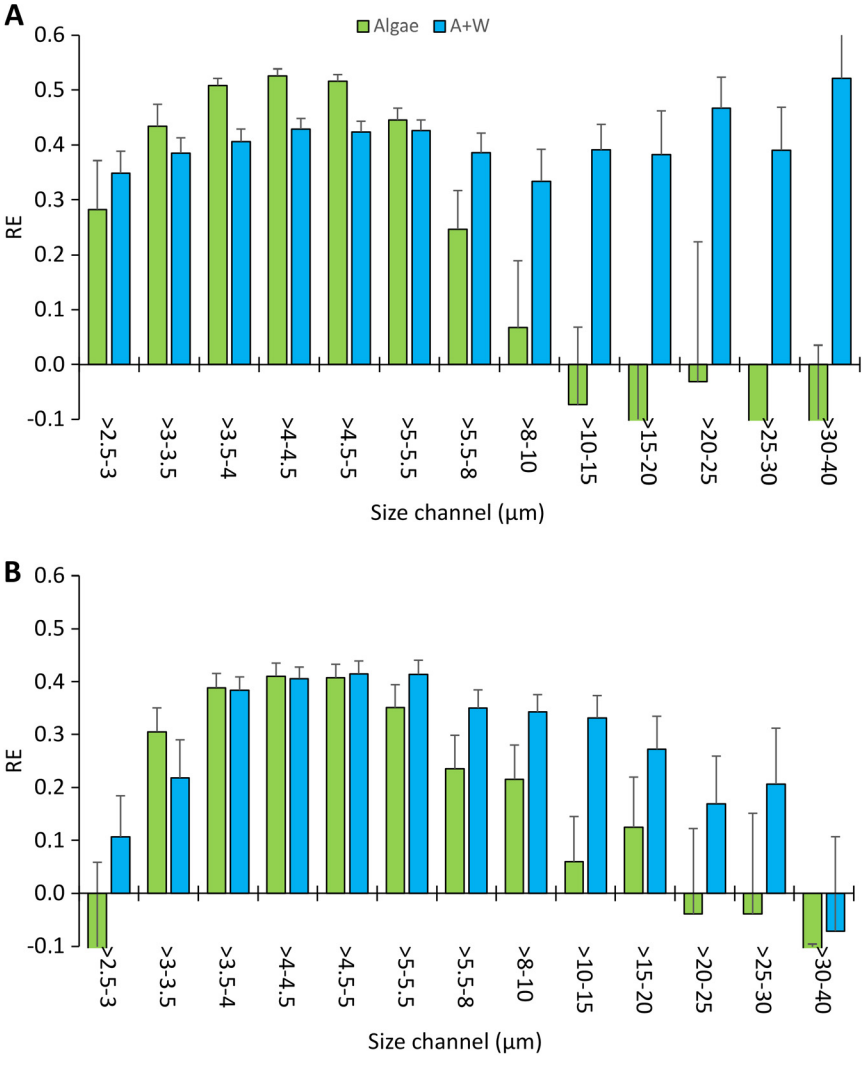

Fig. 4. Mean ± SE for retention efficiency (RE) for the 2 diets Algae and A+W at 2 different tank flow rates of seawater with diet particles: (A) Flow 1 (1000 ml min^{-1} $tank^{-1}$, n = 15); (B) Flow 2 (1590 ml min^{-1} $tank^{-1}$, n = 18). Data are from 80 l tanks stocked with 3 scallops each

3.5 and 5.0 µm for Algae and between 3.5 and 5.5 µm for A+W at both Flow 1 and 2 and declined more rapidly for Algae than for A+W when particle size >5.5 µm. RE was negative for Algae when particles exceeded 10 µm at Flow 1 and 20 µm at Flow 2 (Fig. 4). Maximum RE values for Algae were higher at Flow 1 than at Flow 2, and reached 0.51–0.53 and 0.39–0.41, respectively. Maximum RE values for A+W were similar at Flow 1 and Flow 2, and were 0.38–0.43.

3.3. Feeding experiments, 2017

There was no effect of tanks on any variable (C_{in}/Flow_rate, % particles cleared, FR), and data from the tanks were pooled. There was an effect of dates on all variables at both flows, except on C_{in}/Flow_rate for A+W at Flow 1 and on FR and % particles cleared for both diets at Flow 2. Mean and SD values for C_{in}, food flow rate, FR and % particles cleared based on TPV are given in Table 3. The data are presented for each tank and hence, for 3 individuals. Due to the increased flow of seawater and similar concentrations (particles ml^{-1}) in the diet mixing tanks, mean values for C_{in} decreased at Flow 2 compared to Flow 1, independent of diet, and were 56 and 44 × 10^3 µm^3 ml^{-1} for Algae and 63 and 39 for A+W at Flow 1 and 2, respectively. C_{in} was higher for A+W than for Algae at Flow 1 (significant on 4 out of 5 dates; p = 0.002, 0.001, 0.012 and 0.004) and vice versa at Flow 2 (significant on 2 out of 5 dates; p = 0.025 and 0.045). Food flow rate was higher at Flow 2 than at Flow 1 for Algae (56 vs. 71 × 10^6 µm^3 min^{-1}, respectively), but similar for A+W for the 2 flow rates. Percentage of particles cleared was lower for A+W than for Algae at both Flow 1 and 2 (48 vs. 41 % and 38 vs. 34 %, respectively), but the difference was only significant at Flow 1 (p = 0.041). FR for Algae was significantly higher than for A+W at

Table 3. Mean ± SD values for particle concentration for the inlet samples (C_{in}), food flow rate (FFR), % particles cleared (% PC) and feeding rate (FR) at 2 different flow rates, Flow 1 (1000 ml min^{-1}) and Flow 2 (1590 ml min^{-1}), and the 2 diets Algae and A+W. All values are given per tank (containing 3 individuals each). Superscript letters [(a–d)] show significant differences ($p < 0.05$) in means between diets at each flow rate. A significant difference between diets was also detected for 2 (^{2d}) and 4 (^{4d}) days out of 5

	Flow 1 (n = 15)		Flow 2 (n = 15–16)	
	Algae	A+W	Algae	A+W
C_{in} (×10^3 µm^3 ml^{-1})	55.9 ± 5.7^{2d}	63.1 ± 16.7	44.4 ± 5.7^{4d}	38.6 ± 6.2
FFR (×10^6 µm^3 min^{-1})	55.9 ± 5.7	63.1 ± 16.7	70.6 ± 9.1	61.3 ± 9.8
% PC	47.6 ± 7.4^a	41.2 ± 8.8^b	38.1 ± 8.3	33.8 ± 6.7
FR (×10^6 µm^3 min^{-1})	26.9 ± 6.2	26.6 ± 10.2	27.0 ± 7.4^c	20.8 ± 5.9^d

Flow 2 (27 vs. 21 × 10^6 µm^3 min^{-1}, $p = 0.016$), but was identical for the 2 diets at Flow 1 (27 × 10^6 µm^3 min^{-1}).

3.4. Reproductive ability, 2018

3.4.1. Gonad ww and GSI

Mean and SE gonad ww (Fig. 5A) at the start was 2.3 ± 0.3 g (n = 17) for females and 3.3 ± 0.4 g (n = 13) for males, with no significant difference between the genders ($p > 0.05$). There was also no significant difference in gonad ww between genders at the end when diets were pooled or between diets when genders were pooled. There was a significant difference between start and end ww values for females ($p = 0.011$, diets pooled), but not for males. Mean and SE GSI (Fig. 5B) at the start was 13.6 ± 2.4 (n = 17) for females and 18.8 ± 3.0 (n = 13) for males. However, the means were not significantly different ($p > 0.05$) due to the high variation. Mean GSI for the end samples of the 3 diets were 15.9–16.9% for females and 13.7–13.9% for males, but no significant differences were detected between start and end samples when genders were pooled, or between diets at the end whether genders were pooled or not. However, when genders were not pooled, GSI for males at the start was significantly higher than for males at the end (n = 43, $p = 0.015$) when diets were pooled. There was no effect of tanks on GSI, and data were pooled across tanks.

3.4.2. FAs

The FA composition was very different between the 2 diet components Algae and Waste (Fig. 6A, Tables S1 & S2). There were some variations between the 2 years and the samplings times; however, the general FA profile for the 2 diet components was very much the same for the 2 years. The waste from a salmon farm was dominated by saturated FAs (55–61% of total FAs), especially 16:0 (29–31% of total FAs) and 18:0 (11–20% of total FAs). The monounsaturated FAs (MUFAs) from Waste was 26–32% of the total FAs, and they were dominated by 18:1n-9 (10–13%), but had relatively high levels of long-chain MUFAs, such as 20:1n-9 and 22:1n-11 (2.9–5.1%). Waste had low levels of PUFAs (Table 2), and among these were 18:2n-6, the most dominant FA (2.4–3.4%). In Algae, the PUFAs were the dominant FA group (36–45%), and (n-3) PUFAs were present in higher levels than (n-6) PUFAs, with 20:5n-3 as the dominant FAs (12–15%). The MUFAs were dominated by 16:1n-7 (15–20%), and in the saturated FAs, 14:0 was highest (22–23%).

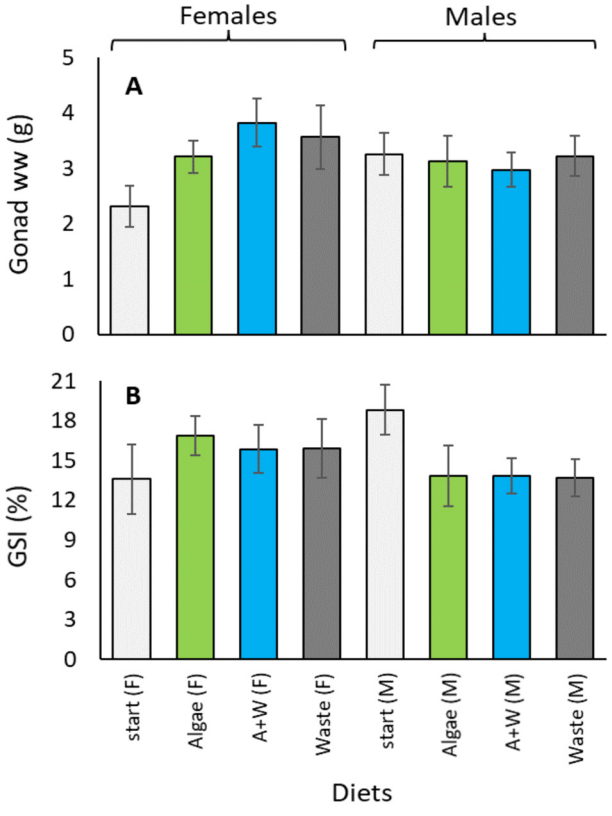

Fig. 5. Mean ± SE for (A) gonad wet weight (ww) and (B) gonado-somatic index (GSI; ww gonad as % of ww somatic tissue), for females (F, n = 13–19) and males (M, n = 10–17) at the start of the experiment and for different diets (Algae, A+W, Waste) at the end (13 wk) of the experiment

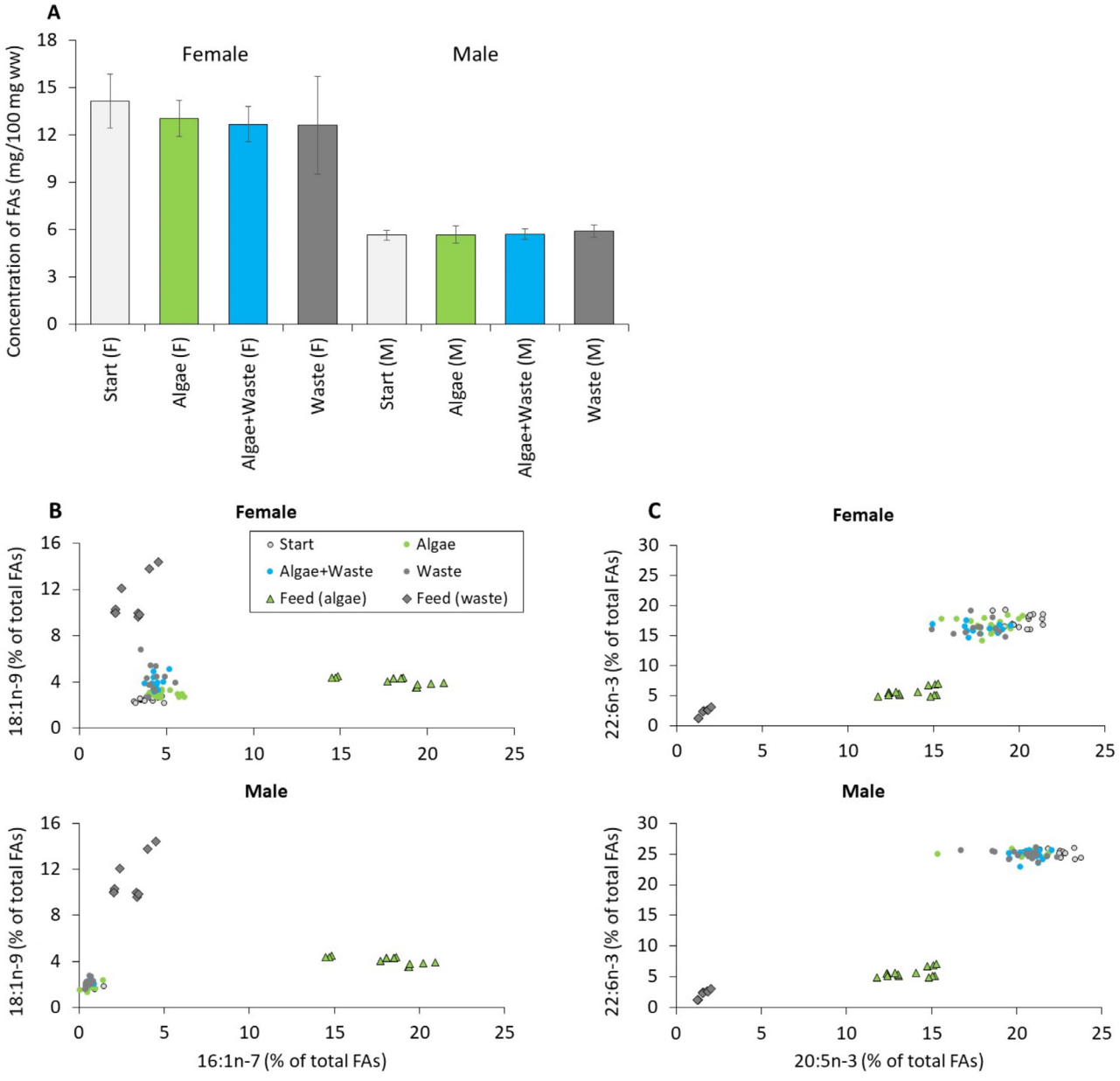

Fig. 6. (A) Concentrations of fatty acids (FAs) (mean ± SD) in the gonads of female (F) and male (M) scallops at the start and end of the experiment (all diets). (B) Relative contribution (% of total FAs) of terrestrial FA (18:1n-9) and diatom FA (16:1n-7) in scallop gonads with the different diets. (C) Relative contribution of essential FAs (20:5n-3 and 22:6n-3) in scallop gonads with the different diets. ww: wet weight

Despite the large differences in the FA composition between the diet components, large differences were not found in the FA profiles in the gonads between the different diets (Table 4, Fig. 6B,C). The gonads of the scallops that were fed Waste had a small increase in 18:1n-9 ($p < 0.0001$ for females and $p = 0.001$ for males) (Table 4).

There were no differences between the feeding groups for the long-chain PUFAs. However, there was a decline from the start and the end of feeding experiment in the relative amount (% of total FAs) of the long-chain PUFA 20:5n-3 in both the ovary and testis ($p < 0.0001$), and an increase for 20:4n-6 in the testis ($p = 0.041$), while the content of 22:6n-3 remained constant in both genders and all treatment groups (Table 4).

The considerable differences between the FA profiles in feed (Waste and Algae) and the ovary and testis are clearly seen in the multivariable PCA (Fig. S1). Algae had relatively higher amounts of the short-chain C_{16} and C_{18} PUFAs, 14:0, 16:1n-7 and 17:1n-6, and Waste had relatively higher amounts

Table 4. Terrestrial fatty acid (FA), diatom FA and essential polyunsaturated FAs (PUFAs) in the gonads (female and male) of Iceland scallop from 2018, at the start of the experiment and with the 3 different diets. Normalised FA data are mean relative amounts (% of sum FA ± SD); superscript letters [(a,b)] show significant differences between treatments analysed by ANOVA followed by pairwise comparison for Groups (Tukey HSD; $p < 0.05$). All FAs are shown in Table S3

	Females				Males			
	Start (n = 15)	Algae (n = 20)	A+W (n = 13)	Waste (n = 13)	Start (n = 14)	Algae (n = 10)	A+W (n = 16)	Waste (n = 17)
Diatom FA								
16:1n-7	4.0 ± 0.6^{b}	4.7 ± 0.7^{a}	4.4 ± 0.3^{ab}	4.3 ± 0.5^{ab}	0.9 ± 0.0.3^{a}	0.6 ± 0.4^{b}	0.5 ± 0.1^{b}	0.5 ± 0.1^{b}
Terrestrial FA								
18:1n-9	2.5 ± 0.2^{b}	3.0 ± 0.2^{b}	3.9 ± 0.6^{a}	4.3 ± 1.1^{a}	1.7 ± 0.2^{b}	1.7 ± 0.3^{b}	2.3 ± 0.13^{a}	2.1 ± 0.3^{a}
Essential PUFAs								
20:4n-6	1.7 ± 0.4	2.0 ± 0.3	1.8 ± 0.2	1.9 ± 0.7	2.8 ± 0.2^{b}	3.3 ± 1.0^{a}	2.9 ± 0.3^{ab}	3.0 ± 0.4^{ab}
20:5n-3	20.2 ± 0.9^{a}	18.4 ± 0.08^{b}	17.7 ± 1.2^{b}	17.0 ± 2.4^{b}	22.4 ± 0.6^{a}	20.3 ± 1.9^{b}	20.8 ± 0.7^{b}	20.3 ± 1.4^{b}
22:6n-3	17.6 ± 1.1	16.9 ± 1.0	16.2 ± 0.8	17.0 ± 2.9	25.1 ± 0.6	25.0 ± 0.5	24.9 ± 0.5	25.0 ± 0.6

of saturated FAs and long-chain $C_{20,}$ C_{22} and C_{24} MUFAs compared to ovary and testis from Iceland scallop.

There were large differences in lipid amounts (relative to dry weight) between the ovaries and the testis, more than double in the ovaries compared with the testis (Fig. 6A, Table S3). The 2 tissues also had large differences between the FA profiles (Table S3). The PCA (Fig. S2) shows that the ovaries had relatively higher amounts of short-chain C_{16} and C_{18} PUFAs, while the testis had relatively higher levels of long-chain C_{20} and C_{22} PUFAs.

3.4.3. Oocytes

The qualitative analysis demonstrated that only 3 dominant reproductive stages (most frequent stages found per animal) were present throughout the study, namely: ripe, partial spawn, and spawn and recovery (Table 5). The most dominant stage at the start and in the diet groups at the end was the partial spawn stage, ranging from 66.7 to 84.6% of scallops in the groups. There was no difference in the gonad stages ripe and partial spawn between the diet groups, including at the start ($p = 0.93$). The spawn and recovery stage was observed only in 1 scallop in the group at the start and in Waste at the end. No animals were found to be completely spent as new primary oocytes were present.

Oocyte mean diameter (µm) at the start was significantly lower than for the different diets at the end ($p < 0.001$ for all 3), but there was no significant difference between the diets at the end (Table 6).

4. DISCUSSION

In this study, we focused on small particles (<41 µm) from farmed-fish waste, which is within the size range we assume to represent particles dispersed into far-field areas (500–1000 m). The diets in our study consisted of similar particle sizes and high (>50%) organic content (% POM), with large differences in the FA composition between the 2 diets, Algae and Waste. The Algae diet had high levels of PUFAs (36–45% of total FAs), while Waste was dominated by saturated

Table 5. Number of individuals with dominant gonad stage at the start of the experiment and for the 3 diets at the end of exposure. n: number of females from each group

Gonad stage	Start	Algae	A+W	Waste
Early maturation	0	0	0	0
Mid maturation	0	0	0	0
Ripe	4	5	2	3
Partial spawn	12	15	11	8
Spawn & recovery	1	0	0	1
Spent	0	0	0	0
n	17	20	13	12

Table 6. Oocyte diameter (mean ± SD) for individuals (n) at the start of the experiment, and at the end for the diets Algae, A+W and Waste. n: number of females; CoV: coefficient of variance (SD as % of means). Superscript letters [(a,b)] show significant differences ($p < 0.05$)

Diet	Oocyte diameter (µm)	n	CoV
Start	45.0 ± 7.3^{a}	17	16.3
Algae	54.8 ± 1.7^{b}	20	3.1
A+W	54.9 ± 3.2^{b}	13	5.8
Waste	52.6 ± 12.3^{b}	12	23.5

FAs (55–61%) and MUFAs (26–32%), and had low levels of PUFAs (5–6%). The low lipid content (≈2%) in Waste and its relative low levels of terrestrial FAs (18:1n-9 ≈ 10%, 18:2n-6 ≈ 2% and 18:3n-3 ≈ 1% of total FAs) indicate that Waste mainly contained salmon faeces and very little salmon feed. Salmon feed has a high lipid content (>20%) and high levels of terrestrial FAs (18:1 n-9 ≈ 30%, 18:2n-6: 10–15% and 18:3n-3: 3–6% of total FAs) (data from Skilbrei et al. 2015). The FA profile in Waste used in the present study was similar to salmon faeces (Nederlof et al. 2019) and was representative of FA profiles that are found in the sediments in the vicinity of salmon farms (White et al. 2017, Woodcock et al. 2019).

4.1. Feeding

There was a significantly higher feeding activity by Iceland scallop using the 100% algae diet (Algae) compared to a diet with 50% fish waste (A+W), but only for the % particles cleared at Flow 1 and for FR at Flow 2. MacDonald et al. (2011) found no consistent differences in other measures of feeding activity, clearance rate (CR, volume cleared of all particles) and absorption efficiency (difference in POM between food and faeces), when mussels *Mytilus edulis* were offered fish food and a microalga in the laboratory for 7 d. Higher feeding activity was indicated *in situ* when they held mussels at a salmon farm compared to mussels at a reference location. However, the mussels were placed within the fish farm sites, and the size distribution of particles would most probably have been very different from the particle size distribution of our study's diets (Law et al. 2014, Broch et al. 2017). Bergvik et al. (2018) showed that CR in juvenile scallops *Pecten maximus* were lower when either salmon feed or faeces were added to the diet of algae mix. This may have been caused by much smaller particle sizes in the salmon feed and faeces than in the algae mix, resulting in differences in RE between the diets and, hence, a difference in CR (Strohmeier et al. 2012). In the present study, the diets were similar in particle sizes, and differences in RE between the diets were small or insignificant. However, Iceland scallop showed higher RE at lower particle sizes (3–5.5 µm) in this study than previously reported for scallops. Vahl (1973) reported that RE in Iceland scallops fed natural seston was high down to a particle size of 4 µm in diameter and reached the highest values above 7 µm. Earlier studies (Møhlenberg & Riisgård 1978, Riisgård 1988) have suggested that RE in scallops is low for particles <5–7 µm due to the gill structure. In contrast to our study, Vahl (1973) only observed particles up to 10 µm, but did not present the size distribution for the diet used, making it difficult to compare the results directly with ours. The small particle sizes of the highest RE in our study compared to Vahl (1973) may be a result of a higher number of small (<8 µm) particle sizes in our diets.

TPV in the diets showed higher values for A+W than for Algae when particle sizes were >5.5 µm. This is consistent with the higher RE for A+W than for Algae at these particle sizes, especially at the lowest flow rate, Flow 1. Refiltration at Flow 1 may explain the higher RE at the lowest particle sizes and at the maximum levels for Algae at this flow rate, but similar trends were not observed for A+W. RE for A+W did, however, show higher levels for particles >10 µm at Flow 1 than at Flow 2. The lowest flow rate in our experiments was equal to 20 l h^{-1} ind.$^{-1}$. Cranford et al. (2016) showed CR for blue mussel *M. edulis* to decrease at flow rates higher than 10–12 l h^{-1}. If this is the case here, Flow 2 was higher than the optimal flow rate and caused a reduction in RE. But the studies of Cranford et al. (2016) differed from the present study in both experimental containers and species (mussels). Different bivalve species have been reported to have different feeding responses to environmental parameters (MacDonald & Ward 2009) and different feeding activity (Shumway et al. 1997)

Feeding in our scallops was calculated for smaller particles (3–8 µm) since the concentration of larger particles was too low to obtain enough data. However, it is most likely that Iceland scallop can also feed on large particles, since feeding on 56–950 µm particles has been reported for other scallop species (Chipman & Hopkins 1954, Shumway et al. 1987).

Like our results showing that % particles cleared was lower at the highest flow rate (Flow 2) than at the lowest flow rate (Flow 1) independent of diet, Filgueira et al. (2006) reported the effect of flow rate on % of particles cleared in mussels. Our % particles cleared values of 41–48% at Flow 1 were above the recommended level of <30% to avoid recirculation and refiltration of water within the containers (Filgueira et al. 2006, Strohmeier et al. 2009), thus some degree of refiltration may have occurred.

4.2. Reproductive ability

There was no indication in our data that the gonads were negatively affected by adding fish waste to the

diet of the adult scallops. In fact, there seemed to be small or no changes in the parameters during the experiment. Gonad maturation level in most animals was similar at the start and at the end in all diet groups, indicating that very little happened in the gonads during the experiment. However, the temporal development throughout the experimental period was not investigated, and a spawning event could therefore have been missed.

Our scallops collected in early April were most likely in a late stage of gonad maturation, since *Chlamys islandica* from Balsfjord spawn during a short period in late June and early July (Sundet & Vahl 1981, Sundet & Lee 1984, Pettersen 1995). This is also indicated by our results that the dominant oocyte stage in May already was partial spawn. It is possible that the essential components of the oocytes and spermatocytes already were in place upon our collection, and that our study's diets therefore had no or little effect on the gonad development.

However, Brokordt & Guderley (2004) showed that during late gonad maturation and spawning, only 10–25% of the energy gain of the ovaries in *C. islandica* was covered by energy loss of the somatic tissue, indicating that the rest of the energy came from feeding. They described a different situation in males, where all the energy gain in testis could be explained by energy loss in somatic tissue. The glycogen reserves of our scallops may then have been depleted by March due to low food abundance during the winter in Balsfjord (Sundet & Lee 1984, Eilertsen & Degerlund 2010), and the scallops needed resources directly from the food to finish the gonad maturation (Sundet & Lee 1984). If energy was more important than essential components, such as FAs, the diet quality may have had less impact than the total energy content.

The lack of dietary effects on gonad maturation in our scallops may have been a result of low total food levels, rather than diet quality. Food amount is shown to play an important role in the development rate of gonads in several bivalves (Delgado & Pérez-Camacho 2007: *Ruditapes philippinarum*; Heasman et al. 1996: *Pecten fumatus*; Utting & Millican 1997: oyster, clam, scallop). Also, this may depend on temperature, as was shown for 2 clam species, *R. philippinarum* and *R. decussatus* (Delgado & Pérez-Camacho 2007). The level of food sufficient for gonad development in Iceland scallop is not known, which made it difficult when designing the feeding regime for the present study. Our food levels were therefore based on knowledge from reports of phytoplankton densities in Balsfjord during summer (Eilertsen & Taasen 1984) when temperatures were as high as in our experiment (Eilertsen & Skarðhamar 2006). The gonad ww in our scallops prior to the start of the experimental on 24 May 2018 matches well with the findings of Sundet & Lee (1984), who described the mean gonad ww of females to be 1.5–2.0 g from post-spawning in July to the end of March. The mean gonad ww then increased to a maximum of a little more than 6.0 g in the beginning of July at the onset of spawning. Male gonads showed the same ww post-spawning and at maximum, but the increase in their ww started already in November (Sundet & Lee 1984). Scallop collection for our feeding experiment was in May 2017 and these scallops had much heavier gonads compared to the scallop gonads from April 2018.

The mean oocyte diameters were 52.6–54.9 µm in our experimental period. Compared to values for *Pecten sulcicostatus* from the southwestern coast of South Africa that were mostly 40–50 µm and peaked at a mean of 55 µm (Arendse et al. 2008), our values were at the uppermost end. Also, the maximum oocyte diameter of 38 µm for bay scallop *Argopecten irradians* prior to spawning was lower than our values (Barber & Blake 1983). Mean oocyte diameter in our study was slightly, but not significantly, lower in scallops fed the Waste diet compared to the other 2 diets. This follows the same trend as in the qualitative results, where complete spawning and recovery activity was found only with the Waste diet.

4.3. FA as biomarker in gonads

Because of the very high levels of terrestrial FAs in today's fish feed, FA analysis is a powerful tool for monitoring the transfer of fish feed into the marine food chain (Redmond et al. 2010, Skilbrei et al. 2015, White et al. 2019, Woodcock et al. 2019). In the present study, we did not find a strong modification of the FA profiles of lipids in either ovary or testis. This may be a consequence of the timing of the experiment that was down-stream from the main gonad maturation but also that the mobilisation of lipids to the gonads are very conservatively selected to obtain a concentration of essential FAs (Soudant et al. 1996, 1997). The lipid analysis was concentrated on gonad tissues, as the main concern about the accumulation of large amounts of terrestrial FAs focuses on the possibility that this may interrupt the reproduction of marine organisms (White et al. 2017, Gonzalez-Silvera et al. 2020). The study would have benefited from analysis of other organs such as the digestive

gland and the mantle, as these organs are more likely to reflect the FA signal from the diet. However, this was not done. The digestive gland is normally the main organ for storage of lipids in bivalves (Caers et al. 1999, Azpeitia et al. 2016), and both blue mussel *M. edulis* (Handå et al. 2012) and great scallop *P. maximus* (Bergvik et al. 2018) have been shown to accumulate terrestrial FATMs from salmon feed into especially the digestive gland.

4.4. Conclusion and further work

There is nothing in our results that indicates an acute negative effect of dietary exposure of Iceland scallops to salmon waste. Although natural phytoplankton is necessary to describe feeding behaviour in nature (Cranford et al. 1998, and references therein), short-term controlled lab experiments using a mix of cultured microalgae instead of natural seston is a first step towards investigating possible effects on Iceland scallops when salmon waste forms part of the diet.

Repeated exposure to non-lethal levels of waste particles may impact scallop physiology over time. Studies on how long the small fish-waste particles stay suspended, degradation rate, and whether they are removed from the water column by other organisms is needed to determine the effect on marine habitats and benthic species living in the outer impact area of fish farms. Once settled on the seabed, these small particles become a food source for filter- and deposit-feeders such as the Iceland scallop. Long-term observations, especially of reproduction success and energetic status, would be the next investigative step. Since Iceland scallops seems to start their oogenesis shortly after spawning (Sundet & Lee 1984, Thorarinsdóttir 1993), effects of fish waste in their diet should be studied from this early stage of gonad maturation. Long-term studies (a year or more) are more relevant if they are carried out in the natural environment, letting the scallops be exposed to the natural variation in diet and temperature. Replicating the natural environment in the lab is very difficult to do, and the lack of effects found in our experiments should be verified *in situ*. A transplant study of Iceland scallop from unaffected areas (control) to areas closer to a salmon farm (within 300–1000 m away from the farm) would therefore be our prioritised suggestion to continue this work. Also, such studies should include FA analysis of other organs such as the digestive gland and the mantle, as these organs are more likely to reflect the FA signal from the diet.

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