

Norwegian red sea cucumber (*Parastichopus tremulus*) fishery and aquaculture north of 60°N latitude: Feasible or fictional?

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Abstract

The high demand for sea cucumbers from the Asian market has led to the interest in new species from the North Atlantic. The Norwegian red sea cucumber, *Parastichopus tremulus*, is one potential species, that has yet to be exploited or cultured. The red sea cucumber is distributed along the entire Norwegian coast, and seems to be abundant north of 60°N. The population is believed to be commercially exploitable, but the lack of knowledge on its life history traits and population structure necessitates more biological investigations before this can be confirmed. Aquaculture of the species is considered, but for this to succeed knowledge about reproduction and early life stages needs to be advanced. In this paper we summarise some of the knowledge currently available for *P. tremulus*, present some recent advances from reproduction studies, and discuss prospects for utilising this species, both through a fishery and aquaculture.

Key words: Norwegian red sea cucumber, *Parastichopus tremulus*, biology, fishery, aquaculture

Introduction

There is a great demand for sea cucumbers from the Asian market and buyers are driven west and north to explore new species to replace vulnerable and depleted species from the Pacific (Purcell et al. 2014). The sea cucumbers of the Atlantic are the next to be targeted for commercial utilisation and face the threat of overexploitation unless: a) more knowledge is obtained about their life-history traits and population dynamics, and b) proper management actions are implemented (González-Wangüemert et al. 2018). Preliminary investigations have shown that the red sea cucumber *Parastichopus tremulus* (Fig. 1), which inhabits Norwegian waters, possesses many important properties favoured by Chinese customers, such as size, body shape, meat content, taste and nutritional composition (Kjerstad et al. 2015). Market introduction of this species is still in the initial phase, but there is increased interest in harvesting and exploiting this resource from the north east Atlantic. Currently, the species is only landed as bycatch in Norway, but the prospects of a lucrative trade and a desire to utilise all bycatch, encourage fishermen, entrepreneurs, and established seafood traders to fish, process and export the species. However, because no commercial fishery licenses are issued, the variable supply of bycatch complicates the development of a new value chain for this resource. Several Asian countries have, over the last decades, developed successful industrial-scale aquaculture of at least three highly appreciated species *Apostichopus japonicus*, *Holothuria scabra* and *Isostichopus fuscus* (Mercier and Hamel 2013), with China being by far the largest producer (Yang

et al. 2015). Therefore, it seems likely that aquaculture production in the future will supplement, or even replace, fisheries as a more sustainable source of sea cucumbers for human consumption. There is increased interest in the aquaculture of species outside of Asia, and several European species have recently been investigated for their aquaculture potential (Santos et al. 2016; Rakaj et al. 2018, 2019; Christophersen et al. 2020; Laguerre et al. 2020). To succeed with the development of sustainable fishery and/or aquaculture, however, several biological, commercial and legislative questions need to be answered. The research institute Møreforskning started work on the utilisation of sea cucumbers in 2004, and it was concluded that there is potential for the commercial utilisation of *P. tremulus* in Norwegian coastal waters (Kjerstad et al. 2015). We report on the current status and thoughts considering the feasibility of catching and producing the Norwegian red sea cucumber *P. tremulus* above 60°N.

Observations and conditions at high latitudes

Although sea cucumbers have been studied since the early days of marine biology, limited information exists on the biology and ecology of the Norwegian red sea cucumber, *P. tremulus* (Gunnerus, 1767) in Norwegian waters. Historically, the species has been recognised under several scientific names (IUCN Red list of Threatened Species): *Stichopus tremulus* (Gunnerus); *Holothuria elegans* O.F. Müller, 1781; *Holothuria tremula* Gunnerus, 1787; *Holothuria ecalcareo* M. Sars, 1859; *Stichopus richardi* Hérourard, 1896 and *Stichopus griegi* Östergren, 1896. The

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Figure 1. An adult specimen of the Norwegian red sea cucumber, *Parastichopus tremulus*. (image: Jan Sunde, Møreforsking)

existing literature is based on observations and studies in a few limited geographical locations: the Bergen and Oslofjord areas in southern Norway (Gunnerus 1767; Nordgaard 1912; Rustad 1940; Jespersen and Lützen 1971; Lønning 1976), the Gullmarsfjord on the west coast of Sweden (Holland 1981; Hudson et al. 2005), and off the western coast of Ireland and the British Isles (Mortensen 1927; Hudson et al. 2004). There is even less documentation on the biology of *P. tremulus* from areas above 60°N (Christoffersen et al. 2020; Schagerström et al. submitted) (Fig. 2).

Habitat and ecology

Parastichopus tremulus mainly lives in waters too deep to be observed by scuba divers, which is one of the reasons why biological and ecological information on the species is scarce. Modern technology, however, such as ROVs (remotely operated vehicles) and towed video rigs, has made deep-sea observations easier. For instance, the Norwegian MAREANO programme³, financed by the Ministry of Fisheries and Coastal Affairs, the Ministry of Environment, and the Ministry of Trade and Industry since 2005, maps the occurrence of different species off the coast of Norway using both video and active sampling gear. Data on benthic organisms are collected, including depth, topography and sediment composition, have provided important information on a variety of underwater nature types and biotopes. Further, information

on species occurrence from historical surveys have been digitised and made accessible through open access databases such as EMODnet⁴ and the Global Biodiversity Information Facility (GBIF).⁵ Recorded occurrences from these data sources show that *P. tremulus* is found in the eastern Atlantic Ocean, from the Arctic Barents Sea to the Canary Islands in the south (Fig. 2), adding new information to the distribution map shown in Madsen and Hansen (1994).

It appears that the species is especially abundant along the Norwegian coast above 60° N (Fig. 2), although it is likely that this is due to the higher survey intensity in this area, particularly through the MAREANO programme. The deepest known occurrence of *P. tremulus* is in the sea between Greenland and Svalbard at a depth of 3193 m (MNHN, Chagnoux S. 2021). This is deeper than the earlier proposed bathymetrical distributions of ca. 20–1900 m (Grieg 1921; Mortensen 1927). The majority of occurrences, however, are from 200 to 400 m depth (Fig. 3). The species has been recorded on a variety of substrates along the Norwegian coastline but appears to be most commonly observed on soft bottom sediments (Fig. 4). It should be noted that data on depth registration and substrate preference might be artefacts of geographical preference for scientific survey activity. On the other hand, the information seems to be substantiated by data from test fisheries and research cruises in Norway, which have found that the highest abundance of the species is on soft bottom habitats at depths between 100 and

³ See <https://mareano.no/en>

⁴ See www.emodnet.eu

⁵ See www.gbif.org

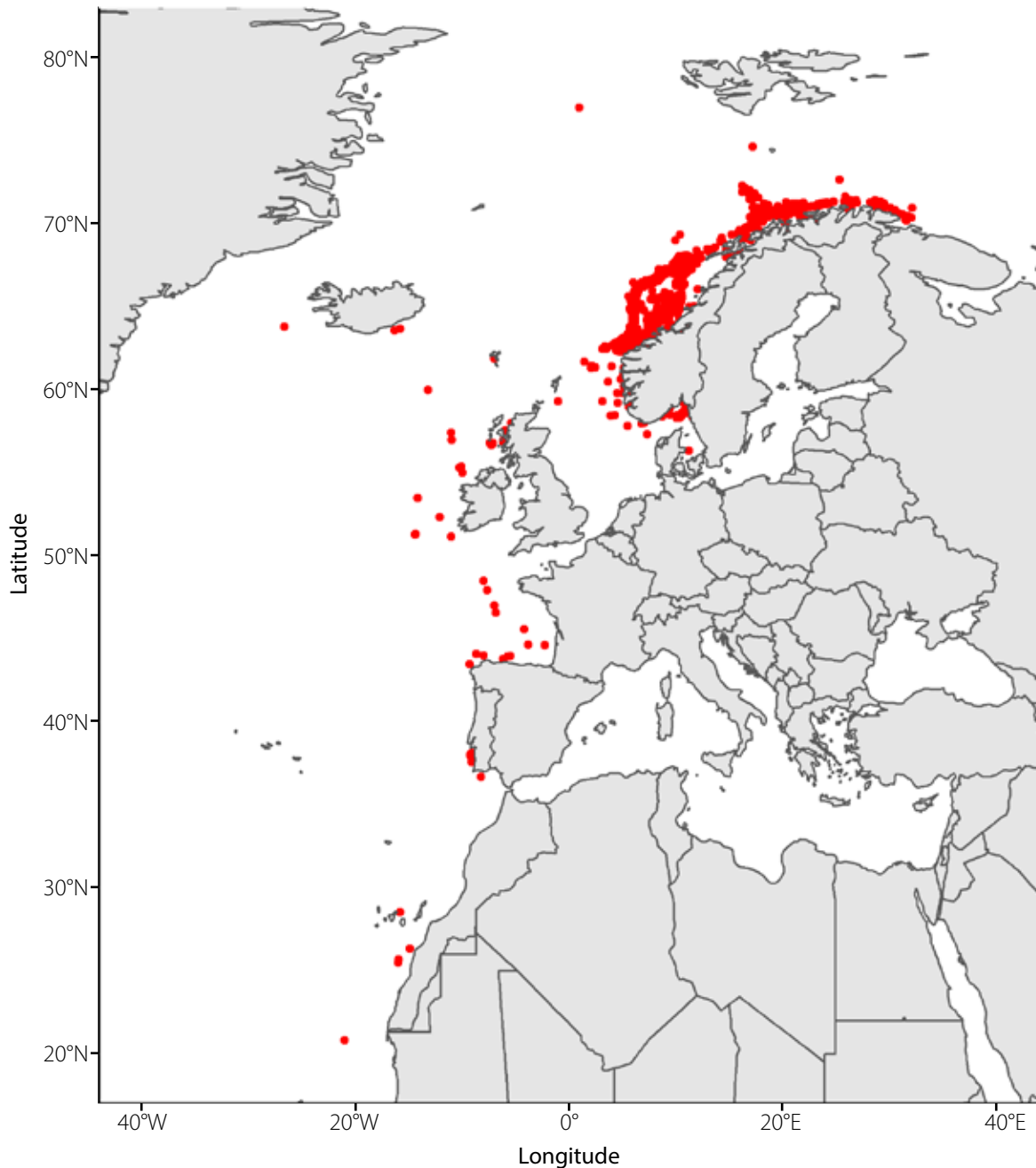


Figure 2. Recorded occurrences of *Parastichopus tremulus*. Data obtained from the MAREANO Marbunn database (www.mareano.no/marbunn), the European Marine Observation and Data Network (EMODnet Biology (2020) Full Occurrence Data and Parameters downloaded from the EMODnet Biology project (<http://www.emodnet-biology.eu>). Available online at <http://www.emodnet-biology.eu/toolbox/en/download/selection/15f9adb20ad111>, consulted on 29 October 2020), and the Global Biodiversity Information Facility (GBIF.org (2 November 2020) GBIF Occurrence Download <https://doi.org/10.15468/dl.u9dvzs>). (n=4319, Duplicate recordings removed from the dataset).

300 m (Kjerstad et al. 2015). Along the coast of northwestern Europe and inside the fjords of Norway, the sea temperature is between approximately 2–8° C at the depths where *P. tremulus* is most abundant (Furevik 2001; Berx and Hughes 2009; Woll et al. 2014), with the lowest temperatures found in the northern part of the species' distribution.

Parastichopus tremulus is a deposit-feeding sea cucumber and extracts nutrients from soft bottom sediments on the sea floor. Jespersen and Lützen (1971) proposed that *P. tremulus* in Norwegian waters might have a seasonal feeding pattern,

and that feeding ceases between mid-October and January, at least in the Oslo fjord. Hauksson (1979) seemed to agree, based on his own observations from the Raune fjord on the west coast of Norway. It is unclear whether this observed cessation of feeding in *P. tremulus* is associated with evisceration of digestive organs (Jespersen and Lützen 1971), or if it merely is a period of aestivation as seen in other holothurioids, most notably *Apostichopus japonicus* (Ji et al. 2008; Yang et al. 2005). We believe this area deserves more research attention. Information is also lacking about feeding preferences and nutritional metabolism of *P. tremulus*.

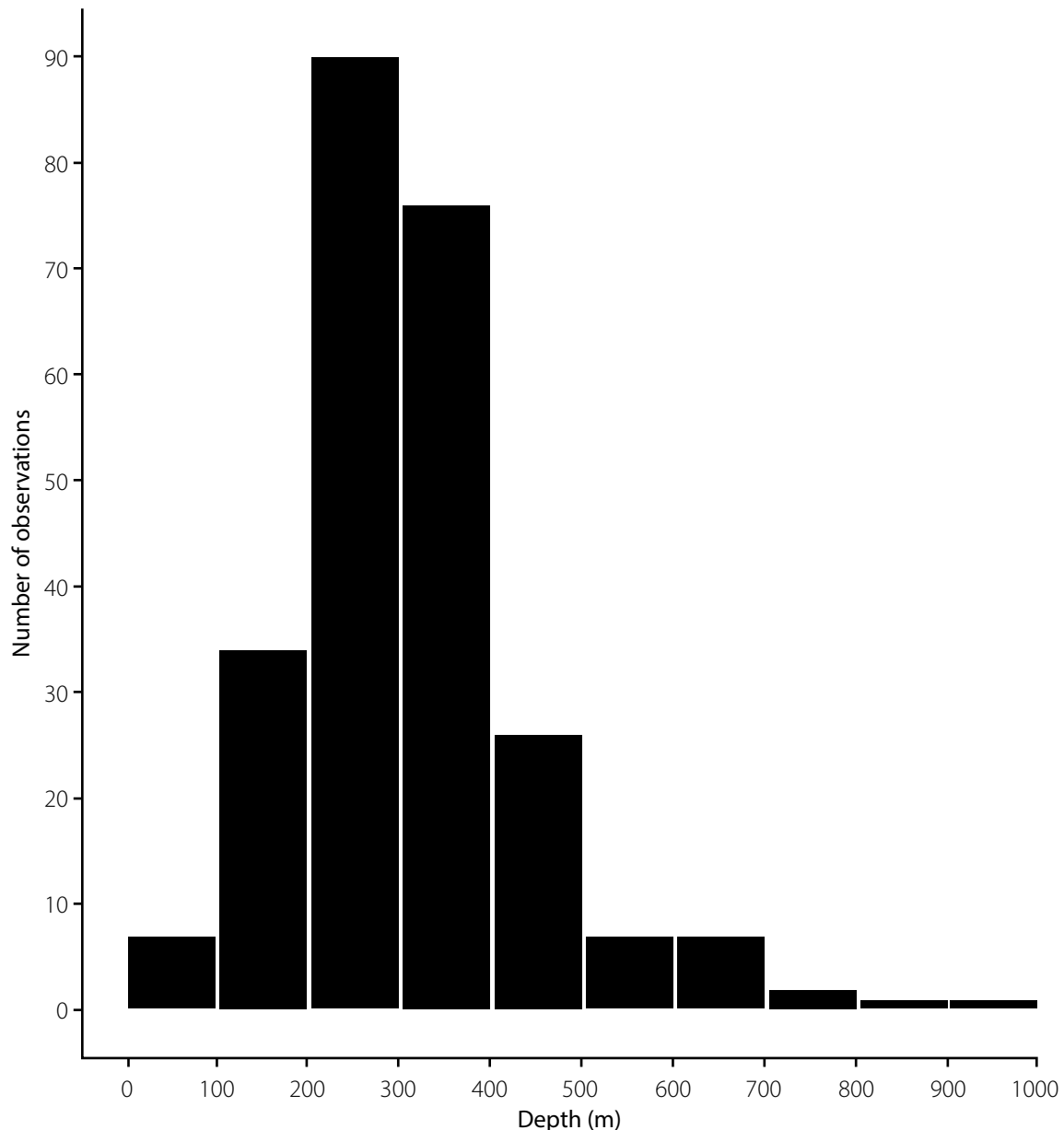


Figure 3. Recorded depth of registration of *Parastichopus tremulus*. Data obtained from the MAREANO Marbunn database (www.mareano.no/marbunn), the European Marine Observation and Data Network (EMODnet Biology (2020) Full Occurrence Data and Parameters downloaded from the EMODnet Biology project (<http://www.emodnet-biology.eu>). Available online at <http://www.emodnet-biology.eu/toolbox/en/download/selection/15f9adb20ad111>, consulted on 29 October 2020), and the Global Biodiversity Information Facility (GBIF.org; 2 November 2020) GBIF Occurrence Download <https://doi.org/10.15468/dl.u9dvzs>). (n=391, Duplicate recordings removed from the dataset).

A comprehensive feeding study on *P. tremulus* was conducted by Hauksson decades ago (1977, 1979), with data from both wild-caught specimens and those in controlled laboratory studies. These studies found that *P. tremulus* shows selective feeding habits with regard to both particle size and organic content, with an estimated average feeding rate of 2 g of sediment per hour. Defecation rates were estimated to be about 20 h for sea cucumbers fed a typical sediment from a Norwegian fjord. A similar defecation rate (~24 h) was also reported by Hudson et al. (2004) who studied the movement of trace particles through the intestine of *P. tremulus* held in sea cages. A higher defecation rate was reported by Jespersen and Lützen (1971) who noted that harvested sea cucumbers had emptied their intestines after about 8–10 h when held in aquaria. In the laboratory studies by Hauksson (1979), an assimilation

efficiency of around 27% was estimated. This is slightly higher than reported for *Parastichopus californicus* feeding on natural sediments (Ahlgren 1998), but significantly lower than estimated assimilation efficiencies for *P. californicus* feeding on sediments high in organic content (Paltzat et al. 2008). Currently, studies are being carried out by Moreforskning that will gain more information on how efficiently *P. tremulus* extracts nutrients from more energy-dense aquaculture feeds.

There are few known predators of *P. tremulus* but it has been reported to be preyed upon by scavenging amphipods, shrimps, starfish and some species of gadoid fish (Francour 1997). Its bright red colour likely provides an efficient camouflage against visual predators in deeper waters as there is little red light to be reflected at these depths. Holothuroids

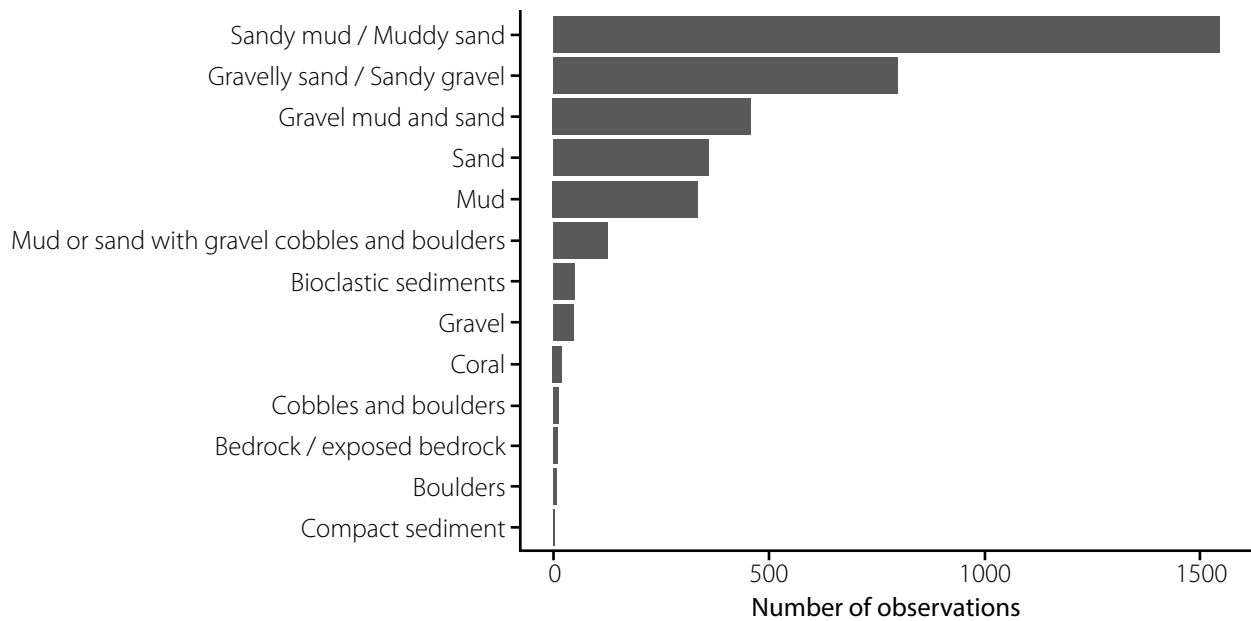


Figure 4. Substrates where *Parastichopus tremulus* have been observed in video surveys. Data from the MAREANO Marbunn database (www.mareano.no/marbunn), n=3783.

are, however, prone to parasitic infections by bacteria, protozoa and metazoa, with the main areas of infestation being the digestive system and the coelom (Eeckhaut et al. 2004). There is no single comprehensive study of the extent and diversity of parasitic infestations in *P. tremulus*, although a few have been reported (Jespersen and Lützen 1971), most notably the gastropod *Enteroxenos østergreni*, which was first described by Bonnevie (1902). Little is known about how *P. tremulus* is affected by this parasite, but a prevalence as high as 35% was reported from the Oslo fjord in Norway (Lützen 1979) and may indicate that *E. østergreni* infestation has little impact. As is the case with other holothurioids, we have frequently observed in our lab copepods on the body of the red sea cucumber, but it is likely this is a commensal, rather than parasitic, relationship (Eeckhaut et al. 2004).

Reproductive cycle

Parastichopus tremulus is a dioecious species, but individuals have no external characteristics that make the two sexes distinguishable. Several dissection studies carried out on specimens from Norwegian waters, suggest a fairly equal sex distribution, with female to male ratios of 0.98:1.00 (Jespersen and Lützen 1971), 1.33:1.00 (Hauksson 1977) and 1.3:1.0 (Christophersen et al. 2020). We have described the annual reproductive cycle of our local population (Christophersen et al. 2020), showing a seasonal pattern typical of other temperate species, with the spawning season commencing in late spring and early summer. Spawning in sea cucumbers can be triggered by light, primary production, changes in temperature and salinity, lunar phase and the presence of gametes in the water (Cameron and Fankboner 1986; Sewell and Bergquist 1990; Hamel and Mercier 1995; Mercier et al. 2007; Morgan 2009). The environmental factor that triggers spawning in *P. tremulus* is unknown. At depths where it is most abundant, the temperature is relatively low and stable (7–9° C) throughout the year (Woll et

al. 2014). It is thus unlikely that any rapid seasonal changes in temperature is a direct spawning cue. At depths of 100–300 m it is more likely that gonad maturation and spawning is induced by phytodetritus, as suggested for some species of deep-water holothurians (Wigham et al. 2003). This could be confirmed in future studies by measuring the organic content in sediment samples from typical habitats during the period of expected gonad development.

Fishery opportunities and constraints

The many observations and occurrence of *P. tremulus* above 60°N could indicate a large harvest potential (Kjerstad et al. 2015). Fishing pressure on new commercial sea cucumber species can be high, and environmental conditions, genetics and fishing pressure are all factors that can affect population dynamics. The study of distribution, abundance and recruitment of indigenous species are of the utmost importance in a management perspective, although most life history traits for *P. tremulus*, such as size at maturity, fecundity, offspring sex ratio and size-specific growth rates are still unknown.

Laws and regulations

Fisheries legislation in Norway does not specifically cover echinoderms, and traditionally only harvesting of low volumes of sea urchins for gonad enhancement has been carried out. Due to increased interest in sea cucumbers, however, the Norwegian Directorate of Fisheries – as a precautionary measure – issued a general ban on targeted sea cucumber fisheries in Norwegian territorial waters and on the Norwegian continental shelf in October 2019 (Regulation J-180-2019). Exemptions to this ban can, however, be given under specific circumstances. As of January 2021, four trial fisheries permits have been issued with the purpose of testing novel fishing gear designs for a potential, future environmentally friendly sea cucumber fishing industry. These permits are limited to

specific geographical areas and require a detailed description of the specific harvesting gear design used in each case. There are, however, large knowledge gaps that need to be filled before a proper legislative framework that will ensure sustainable fisheries management can be implemented.

Population dynamics and landings

The population structure of the Norwegian red sea cucumber has yet to be investigated in detail. Information about spatial and temporal distribution is key to evaluating the prospects of the species as a new fishing resource. Recordings from trial fisheries above 60°N along the Norwegian coast from Møre and Romsdal to Finnmark showed that the size of *P. tremulus* from trawl catches fell within the range of 20–250 mm in length (Kjerstad et al. 2015). In our studies from 2017 to 2019, where the purpose was to examine gonad maturation in sea cucumbers from the Møre and Romsdal region of Norway, lengths from 65 to 302 mm were recorded in animals obtained in trawl or pot fisheries in different seasons (Fig. 5a). Of these, approximately 5% were less than 100 mm in length. Round weight (total wet weight) of the same individuals ranged from 12 to 537 g, encompassing the range of 20–470 g reported by Kjerstad et al. (2015). Biometric relationships show correlations between body length and total wet weight and body wall weight, as well as between total and body wall wet weights (Fig. 5a-c). Gonad weights obtained throughout the year ranged from 0.01 to 26.3 g. A weak but significant relationship was described between body length and gonad wet weight, indicating a positive correlation between fecundity and size (Christophersen et al. 2020). Data on fecundity and reproductive parameters may show local variation between populations of the same species that are tied to latitude-specific environmental factors (Sewell 1992; Hamel and Mercier 1996; Marquet et al. 2017).

Individual measurements in our study (Christophersen et al. 2020) were not considered sufficient for detailed size distribution analyses, and thus too incomplete to obtain an indication on the structure of the local population. Juveniles rarely occur in trawl catches, but specimens as small as 3 cm (Rustad 1940; Jespersen and Lutzen 1971), and 2 cm (Kjerstad et al. 2015) have been recorded. The lack of significant data on recorded juveniles hinders estimations of year class size and recruitment in Norwegian waters. Neither have we (on basis of catch data) been able to establish size at first maturity, another measure that is important for proper management. *P. californicus*, a related species living under similar conditions, reaches first maturation at an age of approximately four years (Whitefield and Hardy 2019), but it remains to be seen if growth rates of the two species are comparable. The smallest sea cucumber we have observed with visible gonad tissue was 79 mm in length (June 2018), slightly shorter than the 84 mm previously reported by Christophersen et al. (2020).

Although the digestion rates and assimilation efficiencies reported for *P. tremulus* is comparable to other species of

sea cucumbers, no studies have reported growth rates. Slow growth has been reported for other sea cucumber species living at higher latitudes, such as *Cucumaria frondosa* (Hamel and Mercier 1996; So et al. 2010) and *P. californicus* (Paltzat et al. 2008). Based on the sea temperatures in the areas where *P. tremulus* is found, it should be considered a cold-water species, which indicates that it might also have a relatively slow growth rate. However, further studies are needed to confirm this and should be prioritised as it is crucial knowledge for future management and aquaculture production.

The volume of reported landings of *P. tremulus* in Norway are mainly low and are caught as bycatch by trawl or pot fishing, both of which target other species (e.g. Nordic shrimp and Norway lobster). Such data are registered by total catch weight. Bycatch is reported to the Norwegian Directorate of Fisheries, and data from 2007–2020 are made public in electronic form.⁶ In these statistics, *P. tremulus* is the only echinoderm identified to the species level, possibly due to its easily recognisable visual appearance. From 2007–2019, 10.4 tonnes of *P. tremulus* were reported as bycatch, whereas 15.6 tonnes were reported in 2020. This recent increase could be indicative of improved bycatch reporting practices but could also reflect an actual increase in catch volume due to the recently issued trial fishery permits. However, we do not think these data can be interpreted as indicative of the abundance of this species in Norwegian waters.

Aquaculture initiatives

Besides being a potentially valuable fishing resource, *P. tremulus* is an interesting candidate for land-based cultivation, sea ranching and integrated aquaculture (Landes et al. 2019). The development of a sea cucumber aquaculture industry in Norway is in its infancy. To succeed with controlled production of a new marine species, large investments in research and development are needed, although competition for funding is a bottleneck. The work related to sea cucumber aquaculture at Møreforsking was initiated through regional projects five years ago and has continued through an ongoing project called “Emerging species for sea cucumber aquaculture”, which is funded by the bilateral SANOCEAN programme of the research councils in Norway and South Africa, and targets several sea cucumber species new to the market. The work covers rearing technology and growth conditions for the different stages of spat production, suitability in IMTA systems and effects of environmental pollution. Within the Nordic network HOLOSUSTAIN⁷, which is coordinated by Møreforsking, North Atlantic sea cucumber species are being promoted as a novel marine resource for the Western market.

Spawning in captivity

Closing the life cycle – meaning having control of spawning, fertilisation, larval development, and growth of specimens until they reach sexual maturity – is required in order to achieve sustainable aquaculture that is independent of wild

⁶ See <http://fiskeridirektoratet.no/Yrkesfiske/Tall-og-analyse/Fangst-og-kvoter/Fangst/Fangst-fordelt-paa-art>. Accessed: 13.01.2021

⁷ See <https://www.holosustain.no/>

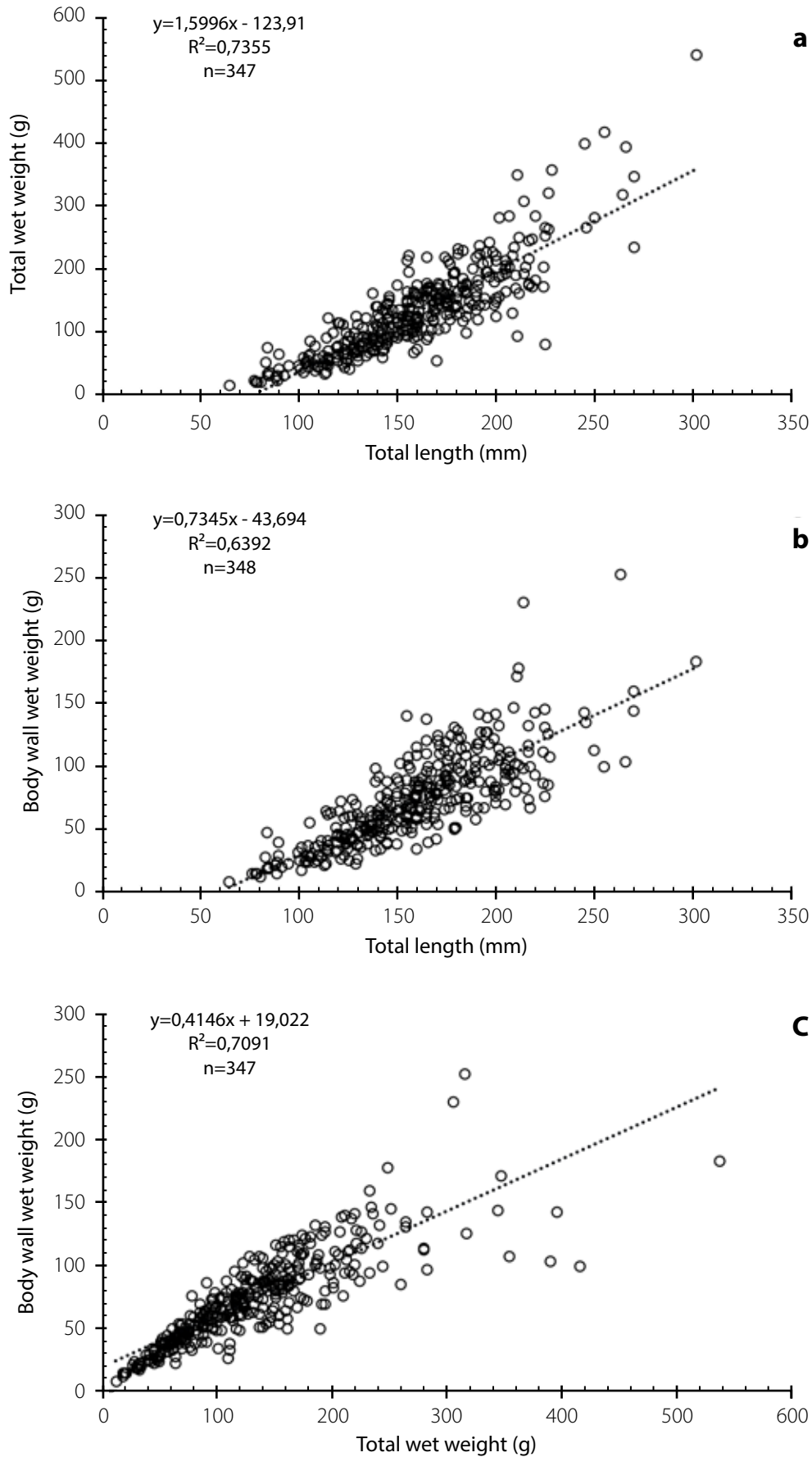


Figure 5. Biometric relationships for red sea cucumber, *Parastichopus tremulus*, caught in Møre and Romsdal, western Norway:
a) length – total weight, b) length – body wall weight, c) total weight – body wall weight.

animals. We have determined the natural spawning season of our local stock of *P. tremulus* (Christophersen et al 2020), which is the starting point for mastering controlled spawning. Until now, spawning trials have relied on newly caught specimens from local fishers within the expected spawning window. Peak gonad index (GI) was observed in May ($7.1 \pm 5.4\%$, mean \pm sd of body wall wet weight) for broodstock collected monthly from the wild. Sea cucumbers held in captivity for several months showed a similar gonad development pattern, but with a significantly lower GI in May and June (Christophersen et al. 2020). *P. tremulus* specimens have been kept alive in our lab for up to four years, but the build-up of gonads in captivity remains uncertain as we have chosen not to sacrifice our stock. Spawning attempts with these animals have failed, most likely due to a lack of a proper conditioning regime. Upcoming experiments will include spawning trials on animals kept in the laboratory from one year to another with year-round feeding. Synchronous spawning is a critical factor for successful hatchery production of juveniles. Thus, providing the environmental conditions that stimulate simultaneous gonad maturation in both sexes is crucial. We have not observed extensive simultaneous spawning in our tanks where groups of sea cucumbers have been kept. Spawning behaviour has been characterised by rather slow-motion events, and the asynchrony in spawning time may be due to variations in gonad status or to the lack of a correct environmental cue in captivity.

To develop aquaculture, it is necessary to develop a method that ensures a reliable production of viable gametes. To obtain sufficient spawning, a large enough group of specimens need to be collected in order to account for individual variation in

spawning willingness on the part of both sexes. The equal sex ratio in this species (see above) suggests that even with a modest number of animals, it should be possible to obtain both male and female gametes. Our experience has been that the animals spawn in pulses over a period of about 1–2 h, and empty the gonads partly at each event. After a resting period of some days (less than a week), we successfully could repeat spawning with the same individuals. Previous studies reporting spawning events in *P. tremulus*, either described fecundity in purely qualitative terms as “a considerable number of eggs” (Rustad 1940), or did not report these data (Holland 1981). At different spawning events in 2019 and 2020 we obtained egg batches of between a few hundred to 165,000 per female, with fertilisation rates of between 7–100% after fertilisation *in vitro* using sperm with good motility. From the most productive females, we collected an accumulated total of between 100,000 and 200,000 eggs from two spawning events. These numbers seem low when compared to the reported fecundity of *A. japonicus* and *P. californicus* of up to 1–2 million and more eggs per female, per spawning event (Chen 2003; Whitefield and Hardy 2019). Our egg numbers most probably represent a fraction of the total number of oocytes developed in the gonad. Successful spawning was associated with typical spawning behaviour (Fig. 6a) and a visibly extruded gonopore (Fig. 6d). The maturation level varied between individuals on the same date, which was believed to be the reason for the variation observed in both egg production and fertilisation success (Sunde and Christophersen unpublished). The reproductive potential and effect of gamete quality on fertilisation success and further larval development of Norwegian red sea cucumber aquaculture is still an area that needs more research.

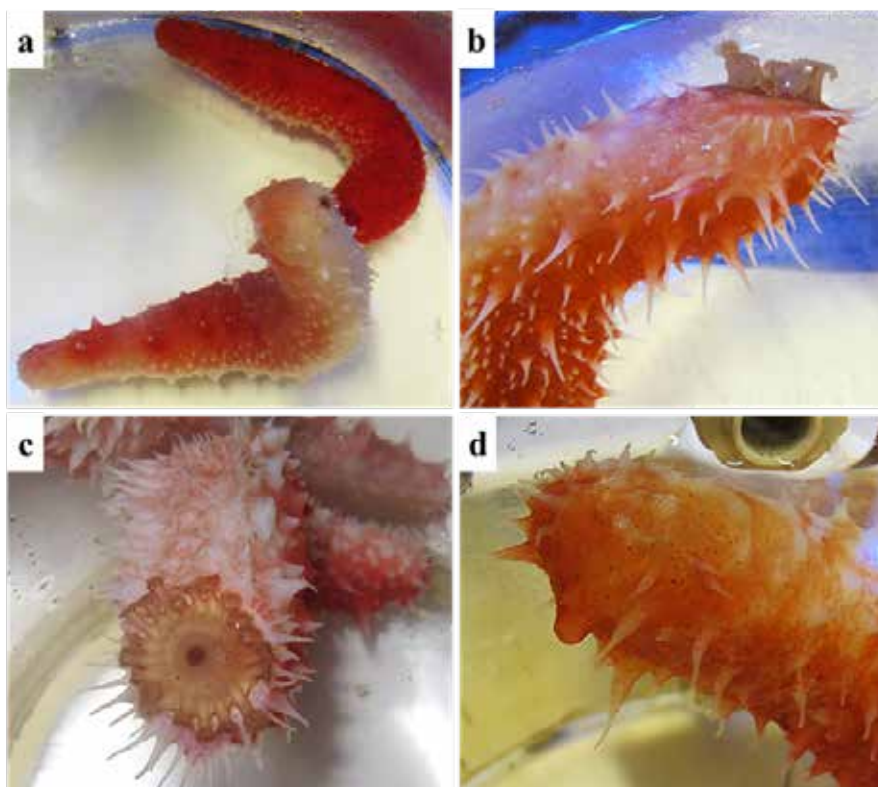


Figure 6. *Parastichopus tremulus* in containers during trials to induce spawning. The sea cucumber with half the body in erect posture is a spawning male (a), protruding mouth parts (b and c) and area (papillae) around the gonopore before spawning (d).
(images: Gyda Christophersen, Møreforsking)

Induced spawning

In 2017, we conducted a study to determine the best method to induce spawning in the laboratory. Sea cucumbers were obtained from the fjord system in the vicinity of Ålesund in western Norway (62°N–6°E). The sea cucumbers were kept in a holding tank at $9.0 \pm 0.2^\circ\text{C}$ (mean \pm sd) until the induced spawning experiments took place. Three groups of four individuals each were either exposed to temperature shock ($\Delta +4\text{--}6^\circ\text{C}$ in seawater), air exposure (desiccation) or salinity reduction (from 35 to 29‰), common methods for stimulating spawning in other species (Ramofafia et al. 2000; Mercier and Hamel 2002; Rakaj et al. 2018). Exposure time was 45 min. After the treatment, the sea cucumbers were transferred to transparent cylindrical containers of two sizes (33.5 cm and 18.5 cm inner diameter) filled with 10 and 5 L from the inlet water, respectively. To minimise disturbance, the water was not exchanged during the observation period. From each treatment group, two individuals were placed in a large container and one in each of two small containers to observe the release of gametes (Fig. 6a-d). The same individuals were stimulated on three occasions; 5, 9 and 12 days after arrival to the laboratory, and spawning activity was observed for up to 6 h. The start time of each spawning event was recorded. The production of eggs or sperm was verified under a dissecting microscope.

Sea cucumbers of both sexes were successfully stimulated to spawn, and the overall spawning success averaged $32 \pm 3.8\%$ (mean \pm sd) for the three trials (Table 1). Spawning was observed both in the containers holding one and two individuals, and spawning events occurred for sea cucumbers given all the stimulation treatments and at the three trial dates. The percentage of sea cucumbers induced to spawn was 42%, 31% and 25% of the groups exposed to increased temperature, air exposure and decreased salinity, respectively (Table 1). In the group given thermal shock, spawning started after 45 and 245 min (date 1), 13 and 32 min (date 2) and 26 min (date 3). Sea cucumbers that were exposed to air started to spawn after 78, 86 and 92 min, respectively, and the animals exposed to lower salinity after 95, 44 and 96 min. Attempts to further stimulate spawning 4–5 h after the initial treatment were unsuccessful. From these trials we found thermal shock to be the best method to stimulate spawning within the natural spawning period June–July. Success has varied between years and between individuals but, to date, we have not observed mass simultaneous spawning events as described for other species (Olavide et al. 2011; Huertas and Byrne 2019; Marquet et al. 2018) when males and females were kept in proximity in tanks within the spawning season.

Prospects for fisheries and aquaculture

P. tremulus is a novel species considered for utilisation in Norway; a species that despite frequent observations has a secret life on the sea floor. Some advancements have been made through recent Scandinavian initiatives on the biology, fisheries and trade of this species since Hamel and Mercier (2008) reported on the status of temperate sea cucumbers in the Northern Hemisphere (Kjerstad et al. 2015; Atanassova and Kjerstad 2019; Christophersen et al. 2020; Clements et al. 2020). The documented occurrence of the species from 60°N and above has spurred Norwegian stakeholders to explore whether catching the species may be a viable option. The Asian market seems to be huge if the product can be traded legally (Atanassova and Kjerstad 2019).

Sustainable exploitation and aquaculture of sea cucumbers in Norway is discussed by Landes et al. (2019), where it is pointed that care must be taken in the interactions between wild and cultured specimens, and possible negative effects on the environment. The development of harvesting gear with negligible impact on bottom habitats must be pursued if a sea cucumber fishery is to prosper. The use of passive gear and ROVs to harvest wild sea cucumbers are being explored by Norwegian fishers but there is a need to map these resources to determine their abundance on small and large scale. Developing a fishery-based sea cucumber industry also needs a proper legal framework in case the selected fishery will be permitted in the future. The authorities of fisheries and seafood safety depend on new species-specific biological knowledge to be able to execute research-based management. For *P. tremulus*, this biological knowledge is missing, and emphasises the need for future studies on the population structure and life history of the species. The potential ecosystem impacts should also be considered. Sea cucumbers, commercial and non-commercial, have important functions within ecosystems in all oceans (Purcell et al. 2016). There is, therefore, a national responsibility to protect benthic community biodiversity in order to maintain bioturbation, cleaning and mixing of sediment layers.

Northern populations of *P. tremulus* may be vulnerable to being heavily fished as we can assume that cold and temperate water species have a slower growth rate than tropical species, thus affecting recruitment and replenishment of fishable stocks. It is, therefore, uncertain which management measures will be most effective in sustaining populations if a commercial fishery is permitted. At present, all catches in Norway originate from bycatch, and the reporting on metrics is inadequate. The use of novel genomic methods for determining

Table 1. Percentage of *Parastichopus tremulus* individuals that spawned after 45 minutes of exposure to increased temperature ($+4\text{--}6^\circ\text{C}$), air exposure and decreased salinity (from 35 to 29‰).

| Trial # | Individual # | Spawne-overall % | Spawned heat % | Spawned air % | Spawned salinity % | Female # | Male # |
|---------|--------------|------------------|----------------|---------------|--------------------|----------|--------|
| 1 | 12 | 33 | 50 | 25 | 25 | 1 | 3 |
| 2 | 11 | 36 | 50 | 33 | 25 | 2 | 2 |
| 3 | 11 | 27 | 25 | 33 | 25 | 1 | 2 |

population structure, origin, divergence and ecosystem function will provide useful information for the sustainable management of wild sea cucumber stocks. Knowledge on the effects of temperature on growth rates through the different life stages – egg, larvae, juvenile and adults – and tolerance to higher temperatures (>8° C) will add the necessary knowledge both for estimating yearly increases in biomass in the wild, and for establishing important aquaculture conditions to maximise growth. The experiments carried out in our lab so far have been with water temperatures varying between 6 and 14° C. It is, therefore, unknown whether *P. tremulus* could tolerate higher temperatures under aquaculture conditions, or whether this may lead to increased growth rates or cause adverse reactions due to stress, thereby affecting gonad maturation and other metabolic processes.

Landes et al. (2019) concluded that polyculture and integrated multi-trophic aquaculture, including with sea cucumbers, as well as monoculture, are conceivable prospects for Norwegian seafood production. Research efforts are, however, needed to fill knowledge gaps related to the early life stages of local sea cucumber species. A predictable supply of robust spat (juveniles) is key to developing aquaculture of the species. Hatchery production may be a viable option, but only if growth from one stage to another until commercial size lies within a time frame that is economically viable for the industry. As age determinations related to size are gaps in our knowledge about the Norwegian red sea cucumber, long-term studies in the laboratory are required to establish this knowledge. Several critical stages must be passed from fertilisation through the pelagic larval stages until metamorphosed benthic life. The development from unfertilised oocyte through the blastula stage has previously been described at 7.5° C (Holland 1981), while larval development beyond this stage has been described for two Scandinavian populations in Schagerström et al. (submitted). So far, protocols for the industrial production of *P. tremulus* juveniles are still far from being developed, and it is foreseen that large investments are needed to develop such intensive production. In addition to land-based production, flow-through or recirculating systems, sea ranching or fishery-based aquaculture may be possible cultivation methods once the technology for spat production is established. Because *P. tremulus* is a deposit feeder, it may also be suitable for reducing the particular nutrient discharges from traditional fed aquaculture, while converting it into valuable biomass. For such integrated circular systems to evolve, changes to current regulatory frameworks to facilitate the polyculture of several species for human consumption must be created.

Norway has a long tradition of harvesting and cultivating coldwater seafood species above 60°N, and decades of work has led to a comprehensive national science-based management. The seafood industry in Norway is characterised by a thriving entrepreneurial industry, that has the necessary market knowledge, and already established seafood processing infrastructure and value chains. Given the long fishery and aquaculture tradition in Norway, we believe it is likely that we will have a future industry based on the exploitation of Norwegian *P. tremulus*. The need to fill the knowledge gaps highlighted above is, however, pivotal for this development

to be sustainable, and will require substantial research effort. A strategic coordinated progress plan should involve industry, research and regulatory authorities.

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References

- Ahlgren M.O. 1998. Consumption and assimilation of salmon net pen fouling debris by the red sea cucumber *Parastichopus californicus*: Implications for polyculture. *Journal of the World Aquaculture Society* 29(2):133–139.
- Atanassova M. and Kjerstad M. 2019. Eastern and western sea cucumber markets: Differences in consumer trends and formats. A review. In: *International Perspectives on Regional Research and Practice*. Akslen-Hoel L.K. and Egilsson B. (eds). Møreforsking Anthology, Orkana: Forlag, Norway.
- Berx B. and Hughes S.L. 2009. Climatology of surface and near-bed temperature and salinity on the north-west European continental shelf for 1971–2000. *Continental Shelf Research* 29(19):2286–2292.
- Bonnevie K. 1902. *Enteroxenos östergreni*, ein neuer Holothurien schmarotzender Gastropode. *Zoologische Jahrbücher* 15:730–792. (In German).
- Cameron J.L. and Fankboner P.V. 1986. Reproductive biology of the commercial sea cucumber *Parastichopus californicus* (Stimpson) (Echinodermata: Holothuroidea). I. Reproductive periodicity and spawning behavior. *Canadian Journal of Zoology* 64(1):168–175.
- Chen J. 2003. Overview of sea cucumber farming and sea ranching practices in China. *SPC Beche-de-mer Information Bulletin* 18:18–23.
- Christophersen G., Bjørkevoll I., Bakke S. and Kjerstad M. 2020. Reproductive cycle of the red sea cucumber, *Parastichopus tremulus* (Gunnerus, 1767), from western Norway. *Marine Biology Research* 16(6–7):423–430.
- Clements J.C., Schagerström E., Dupont S., Jutfelt F. and Ramesh K. 2020. Roll, right, repeat: Short-term repeatability in the self-righting behaviour of a cold-water sea cucumber. *Journal of the Marine Biological Association of the United Kingdom* 100(1):115–120.
- Eeckhaut I., Parmentier E., Becker P., Gomez da Silva S. and Jangoux M. 2004. Parasites and biotic diseases in field and cultivated sea cucumbers. p. 311–325. In: Lovatelli A., Conand C. Pucell S., Uthicke and Hamel J.F. (eds). *Advances in Sea Cucumber Aquaculture and Management*. FAO Fisheries Technical Paper. 463. Rome: FAO.

- Francour P. 1997. Predation on holothurians: A literature review. *Invertebrate Biology* 116(1):52–60.
- Furevik T. 2001. Annual and interannual variability of Atlantic water temperatures in the Norwegian and Barents Seas: 1980–1996. *Deep Sea Research Part I: Oceanographic Research Papers* 48(2):383–404.
- González-Wangüemert M., Domínguez-Godino J.A. and Cánovas F. 2018. The fast development of sea cucumber fisheries in the Mediterranean and NE Atlantic waters: From a new marine resource to its over-exploitation. *Ocean and Coastal Management* 151:165–177.
- Grieg J.A. 1921. Echinodermata. Trustees of the Bergen Museum. Grieg, In: Report of the scientific results of the Michael Sars North Atlantic Deep Sea Expedition 1910. The Trustees of the Bergen museum, Vol. III Part 2., Bergen, Norway.
- Gunnerus J.E. 1767. Beskrifning på trenne Norrska sjö-kräk, sjö-pungar kallade. Kongliga Vetenskaps Akademiens Handlingar 28 (4–6):114–124, Tab. IV. Stockholm. (In Swedish)
- Hamel J.F. and Mercier A. 1995. Spawning of the sea cucumber *Cucumaria frondosa* in the St Lawrence Estuary, eastern Canada. *SPC Beche-de-mer Information Bulletin* 7:12–18.
- Hamel J.F. and Mercier A. 1996. Early development, settlement, growth, and spatial distribution of the sea cucumber *Cucumaria frondosa* (Echinodermata: Holothuroidea). *Canadian Journal of Fisheries and Aquatic Sciences* 53(2):253–271.
- Hamel J.F. and Mercier A. 2008. Population status, fisheries and trade of sea cucumbers in temperate areas of the Northern Hemisphere. p. 257–291. In: Toral-Granda V., Lovatelli A. and Vasconcellos M. (eds). *Sea cucumbers. A global review of fisheries and trade*. FAO Fisheries and Aquaculture Technical Paper. No. 516. Rome: FAO.
- Hauksson E. 1977. Ernæringsøkologiske studier av *Stichopus tremulus* (Gunnerus), en detritusetende holothurioid. Cand. real. thesis, University of Bergen, Norway. 119 p. (In Norwegian).
- Hauksson E. 1979. Feeding biology of *Stichopus tremulus*, a deposit-feeding holothurian. *Sarsia* 64(3):155–160.
- Holland N.D. 1981. Electron microscopic study of development in a sea cucumber, *Stichopus tremulus* (Holothuroidea), from unfertilized egg through hatched blastula. *Acta Zoologica* 62(2):89–111.
- Hudson I.R., Wigham B.D. and Tyler P.A. 2004. The feeding behaviour of a deep-sea holothurian, *Stichopus tremulus* (Gunnerus) based on in situ observations and experiments using a Remotely Operated Vehicle. *Journal of Experimental Marine Biology and Ecology* 301(1):75–91.
- Hudson I.R., Wigham B.D., Solan M. and Rosenberg R. 2005. Feeding behaviour of deep-sea dwelling holothurians: Inferences from a laboratory investigation of shallow fjordic species. *Journal of Marine Systems* 57(3–4):201–218.
- Huertas V. and Byrne M. 2019. Observation of mass spawning of the sea cucumber *Holothuria coluberat* Lizard Island, Great Barrier Reef, Australia. *SPC Beche-de-mer Information Bulletin* 39:79–80.
- Jespersen A. and Lützen J. 1971. On the ecology of the aspidochirote sea cucumber *Stichopus tremulus* (Gunnerus). *Norwegian Journal of Zoology* 19:117–132.
- Ji T., Dong Y. and Dong S. 2008. Growth and physiological responses in the sea cucumber, *Apostichopus japonicus* Selenka: Aestivation and temperature. *Aquaculture* 283(1–4):180–187.
- Kjerstad M., Ringvold H., Søvik G., Knott E.K. and Thangstad T.H. 2015. Preliminary study on the utilisation of Norwegian red sea cucumber, *Parastichopus tremulus* (Gunnerus, 1767) (Holothuroidea, Echinodermata), from Norwegian waters: Resource, biology and market. p 109–132. In: Gundersen A.C. and Velle L.G. (eds). *Blue Bio-resources* Orkana Forlag: Norway.
- Laguerre H., Raymond G., Plan P., Améziane, N., Bailly X. and Le Chevalier P. 2020. First description of embryonic and larval development, juvenile growth of the black sea-cucumber *Holothuria forskali* (Echinodermata: Holothuroidea), a new species for aquaculture in the north-eastern Atlantic. *Aquaculture* 521:734961.
- Landes A.M., Sunde J. and Christophersen G. 2019. Atlantic sea cucumber species in the spotlight – prospects for Norwegian aquaculture. p 19–49. In: *International Perspectives on Regional Research and Practice*. Akslen-Hoel L.K. and Egilsson B. (eds). Orkana Forlag: Norway.
- Lønning S. 1976. Reproductive cycle and ultrastructure of yolk development in some echinoderms from the Bergen area, western Norway. *Sarsia* 62(1):49–72.
- Lützen J. 1979. Studies on the life history of *Enteroxenos Bonnevie*, a gastropod endoparasitic in aspidochirote holothurians. *Ophelia* 18(1):1–51.
- Madsen F.J. and Hansen B. 1994. Echinodermata, Holothuroidea. *Marine Invertebrates of Scandinavia* Number 9. Oslo: Scandinavian University Press.
- Marquet N., Conand C., Power D.M., Canário A.V. and González-Wangüemert M. 2017. Sea cucumbers, *Holothuria arguinensis* and *H. mammata*, from the southern Iberian Peninsula: Variation in reproductive activity between populations from different habitats. *Fisheries Research* 191:120–130.
- Marquet N., Hubbard P.C., da Silva J.P., Afonso J. and Canário A.V.M.M. 2018. Chemicals released by male sea cucumber mediate aggregation and spawning behaviours. *Scientific Reports* 8(1):1–13.

- Mercier A. and Hamel J.F. 2002. Perivisceral coelomic fluid as a mediator of spawning induction in tropical holothurians. *Invertebrate Reproduction and Development* 41(1–3):223–234.
- Mercier A., Ycaza R.H. and Hamel J.F. 2007. Long-term study of gamete release in a broadcast-spawning holothurian: predictable lunar and diel periodicities. *Marine Ecology Progress Series* 329:179–189.
- Mercier A. and Hamel J.F. 2013. Sea cucumber aquaculture: Hatchery production, juvenile growth and industry challenges. p. 431–454. In: *Advances in Aquaculture Hatchery Technology*. Cambridge, UK: Woodhead Publishing Limited.
- MNHN (Muséum national d’Histoire naturelle. The echinoderm collection (IE) of the Muséum national d’Histoire naturelle (MNHN - Paris), Chagnoux S. 2021. Version 75.194. Occurrence dataset. Accessed via GBIF.org on 15 January 2021. <https://doi.org/10.15468/tp2nxo>
- Morgan A.D. 2009. Spawning of the temperate sea cucumber, *Australostichopus mollis* (Levin). *Journal of the World Aquaculture Society* 40(3):363–373.
- Mortensen T. 1927. *Handbook of the Echinoderms of the British Isles*. Oxford, UK: Oxford University Press.
- Nordgaard O. 1912. Faunistiske og biologiske iakttagelser ved den biologiske station i Bergen. *Det Kongelige Norske Videnskabers Selskabs Skrifter* 1911, no. 6:1–58.
- Olavide R.D., Rodriguez B.D. and Juinio-Meñez M.A. 2011. Simultaneous mass spawning of *Holothuria scabra* in sea ranching sites in Bolinao and Anda municipalities, Philippines. *SPC Beche-de-mer Information Bulletin* 31:23–24.
- Paltzat D.L., Pearce C.M., Barnes P.A. and McKinley R.S. 2008. Growth and production of California sea cucumbers (*Parastichopus californicus* Stimpson) co-cultured with suspended Pacific oysters (*Crassostrea gigas* Thunberg). *Aquaculture* 275(1–4):124–137.
- Purcell S.W., Conand C., Uthicke S. and Byrne M. 2016. Ecological roles of exploited sea cucumbers. *Oceanography and Marine Biology: An Annual Review* 54:367–386.
- Purcell S.W., Polidoro B.A., Hamel J.F., Gamboa R.U. and Mercier A. 2014. The cost of being valuable: predictors of extinction risk in marine invertebrates exploited as luxury seafood. *Proceedings of the Royal Society B: Biological Sciences* 281:20133296.
- Rakaj A., Fianchini A., Boncagni P., Lovatelli A., Scardi M. and Cataudella S. 2018. Spawning and rearing of *Holothuria tubulosa*: A new candidate for aquaculture in the Mediterranean region. *Aquaculture Research* 49(1):557–568.
- Rakaj A., Fianchini A., Boncagni P., Scardi M., and Cataudella S. 2019. Artificial reproduction of *Holothuria polii*: A new candidate for aquaculture. *Aquaculture* 498:444–453.
- Ramofafia C., Battaglione S.C., Bell J.D. and Byrne M. 2000. Reproductive biology of the commercial sea cucumber *Holothuria fuscogilva* in the Solomon Islands. *Marine Biology* 136(6):1045–1056.
- Rustad D. 1940. The early development of *Stichopus tremulus* (Gunn.) (Holothurioidea). *Bergens Museums Aarbok* 1938, John Grieg 8:1–21.
- Santos R., Dias S., Pinteus S., Silva J., Alves C., Tecelão C., Pedrosa R. and Pombo A. 2016. Sea cucumber *Holothuria forskali*, a new resource for aquaculture? Reproductive biology and nutraceutical approach. *Aquaculture Research* 47(7):2307–2323.
- Schagerström E., Christophersen G., Sunde J., Bakke S., Matusse N.R., Dupont S. and Sundell K.S. Controlled spawning and rearing of the sea cucumber *Parastichopus tremulus* auricularia larvae. Submitted to *Journal of the World Aquaculture Society*.
- Sewell M.A. 1992. Reproduction of the temperate aspidochirote *Stichopus mollis* (Echinodermata: Holothuroidea) in New Zealand. *Ophelia* 35(2):103–121.
- Sewell M.A. and Bergquist P.R. 1990. Variability in the reproductive cycle of *Stichopus mollis* (Echinodermata: Holothuroidea). *Invertebrate Reproduction and Development* 17(1):1–7.
- So J.J., Hamel J.F. and Mercier A. 2010. Habitat utilisation, growth and predation of *Cucumaria frondosa*: Implications for an emerging sea cucumber fishery. *Fisheries Management and Ecology* 17(6):473–484.
- Whitefield C.R. and Hardy S.M. 2019. Estimates of reproductive potential and timing in California sea cucumbers *Parastichopus californicus* (Stimpson, 1857) from southeast Alaska based on natural spawning. *Journal of Shellfish Research* 38(1):191–199.
- Wigham B.D., Tyler P.A. and Billett D.S.M. 2003. Reproductive biology of the abyssal holothurian *Amperima rosea*: an opportunistic response to variable flux of surface derived organic matter? *Journal of the Marine Biological Association of the United Kingdom* 83(1):175–188.
- Woll A.K., Bakke S. and Larssen W.E. 2014. Velferd og kvalitet i verdikjeden for levende sjøkreps og hummer. Report no. MA 14-02 (In Norwegian with English summary), Møreforskning Marin, Ålesund. 58 p.
- Yang H., Hamel J.F. and Mercier A. (eds). 2015. *The sea cucumber *Apostichopus japonicus*: History, biology and aquaculture*. Cambridge, MA, USA: Elsevier, Academic Press. 478 p.
- Yang H., Yuan X., Zhou Y., Mao Y., Zhang T. and Liu Y. 2005. Effects of body size and water temperature on food consumption and growth in the sea cucumber *Apostichopus japonicus* (Selenka) with special reference to aestivation. *Aquaculture Research* 36(11):1085–1092.