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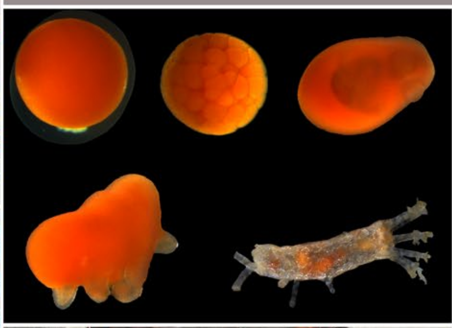
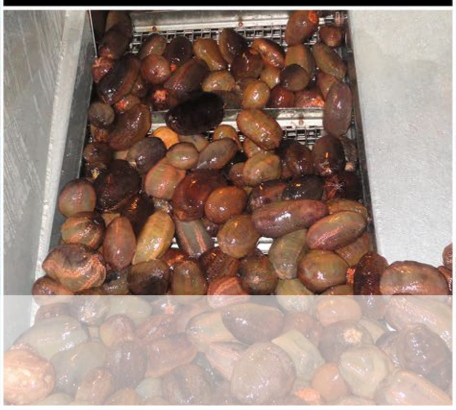
The biology and management of *Cucumaria frondosa*



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A guide to northern sea cucumbers

The biology and management of *Cucumaria frondosa*

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Preparation of this document

This technical guide is intended as an introduction to northern sea cucumbers, focusing on the biology, ecology, and commercial exploitation of *Cucumaria frondosa*, also known as the orange-footed or the Atlantic sea cucumber. The primary goal is to make some 40 years of scientific knowledge accessible to a non-scientific audience and to explore best practices at all levels of the value chain. Because *C. frondosa* differs fundamentally from the other commonly exploited species of sea cucumber worldwide, the guide provides a key tool to assist stakeholders and guide the management of the species across its Arctic, North American and North European range. It is also meant as a basis for discussions around the sustainability of large-scale industrial fisheries, the conservation of sea cucumbers, and the most promising avenues for research and development as the species is rapidly gaining commercial momentum.

It is fitting for this document to be published as an FAO Fisheries and Aquaculture Technical Paper, in line with FAO's strategy to build an understanding of sea cucumber exploitation, management and trade worldwide, launched 20 years ago at a workshop on Advances in Sea Cucumber Aquaculture and Management (Dalian, China, 2003). Complementing the initial focus on tropical and temperate species from the Indo-Pacific and East Asia, this document proposes a first foray into the unique problematics surrounding the harvesting and commercial trade of northern, cold-water, sea cucumbers.

Preamble

Boreal oceans, in particular the Northwest Atlantic and its famous Grand Banks, have traditionally been regarded as fishing havens. However, with the downturn in valuable assets such as crab and shrimp and an uncertain return of the cod fishery, the seafood sector is now actively seeking to diversify and explore underutilized species. One such species is the North Atlantic sea cucumber *Cucumaria frondosa*, which, for many regions, has shown great promise. However, the sea cucumber fishery in northern countries remains relatively new, *C. frondosa* having been harvested at commercial scales for 40 years at the most.

The sustainable exploitation of any emerging marine resource demands that management bodies gather thorough scientific information about all aspects of the target species to assess and properly manage the stocks. Other stakeholders seek similar knowledge to develop adapted markets and assess the potential of parallel commercial activities such as aquaculture. Newcomers to this sector soon discover that sea cucumber production is among the most lucrative and fastest developing seafood sector in the world. The commonly traded product in many Asian countries (Purcell *et al*., 2013), known as beche-de-mer or trepang, consists of the eviscerated, boiled, and dried form. In China alone, where most of the demand comes from due to centuries-old cultural attachment, sea cucumber is now mainly derived from a multi-billion dollar aquaculture industry (Yang, Hamel and Mercier, 2015). In several other countries in Asia and the Indo-Pacific, the frenetic demand for sea cucumber has created boom-and-bust patterns of exploitation that have recently driven major stock depletions and threatened prized species (Purcell *et al*., 2014). Such alarming trends emphasize the need for a cautious approach to any new sea cucumber fishery, and demand that stakeholders try to balance the economic interests with carefully devised conservation measures. This starts by understanding the species that is being targeted. While knowledge on sea cucumbers in general is rich and diverse, including many reviews and practical guides, northern sea cucumbers such as *C. frondosa* cannot be managed like other commercial species, because they have a markedly different biology, and they are the target of a very different fishery.

Most commercial sea cucumber species are hand-caught and destined to luxury seafood and pharmaceutical markets, whereas in the North Atlantic, the resource is most often trawled using a special drag or rake and landed in ice or slurry. Initially, processing was done by hand; however recent development of machinery has allowed for automation of the evisceration process with greater efficiency and increased volume handling capacity. Unfortunately, because of the economic urgency and technological means, the northern sea cucumber fishery has been developed under a high-volume low-value model, following the footsteps of groundfish and shrimp. To make things worse, *C. frondosa* is unlike other sea cucumbers in several respects. It is a subtidal cold-water species that chiefly captures and feeds on live phytoplankton; it reproduces once a year by producing few large yolky oocytes/eggs; and it is both slow-growing and late maturing. Most other commercial sea cucumber species are distributed in shallow waters and coral reefs along tropical or temperate coasts; they are deposit feeders that ingest organically rich mud and detritus; they reproduce several times annually by producing millions of tiny oocytes/eggs; and they grow an order of magnitude faster. This means that general information about other sea cucumber species cannot readily be applied to *C. frondosa*. Most stakeholders either do not know, or do not fully grasp this, creating some unique challenges.

On the positive side, the body of knowledge on *C. frondosa* was already quite solid even before its commercial exploitation began; it has continued to grow ever since and has recently been synthesized in a scientific review (Gianasi *et al*., 2021). Furthermore, the fact that *C. frondosa* is a plankton feeder makes it a potentially unique source of valuable natural products, including antioxidants, vitamins and phospholipids that may hold great health benefits for humans (Mamelona *et al*., 2007; Vaidya and Cheema, 2014). In addition, the virgin stocks of *C. frondosa* are often unparalleled and their exploitation has not yet begun in the northernmost regions of its distribution. There is hope yet to move from a high-volume fishery to a high-value one.

The present guide aims to help the various existing and future stakeholders gain a deeper understanding of northern sea cucumbers and come to appreciate their intricate biology and unique qualities. It will hopefully promote a fuller utilization of a currently abundant yet already fragile resource, along with more sustainable fishing and handling practices, leading to increased value through quality preservation. As the industry expands, emphasis on value and quality should ultimately allow further investment by the sector and provide greater benefits to many local economies and livelihoods.

Abstract

This document synthesising knowledge on the northern sea cucumber *Cucumaria frondosa* was prepared for all stakeholders, including industry participants, government scientists, policymakers, and academic researchers. Its aim is to highlight the uniqueness of this marine resource to guide the industry forward and to emphasize areas that deserve further investigation. Available data from eastern and northern Canada, eastern United States of America, Greenland, northern Europe and the Russian Federation are presented. Topics covered include the taxonomy, distribution, biology, and ecology of the species, the natural threats it faces, the current harvesting, processing and marketing practices, and the prospects for aquaculture development. Relying on a knowledge base gathered over more than 40 years, this contribution compares *C. frondosa* with other common commercial species of sea cucumbers to tease out the major aspects that set it apart. A final segment provides a number of key recommendations for its management and conservation.

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Graphic design and layout was carried out by José Luis Castilla Civit while Massimiliano Lipperi (@studiowildart) produced the illustrations in Figure 1 and in Figure 19.

Acronyms and abbreviations

ABA	active buoyancy adjustment
CPUE	catch per unit effort
DFO	Department of Fisheries and Oceans (Canada)
FAO	Food and Agriculture Organization of the United Nations
IMTA	integrated multitrophic aquaculture
MPA	marine protected area
NAFO	Northwest Atlantic Fisheries Organization
PIT	passive integrated transponder
PSU	practical salinity unit
TAC	total allowable catch

mm	millimetre
cm	centimetre
m^2	square metre (1 metre x 1 metre)
ml	millilitre (0.001 litre)
kg	kilogram (1 000 grams)
tonne	1 000 kilograms

Glossary

Ambulacrum	Each of the radially arranged bands, together with their underlying structures, through which the rows of tube feet protrude. Sea cucumbers and other echinoderms generally have 5 ambulacra.
Aquapharyngeal bulb	Bulb-like anterior part of a sea cucumber, containing the pharynx and water vascular system.
Asexual reproduction	Reproduction that occurs without the fusion of male and female gametes, usually by splitting of the body into two parts that regenerate. The genetically identical offspring of asexual parents are clones.
Autotomy	A defensive process of self-mutilation initiated in response to adverse stimuli. It involves loss of portions of the body, such as the intestine and respiratory tree in several species of sea cucumbers.
Beche-de-mer	Boiled and dried (sometimes smoked) eviscerated body wall of sea cucumbers.
Blastula	Early stage of embryonic development.
Broadcast (spawning)	The action of releasing gametes (sperm and eggs) in the external environment (generally the water).
Brooding	Reproductive mode in which the embryos are protected on, in, or beneath the parent, and emerge as tiny, crawl-away juveniles.
Broodstock	A group of mature individuals used in aquaculture for breeding purposes.
Buccal	Related to the mouth.
Calcareous ring	A calcified ring surrounding the pharyngeal region of sea cucumbers. It forms a point of insertion for longitudinal muscles and, when present, for retractor muscles.
Chlorophyll-α	A specific form of chlorophyll, the natural green pigment that allows algae and plants to undergo photosynthesis.
Cloaca	In sea cucumbers, the posterior part of the intestine that opens to the outside; it carries the openings to the respiratory tree(s) and Cuvierian tubules, when present. Although slightly different anatomically, it is often synonymized with anus.
Deposit feeding	Ingestion of particles that cover the seafloor.
Doliolaria	A type of free-swimming non-feeding sea cucumber larva. It is barrel-shaped, has several transverse rings of cilia, and lacks a mouth. Also called vitellaria.
Egg	Mature (fertilized) female gamete.
Embryo	An early developmental stage that is enclosed in a fertilization membrane or protected by the body of the parent.
Enzyme	A substance (generally a protein) that acts as a biological catalyst by modulating the rate at which chemical reactions proceed.

Evisceration	In sea cucumbers, expulsion of the digestive tract and associated organs; in some species, the anterior end of the body ruptures and the calcareous ring and associated organs are expelled. Can be actively used by some species as a defensive mechanism.
Gametogenesis	Steps of gamete synthesis happening inside the testis in males and the ovary in females.
Gastrula	Stage of embryonic development following the blastula.
Genital papilla	The fleshy or protruding outlet of the gonoduct through which gametes are expelled.
Gonad	Reproductive gland that produces the gametes (see Ovary, Testis).
Gonoduct	Genital duct that carries gametes from the gonad to an external genital opening.
Humoral factor	Factor (e.g. protein or other molecule) that is transported by the circulatory system.
Interradial (interradius)	Referring to inter-ambulacral sectors of the body.
Introvert	Strictly speaking, the collar of flexible tissue behind the tentacles that is pulled into the body by retractor muscles. Sometimes used to designate the whole of the retractable oral region, including tentacles, aquapharyngeal bulb and associated structures.
Larva (plural larvae)	An intermediate developmental stage that is independent of the fertilization membrane; when present it follows the embryo and precedes the juvenile.
Lecithotrophy	A mode of reproduction in which free-swimming larvae develop using nutrients (yolk) laid down in the oocyte/egg.
Madreporite	A plate with numerous perforations that is connected to the water-vascular ring by a so-called stone canal. In most sea cucumbers, it is internal; in most other echinoderms, it opens to the exterior.
Nutraceutical	A substance that is either food or part of a food that can provide medical or health benefits, including prevention and treatment of disease.
Oocyte	Developing female gamete when still inside the ovary; once fully mature (usually at the fertilization stage), it will become the egg.
Oral	A part of the body on the same surface as the mouth.
Ossicle	A small, usually microscopic, calcified element of the skeleton of sea cucumbers and other echinoderms. Commonly found in the body wall but also present other tissues and organs.
Ovary	Female reproductive organ.
Pelagic	Found inside the water column, passively floating or actively swimming.
Pentactula	The last larval developmental stage of sea cucumbers, which immediately precedes the juvenile; it has an anterior mouth, buccal podia, and one or two tube feet (but the digestive tract is not yet open).
pH	Measure of how acidic or basic water is.
Pheromone	A substance secreted to the outside by an individual that is received by a second individual (generally of the same species) in which it elicits a reaction.

Photoperiod	Day length.
Phylum	Scientific term grouping together related species on the basis of their common fundamental characteristics; a principal taxonomic category that ranks above class and below kingdom.
Phytoplankton	Microscopic plant-like organisms; portion of the plankton that grows through photosynthesis; also known as microalgae.
Plankton	Generally small, often microscopic, organisms that drift or float in the water (see Phytoplankton and Zooplankton).
Planktotrophy	The mode of development of free-swimming larvae that feed externally on particulate matter, usually phytoplankton.
Podium (plural podia)	Fluid-filled, small active tubular projection on the oral and dorsal sides of sea cucumbers and other echinoderms (also called tube foot/feet).
Propagule	Any of various structures that can give rise to a new individual organism (e.g. egg, embryo, larva).
Respiratory tree	Usually paired respiratory organs of some sea cucumbers. They are attached to the cloaca, and project anteriorly in the body cavity.
Recruitment	In biology, the process by which individuals are added to a population.
Salinity	Saltiness or amount of salts dissolved in water.
Suspension feeding	Interception and ingestion of living and non-living particles that are floating in the water.
Spawning	Action of releasing male or female gametes out of the body (for sea cucumbers, mostly in the water surrounding them).
Species	Related organisms that share common traits and are capable of reproducing; lowest taxonomic unit, denoted by a Latin binomial (e.g. *Cucumaria frondosa*).
Spermatozoon (plural spermatozoa)	The male reproductive cell (often called sperm).
Stone canal	A tube, usually reinforced with ossicles, leading from the madreporite to the water-vascular ring canal.
Tentacle	In sea cucumbers, feeding structures in the form of highly modified tube feet arranged in a ring around the mouth.
Testis	Male reproductive organ.
Tube foot	Fluid-filled, small active tubular projection on the oral and dorsal sides of sea cucumbers and other echinoderms (also called podium/podia).
Vitellaria	A type of free-swimming non-feeding sea cucumber larva. It is barrel-shaped, has several transverse rings of cilia, and lacks a mouth. Also called doliolaria/doliolariae.
Zooplankton	The animal component of the plankton community that swim weakly and drift passively with the currents.

1. Introduction to sea cucumbers

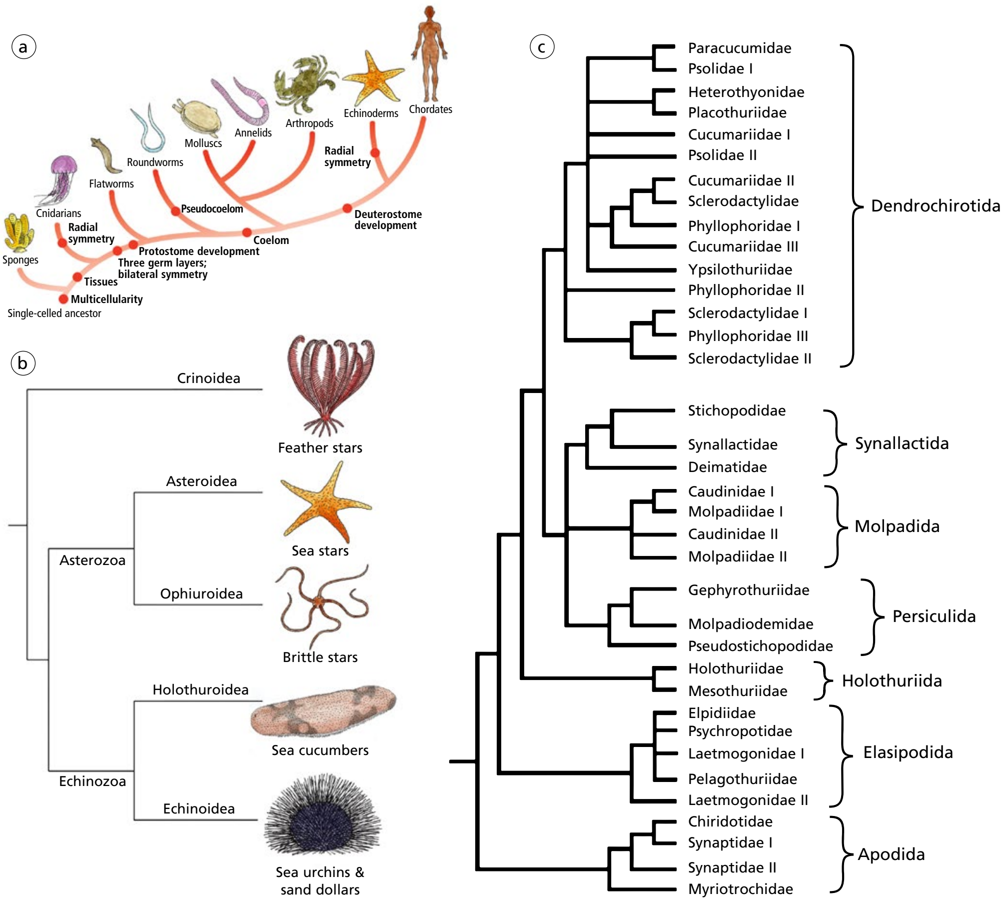
1.1 WHAT IS A SEA CUCUMBER?

Sea cucumbers get their common name from their elongated, cylindrical, barrel-like shape that evokes the garden vegetable. However, sea cucumbers are not vegetal; they are part of a large animal group, or phylum, called Echinodermata or echinoderms. While it may be difficult to imagine, echinoderms sit right next to chordates (the phylum that includes humans and other mammals) in the evolutionary tree (Figure 1a). Most people know of their close cousins, sea stars and sea urchins, which are two other recognizable members of the Echinodermata phylum (Figure 1b). In scientific documents, sea cucumbers may be referred to as holothuroids or holothurians, which are terms broadly derived from their position inside the taxonomic class Holothuroidea (Figure 1b). There are about 1 700 species of sea cucumbers found all around the world, which are themselves divided in several families (Figure 1c). However, new species are discovered and described by scientists every year, so this number is constantly changing.

FIGURE 1

Classification of sea cucumbers

(a) Sea cucumbers are part of a large group (phylum) of animals called Echinodermata or echinoderms that sits closest to chordates, which is the phylum that includes humans and other mammals. (b) The Echinodermata phylum is divided into five main classes, called Crinoidea (feather stars), Asteroidea (sea stars), Ophiuroidea (brittle stars), Echinoidea (sea urchins) and Holothuroidea (sea cucumbers). (c) The class Holothuroidea is further subdivided into seven orders, each containing a number of families. *Cucumaria frondosa* belongs to order Dendrochirotida, and the family Cucumariidae



Sea cucumbers can range in size from under 1 cm to about 50–60 cm in length and from a few grams to several kilograms in weight. They are generally soft-bodied, and they live on the sea floor, mostly laying on its surface but sometimes burrowing inside the sediment. They are exclusively found in salt water, colonizing estuaries, seas and oceans from tropical to polar regions, and from nearshore intertidal environments to the deepest abyssal trenches thousands of metres deep (Mercier *et al*., 2024). Depending on the species, their colour varies from transparent or white to completely black, encompassing nearly all the intermediate shades of grey, brown, yellow, red, and mixes of them all (Mercier *et al*., 2024).

Sea cucumbers as a whole play important ecological roles (Purcell *et al*., 2016). Some species are considered ecosystem engineers because they modify the habitat in which they live. In a process called bioturbation, they can displace pebbles, sand and mud while foraging or burrowing in it, bringing oxygen deeper into the soft substrates (Costa, Mazzola and Vizzini, 2014; Uthicke and Klumpp, 1998). Other species are known to buffer pH levels inside coral-reef ecosystems (Schneider *et al.*, 2011), an important action considering the growing concern about ocean acidification driven by climate change. Sea cucumbers are an integral part of the cycle of nutrients in marine ecosystems. The deposit-feeding species process organic material at the surface of sediments, while suspension-feeding species contribute to a phenomenon called pelagic-benthic coupling, linking the water column with the seabed as they consume plankton and release solid and liquid wastes. These biological processes can aid in the redistribution of sediments across the seafloor and the remineralisation of organic matter (Purcell *et al*., 2016).

1.2 COMMERCIAL EXPLOITATION OF SEA CUCUMBERS

Sea cucumbers have been consumed as food in Asia since at least the period of the Three Kingdoms (200–280 CE), with some accounts mentioning sea cucumbers going back as early as the period of the Warring States in 475–221 BCE (Yang and Bai, 2015). Sea cucumbers are also known as "sea ginseng" in China, Korean Peninsula, and Viet Nam (海參, 해삼, hải sâm, respectively) and as "sea rat" in Japan (海鼠 or ナマコ). An archaic term for sea cucumbers in Chinese is "sand spurting out of the mouth" (沙噀). In Korean, sea cucumbers are also known by other aliases: mu (뮈), mi (미), haenam (해남자) and heukchung (흑충).

As a luxury food item, sea cucumbers are often served at wedding banquets and other important events (Fabinyi *et al.*, 2012; Purcell, 2014). In addition, they have been consumed as part of Asian folk medicine for the promotion of health and well-being (Fabinyi *et al.*, 2012; Gianasi *et al.*, 2021; Hamel, Phelps Bondaroff and Mercier, 2024; Yang, Hamel and Mercier, 2015). Traditional culinary and medicinal uses exist in the Catalan region of Spain (Ramón, Lleonart and Massutí, 2010). The Inuit of Sanikiluaq (Nunavut, Canada) also have a persisting tradition of consuming sea cucumbers, in Inuktitut known as ᖁᖅᓱᔪᒃ or qursujuk or quursujuuq (Wein, Freeman and Makus, 1996).

Today, a variety of species of sea cucumbers are commercially exploited to meet the increasing demand that chiefly comes from Asian communities (including overseas diasporas). Although sea cucumbers account for about 0.05 percent of all marine species (fishes and invertebrates combined) harvested globally (FAO, 2022), they can fetch among the highest prices for seafood per unit weight (Yang, Hamel and Mercier, 2015). With the exception of a few temperate-cold species, including *Apostichopus japonicus* in Asia and *A. californicus* on the western coast of North America, most commercial species inhabit warm-temperate and tropical latitudes of the Indo-Pacific, Caribbean, Central and South America, Africa, Southeast Asia, India and Sri Lanka, and part of the Mediterranean Sea (Purcell *et al.*, 2013; 2023). High demand and high prices have created boom-and-bust patterns of exploitation for many sea cucumber species, which has led to the emergence of illegal, unreported, and unregulated fisheries (IUU). Global pressure has resulted in the overexploitation of stocks, such that at least 21 percent of commercially harvested sea cucumber species, representing over 70 exploited species, are now considered endangered or vulnerable (Purcell, 2014; Purcell *et al.*, 2016).

As demand is steadily increasing and the most commonly fished sea cucumber species become rarer, high-latitude species distributed in cold temperate and polar waters are increasingly exploited in various regions of North America and northern Europe (Purcell *et al.*, 2023). Among the new species, *Cucumaria frondosa* has progressively gained importance in recent decades. Following years of exploratory development in Canada, the United States of America and northern European countries (Hamel and Mercier, 2008) it has now reached full commercial status and provides the highest catches of wild sea cucumber. From a low value species a few years ago, *C. frondosa* now commands medium value as its presence and appreciation on the markets continue to evolve.

2. *Cucumaria frondosa*: names, appearance and anatomy

2.1 COMMON NAMES

The sea cucumber *Cucumaria frondosa* is mainly known by the common name "orange-footed sea cucumber" (Figure 2) in reference to the colour often seen on the ventral surface and along the rows of tube feet. Other vernacular and market names that are in use (Table 1) include the northern sea cucumber (Canada), the Atlantic sea cucumber (United States of America), the phenix sea cucumber (Canada), and pumpkin (Canada). Notably, pumpkin tends to refer to only the orange and grey-beige individuals.

FIGURE 2
The orange-footed sea cucumber *Cucumaria frondosa*, also called the northern sea cucumber or the Atlantic sea cucumber
(a) Fully extended posture with buccal tentacles deployed (top) and rows of tube feet visible (mainly along the right side). (b) Contracted posture with tentacles nearly completely retracted into the body cavity

TABLE 1
List of common names for the sea cucumber *Cucumaria frondosa*

Common name (in Latin alphabet)	English meaning (original language)	Region / Country
Orange-footed sea cucumber	–	Canada; United States of America
Northern sea cucumber	–	Canada
Atlantic sea cucumber	–	Russian Federation; United States of America
Phenix sea cucumber	–	Canada
Pumpkin	–	Canada
Pickle	–	United States of America
Holothurie touffue	Bushy holothuroid (French)	Québec / Canada
ᖁᖅᓱᔪᒃ (qursujuk or quursujuuq)	The thing that folds in (Inuktitut)	Arctic / Canada
Schwarze Seegurke	Black sea cucumber (German)	Germany
Brunpølse	Brown sausage (Norwegian)	Norway
北大西洋瓜参 (běidàxīyángguāshēn)	Cucumariidae of the North Atlantic (Chinese)	China

Source: Authors' own elaboration.

Referencing the shape of the sea cucumber, the name pickle is used by harvesters in Maine, United States of America (Feindel, Bennett and Kanwit, 2011). The species is also known as "holothurie touffue" in French, which translates to "bushy holothuroid" in reference to its finely ramified tentacles. In Inuktitut (the language of Inuit) sea cucumbers are collectively known as ᖁᖅᓱᔪᒃ (qursujuk or quursujuuq) (Rapinski *et al.*, 2018), which means "the thing that folds in" perhaps in reference to the retraction of the tentacles upon stimulation. In Europe, *C. frondosa* is also known as "Schwarze Seegurke", which is German for "black sea cucumber" in reference to the typical dark body colour, and as "brunpølse", which is Norwegian for "brown sausage", referencing both the dark colouration and shape (www.mindat.org/taxon-5188240.html). In China, *C. frondosa* is known as 北大西洋瓜, which means "Cucumariidae (瓜参科) of the North Atlantic Ocean (北大西洋)" in reference to the taxonomic family to which the species belongs and its general distribution in the North Atlantic (Table 1).

2.2 SCIENTIFIC NAME

Taxonomy is the branch of science concerned with the classification of species. In the taxonomic system, *Cucumaria frondosa* belongs to the phylum Echinodermata, the class Holothruoidea and the order Dendrochirotida (it is a dendrochirotid). Notably, most exploited sea cucumbers are in the order Holothuriida (they are holothuriids, formerly known as aspidochirotids). The species was originally described by Gunnerus in 1767 under the name *Holothuria frondosa* and, in the past, it was known by other scientific names until they were all synonymized with the currently accepted name *Cucumaria frondosa* (WoRMS, 2023). *Cucumaria* represents the genus and *frondosa* the species, both of which are conventionally italicized.

2.3 EXTERNAL APPEARANCE

Like most sea cucumbers, adults of *Cucumaria frondosa* have a cylindrical and elongated body with a mouth and anus on opposite ends of the body (Figure 2). Large individuals measure 20–30 cm long with a mid-body circumference (girth) between 10 and 35 cm (Gudimova, 1998b; So *et al.*, 2010). Some exceptionally large individuals can attain an atypical length of up to 50 cm. Adults individuals can weigh between 0.5–2 kg (Feindel, Bennett and Kanwit, 2011; Hamel and Mercier, 2008).

The mouth is surrounded by ten ramified (dendritic) flexible tentacles (Edwards, 1910) that can be deployed to feed (Figure 2a). When an individual is disturbed, its tentacles retract into its body (Figure 2b) and, usually simultaneously, its body contracts into a tight oval or spherical shape (Clark, 1904; Edwards, 1910; Trenholm *et al.*, 2024).

The anus (or cloaca) is not only used to evacuate waste material but is also used to respire (or "breathe") by pumping oxygenated seawater inside sac-like organs called the respiratory trees which possess a thin membrane allowing gas exchange to occur.

Each individual has five rows (ambulacra) of tube feet, which may also be referred to as podia (Figure 3). Tube feet are used for locomotion (crawling) and attachment to surfaces. On the bottom-facing surface of the body (ventral side) there are three distinct rows of tube feet, collectively called the trivium. The remaining two rows of tube feet on the upward-facing surface (dorsal side) is known as the bivium, which may not be as noticeable as the trivium (Figure 3).

FIGURE 3
An emerged sea cucumber *Cucumaria frondosa* showing rows of ambulacral podia or tube feet
(a) Dorsal view showing modified podia/tube feet along two rows, called the bivium. (b) Ventral view of three defined rows of more prominent podia/tube feet, called the trivium. Anterior part of the sea cucumber is at the top of the images. Scale bars represent 2 cm

The typical external colouration (or colour morph) of most adult individuals is dark brown or greyish brown (Figure 4b, c). For a given individual, the dorsal surface is usually a darker shade than the ventral surface. A wide range of less common pigmentations can be observed, including deep black (Figure 4a), light to bright orange (Figure 4d, e), and paler shades of beige or white (Montgomery *et al.*, 2019). Consisting of about 0.5 percent of a population in eastern Canada, orange-coloured individuals are colloquially known as "pumpkins". Beige and white individuals (Figure 4f, g) are rarer still, comprising less than 0.2 percent of the population (Montgomery *et al.*, 2019).

BOX 1

Colour morphs of sea cucumbers

Besides size and texture, colour is a key factor in determining the value of beche-de-mer or the dried body wall of sea cucumbers (Xing *et al*., 2017). Different colour morphs have been documented in the Japanese sea cucumber, *Apostichopus japonicus* (Xing *et al*., 2017), the giant sea cucumber, *Isostichopus fuscus* (Fernández-Rivera Melo *et al*., 2015), the brown sea cucumber, *Ocnus planci* (Casellato and Soresi, 2006), and the orange-footed sea cucumber, *Cucumaria frondosa* (Montgomery *et al.*, 2019).

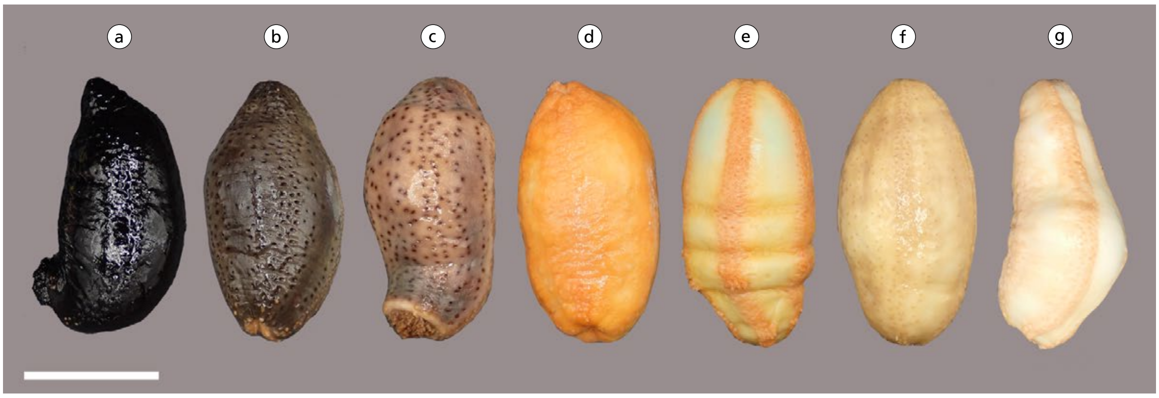
In addition to affecting the market price of sea cucumbers, colour variation can influence its taste (Kang *et al*., 2011). At present, there are no separate markets for the different colour morphs of *C. frondosa*. Rarer colour morphs that are chromatically orange (pumpkin), beige, even white (Figure 4d, e, f, g) should probably be processed separately from the regular dark coloured individuals and marketed at a higher price point depending on demand, as is the case with *A. japonicus* (Tse, 2015). Further work may be required to assess any nutritional and taste-related differences between these light-coloured pumpkins and the more common dark-coloured varieties.

Blue-black-coloured individuals are the rarest. Research into colour variations, and their respective drivers and values, is not as advanced in *C. frondosa* as it is in the prime species *Apostichopus japonicus* (Box 1).

FIGURE 4

Variability in the external colour of the sea cucumber *Cucumaria frondosa*

(a) Black individual. (b–c) Dark-brown and greyish-brown individuals. (d–e) Bright orange individual. (f) Pale beige individual. (g) White individual. Scale bar represents 5 cm for (a–f) and 3 cm for (g)



Source: Modified from Montgomery *et al*. (2019). Albinism in orange-footed sea cucumber (*Cucumaria frondosa*) in Newfoundland. *The Canadian Field-Naturalist*, 133(2): 113–117.

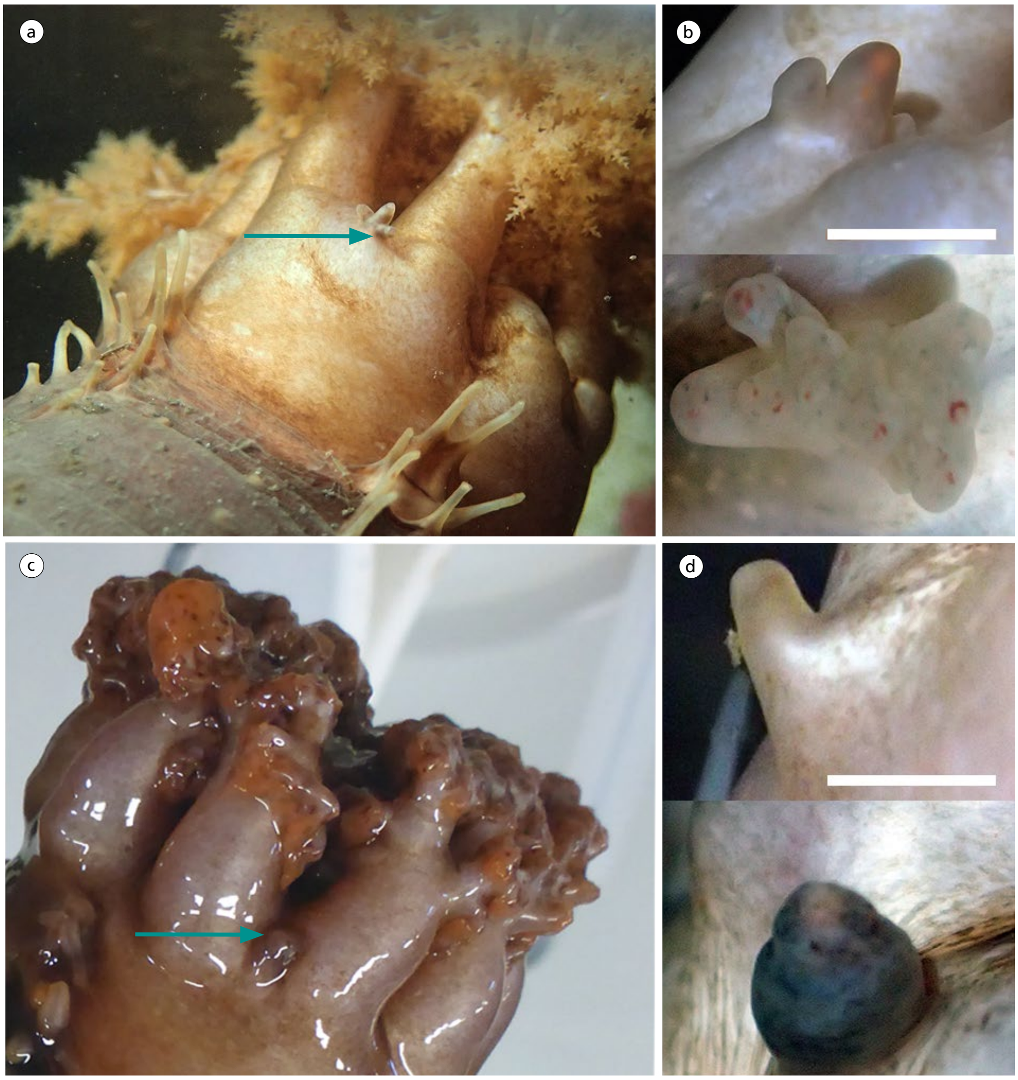
2.4 SEXUAL DIMORPHISM (DIFFERENCE BETWEEN SEXES)

Most species of sea cucumbers, including *Cucumaria frondosa*, have two separate sexes. While they look quite similar externally, males and females can be distinguished at closer range. When the tentacles surrounding the mouth are deployed, a nipple-like protuberance called the genital papilla can be observed at the base of one of them. Its appearance differs between males and females. This papilla is digitate, meaning it is composed of multiple branches, in males (Figure 5a, b, c, d) while it consists of a simple cone-like protuberance in females (Figure 5e, f) (Montgomery *et al.*, 2018). In both sexes, the papilla is connected to the reproductive organ (see Section 2.11) and used to release the gametes (oocytes and spermatozoa) through the gonopore into the water column.

FIGURE 5

Genital papillae in the sea cucumber *Cucumaria frondosa* are located between two buccal tentacles

(a) The male genital papilla (arrow) is ramified or branched, with multiple orifices. b) Close-ups of the male genital papilla. (c) The female genital papilla (arrow) is cone-shaped, with a single orifice. (d) Close-ups of female genital papilla. Scale bar in (b) and (d) represents 0.5 cm

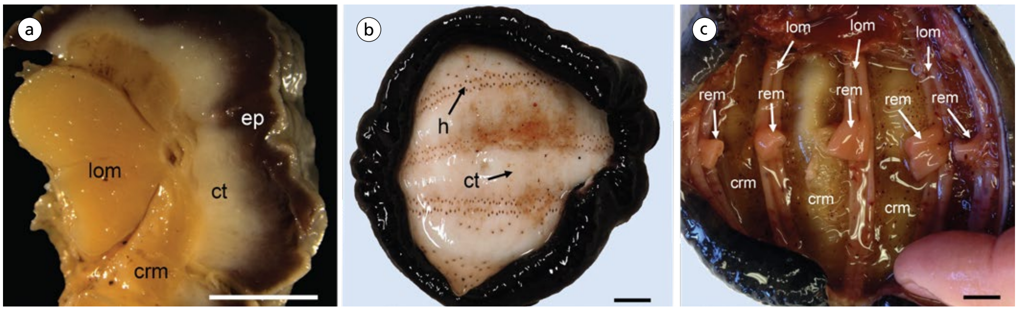


2.5 BODY WALL

The body wall that surrounds the entire individual is made up of several main layers: the epidermis (epithelium), the dermis (white collagenous tissue), and bands of circular and longitudinal muscles (Figure 6a). The skin usually refers to both the epidermis and dermis. The dermis is a layer of white connective tissue (Figure 6a, b) which primarily consists of collagen and has an impressive capacity to stretch and retract (Koob-Emunds *et al.*, 1996; Trotter *et al.*, 1996). Along the body wall, there are longitudinal rows of tiny tube feet (Figure 3c), or podia, connected to and activated by the internal water-vascular or hydrovascular system (see Section 2.8).

Embedded in the body wall and other structures, such as the tentacles and tube feet, are tiny calcareous structures known as ossicles that form the endoskeletal system (Figure 7). They are microscopic in size (92–370 µm or 0.092–0.370 mm) and come in a variety of shapes; they can have knobbly features, and can exhibit as many as 65 holes in each of them (Levin and Gudimova, 2000). The shape and size of ossicles vary depending on their location in the body. For instance, the ossicles around the

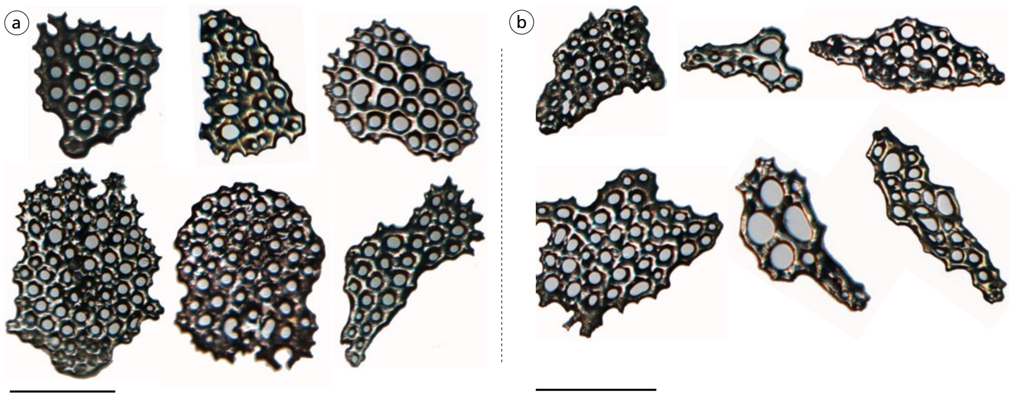
FIGURE 6
The body wall of the sea cucumber *Cucumaria frondosa*
(a) Cross-section of the body wall showing the epidermis (ep), connective tissue (ct), circular muscle (crm), and longitudinal muscle (lom). (b) Body wall without muscle tissues showing the connective tissue (ct) and the holes (h) that accommodate the ambulacral podia. (c) Arrangement of longitudinal muscles (lom), circular muscles (crm), and introvert retractor muscles (rem). Scale bars represent 5 mm in panel (a) and 10 mm in panels (b–c)



Source: Gianasi, B.L., Hamel, J.-F., Montgomery, E.M., Sun, J. & Mercier, A. 2021. Current knowledge on the biology, ecology, and commercial exploitation of the sea cucumber *Cucumaria frondosa. Reviews in Fisheries Science and Aquaculture*, 29(4): 582–653.

mouth are elongated while those embedded in the tentacles tend to be rod-like in shape (curved and/or straight rods) and those in the tube feet are usually wide with a tapering end (Figure 7). In addition to the body wall, tentacles and tube feet, ossicles can be found in the calcareous ring canal, the stone canal, and the madreporite, among others.

FIGURE 7
Ossicles of the sea cucumber *Cucumaria frondosa*
(a) Ossicles from the body wall and (b) ossicles from a tentacle. Scale bars represent 100 μm



Source: Gianasi, B.L., Hamel, J.-F., Montgomery, E.M., Sun, J. & Mercier, A. 2021. Current knowledge on the biology, ecology, and commercial exploitation of the sea cucumber *Cucumaria frondosa. Reviews in Fisheries Science and Aquaculture*, 29(4): 582–653.

2.6 ORAL COMPLEX

Cucumaria frondosa, like other dendrochirotid sea cucumbers, possesses a well-developed oral region held by a collar of flexible tissue (the introvert) that can be pulled into the body by retractor muscles. The main components associated with the oral complex are the tentacles surrounding the mouth, the aquapharyngeal bulb (a muscular bulb-like structure), the retractor muscles (responsible for retracting the oral complex inside the body), the water ring or ring canal with the attached Polian vesicle, the calcareous ring, the stone or sand canal, and madreporite (Figure 8). Because of its appearance evoking a corolla when it is dry, the oral complex, mainly the aquapharyngeal bulb with the attached tentacles, is known as the “flower” in the sea cucumber industry.

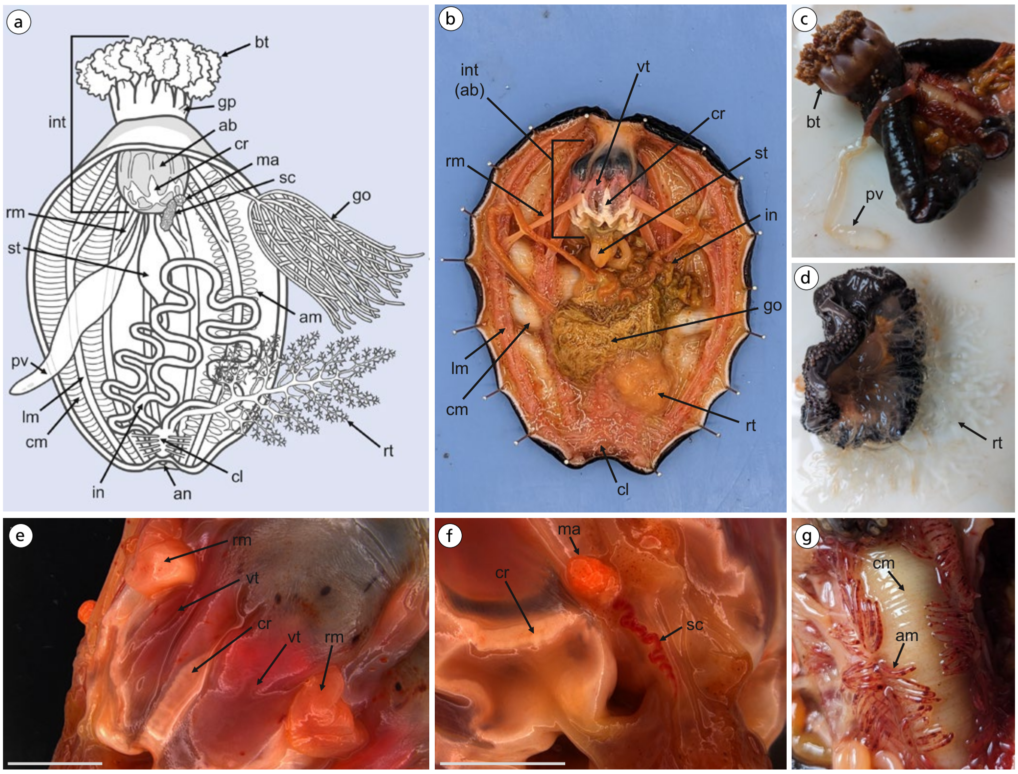
2.7 MUSCULAR SYSTEM

Cucumaria frondosa possesses a complex network of muscles, helping it to contract, extend and move around. This species is especially renowned for its ability to modify its shape when touched (Figure 3). The muscle system is composed of longitudinal muscles, circular muscles, and introvert retractor muscles (also known as pharynx retractor muscles) located in different parts of the body (Figure 6c and Figure 8a, b). Specifically, each individual has five longitudinal muscle bands and five corresponding retractor muscles. The five longitudinal muscle bands are attached perpendicular to a series of several circular muscle bands which in turn are attached to the dermis (Figure 6c). Together these muscles are typically considered part of the body wall (i.e. the meat in the industry) and they are all pinkish in colour. The combined effect of using both types of muscles lining the body wall creates a wave-like movement for locomotion (also known as peristaltic movement) and to modify the shape of the body as needed. The retractor muscles of the introvert (oral complex) connect with the aquapharyngeal bulb (Figure 8), allowing the sea cucumber to retract its tentacles or change their orientation and to move the anterior end (where the mouth is found) of its body from side to side (lateral movement).

FIGURE 8

Anatomy of the sea cucumber *Cucumaria frondosa*

(a) Schematic drawing and (b) a dissected individual with tentacles retracted, showing the main anatomical components. (c) Close-up on the crown of tentacles and visible Polian vesicle. (d) Photo showing an inflated respiratory tree (clear ramifications spread outside the open individual). (e) Close-up of the aquapharyngeal bulb, showing the vesicles of the tentacles, calcareous ring, and the location where the retractor muscles are connected to the aquapharyngeal bulb. (f) Close-up of the aquapharyngeal bulb showing the madreporite and the stone canal, which are located near the calcareous ring. (g) Internal view of the body wall showing the ampullae of the tube feet. Labels in alphabetical order: ab = aquapharyngeal bulb, am = ampulla of the tube foot, an = anus, bt = buccal tentacles, cm = circular muscle, cl = cloaca, cr = calcareous ring, go = gonad, gp = genital papilla, in = intestine, int = introvert + oral complex, lm = longitudinal muscle, pv = Polian vesicle, rm = retractor muscle, rt = respiratory tree, sc = stone canal, st = stomach, vt = vesicle of the tentacle. Scale bars in E and F represent 5 mm; scale bars not available for panels b, c, d, and g



2.8 WATER VASCULAR SYSTEM

The water vascular system or hydrovascular system of *Cucumaria frondosa* (and other species) is a semi-closed hydraulic system that is used for locomotion, respiration, immune defence, transportation of food and waste, and the deployment of tentacles and tube feet. It is composed a large network of canals, reservoirs, valves and filters. Its main components include the tube feet (podia and ampullae, Figure 8d), radial canals (Figure 8d), the water ring (Figure 8c), the Polian vesicle(s) (Figure 8a, b), the stone canal (Figure 8c), the madreporite (Figure 8c), tentacles (Figures 2b, 8a), and vesicles of the tentacles (Figure 8c). Most of the immune cells can be found in this system (Caulier, Hamel and Mercier, 2020).

The madreporite (Figure 8c) acts as a pressure-equalizing valve to filter water into (and possibly out of) the hydrovascular system. As this system is pressurized and subject to leaks (from tears in the tube feet or tentacles), the madreporite allows water to enter the system as required, via the stone canal (Figure 8c), and rebuild the pressure. The Polian vesicle (Figure 8a, b) serves as a reserve of fluid or as an expansion chamber to regulate pressure in this system. Ordinarily, each individual has one Polian vesicle, but in some cases two or more can be observed in *C. frondosa* (Edwards, 1910). The vesicles of the tentacles (Figure 8c) – located at the tentacle base – are used as a fluid reserve to assist with their extension and retraction. Each cylinder-shaped tube foot also has an ampulla that help controls the extension and retraction of the podium (Levin and Gudimova, 2000).

2.9 DIGESTIVE SYSTEM

The mouth, pharynx, stomach, intestine, and cloaca or anus (Figure 3 and Figure 8) are the main parts of the digestive system that *Cucumaria frondosa* uses to convert food into energy and nutrients. Food enters the body through the mouth and passes into the pharynx, then into the stomach. The stomach produces a protein (more specifically an enzyme) called "lipase", which breaks down fats (Mayer *et al.*, 1997). The food then goes through the intestine (Figure 8a, b), which is sub-divided into three sections: the descending anterior intestine, the ascending anterior intestine, and the posterior intestine. The intestine is a winding tube that can be up to 30 cm in length (in a mature adult) when fully extended. Each section of the intestine has a slightly different function as evidenced by slightly different composition of cells. The first section of the intestine (or the descending anterior intestine) produces enzymes known as "glucosidase" to aid in the breakdown of starches and sugars and esterase to digest a class of chemical compounds known as esters. The last sections possess high levels of a group of enzymes called proteases, which are used to break down proteins (Filimonova and Tokin, 1980). The terminal portion of the digestive system connects with the respiratory system before opening to the outside environment, which is why it is sometimes called a cloaca instead of an anus (Figure 3 and Figure 8). The digestive tract is one of the organ systems that sometimes gets expelled accidentally in *C. frondosa* (Box 2).

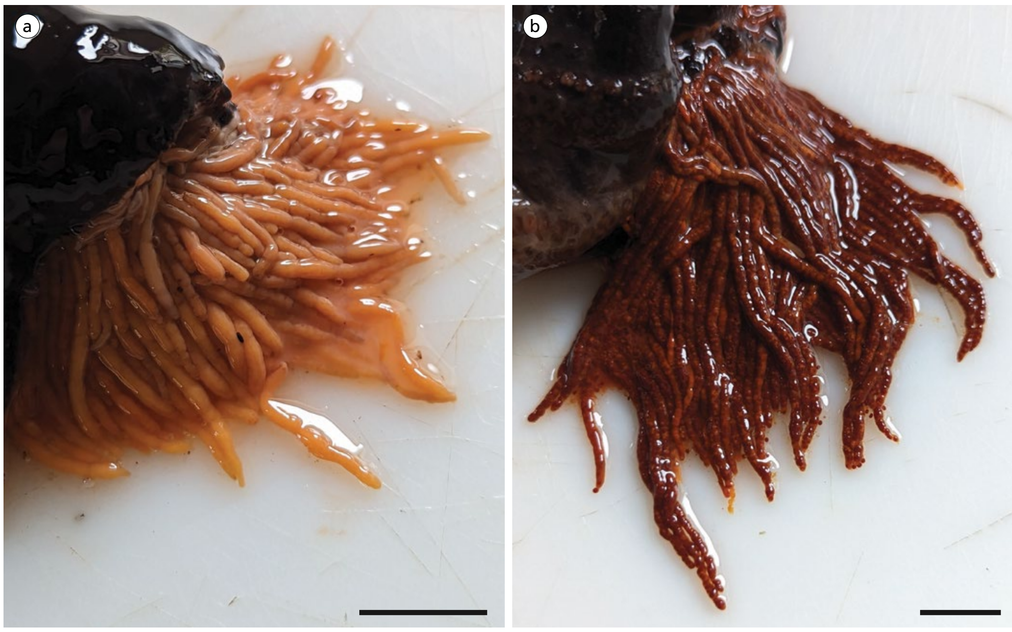
2.10 HAEMAL SYSTEM

Like all echinoderms, *Cucumaria frondosa* lacks a true blood vascular system. Instead, it has a series of canals and follicles, known as the haemal system, which is visually associated with the digestive tract (Figure 8). Although its functionality has not yet been fully elucidated, this system delivers processed food and nutrients to all body parts. Brownish in colour in *C. frondosa* and visible during the spring, summer and autumn when food is abundant, the haemal system almost disappears (degenerates) during the winter, when feeding is very limited.

2.11 REPRODUCTIVE SYSTEM

Internally, each individual of *Cucumaria frondosa* possesses a reproductive organ, or gonad, comprised of 100–300 tubules that vaguely look like noodles, except for the colouration. Each tubule can reach up to ~16 cm long in mature individuals (Hamel and Mercier, 1996c). The male gonad is also referred to as the testis, which produces spermatozoa, and the female gonad is known as the ovary, which produces oocytes (fully developed fertilized oocytes are referred to as eggs). In mature adults, the ripe gonad tubules are light pink or orange in the males and dark red or burgundy in the females (Figure 9) (Gianasi, Hamel and Mercier, 2019c; Hamel and Mercier, 1996c; Singh *et al.*, 2001). All the tubules are connected to a single gonoduct leading to the genital papilla, which has one or numerous tiny opening(s) collectively known as the "gonopore", through which the gametes are released in the sourrounding water (Figure 5).

FIGURE 9
Gonad of the sea cucumber *Cucumaria frondosa*
(a) Whole male gonad and (b) whole female gonad. Scale bar represents 1 cm



2.12 RESPIRATORY SYSTEM

Sea cucumbers have evolved specialized organs called respiratory trees (somewhat analogous to lungs in humans) to facilitate gas exchange or "breathing". A small amount of oxygen, however, may be directly taken up through the body wall (skin) or the tube feet (Brown and Shick, 1979; Doyle and McNiel, 1964). Each individual of *Cucumaria frondosa* has two respiratory trees, which are highly branched translucent cavities surrounded by a thin membrane (Figure 8). These organs are connected to the cloaca, through which oxygenated seawater is drawn in at regular intervals before being expelled (along with metabolic wastes) out the same way. Yes, sea cucumbers breathe through their rear end! Each branch of the respiratory tree terminates with vesicles that are believed to facilitate gas exchange with nearby tissues and organs (Doyle and McNiel, 1964) similar to alveoli in human lungs. These arborescent bags occupy most of the internal body space when filled with seawater. The water spouting from a sea cucumber that is being handled usually comes from the respiratory tree(s).

BOX 2

Evisceration

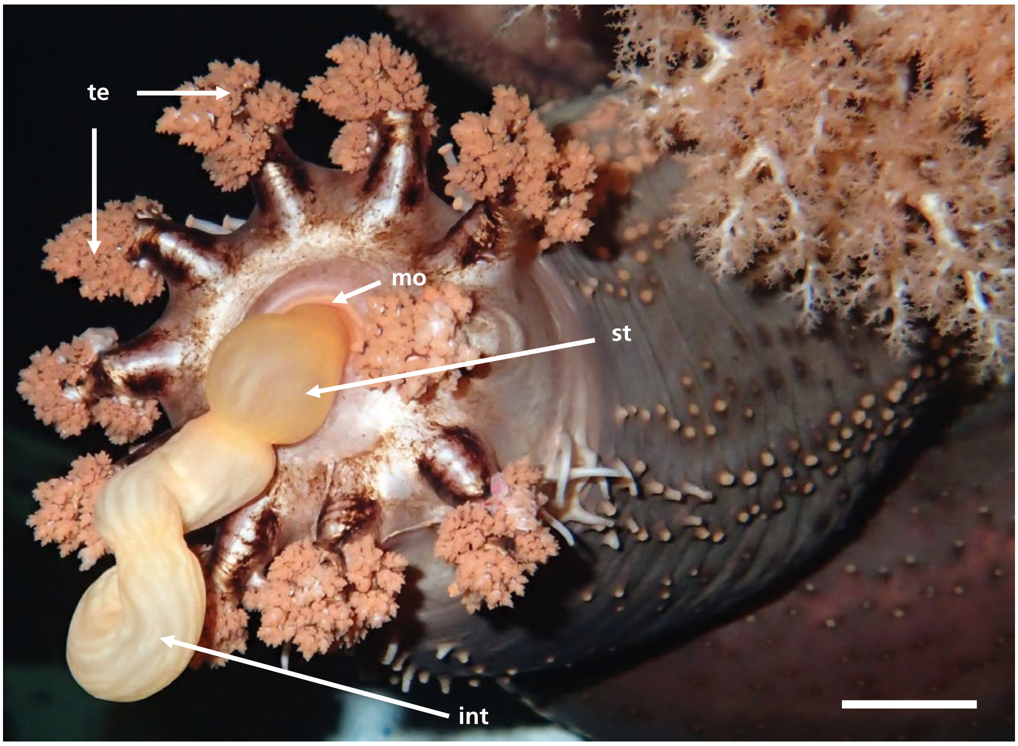
Many sea cucumbers can expel all or part of their internal organs (intestine, gonad, respiratory tree), in a process called "evisceration", as an active response to stress such as manipulation or interactions with a predator (Emson and Wilkie, 1980). Some species of *Apostichopus* even undergo seasonal evisceration (aestivation) as a means of withstanding physiologically demanding environmental conditions (Ji, Dong and Dong, 2008). In species that naturally resort to evisceration, the internal organs are totally discarded and subsequently regenerated inside a few weeks.

However, natural evisceration has never been documented in *Cucumaria frondosa*. Nevertheless, the ejection of the stomach and part of the digestive tract through the mouth has frequently been observed after harvesting of *C. frondosa* (Figure 10). This partial evisceration is probably induced by the pressure applied to sea cucumbers piled in the ship haul or in vats during transport to the docks or the processing plant. This condition is generally, but not always, irreversible. While most affected individuals ultimately die, some of them were shown to make a full recovery in the laboratory, whereby the organs were reintegrated inside the body cavity (Gianasi *et al.*, 2021).

FIGURE 10

Partial evisceration of the stomach and the intestine through the mouth in the sea cucumber *Cucumaria frondosa*

Labels: int = intestine, mo = mouth, st = stomach, te = tentacle. Scale bar represents 1 cm

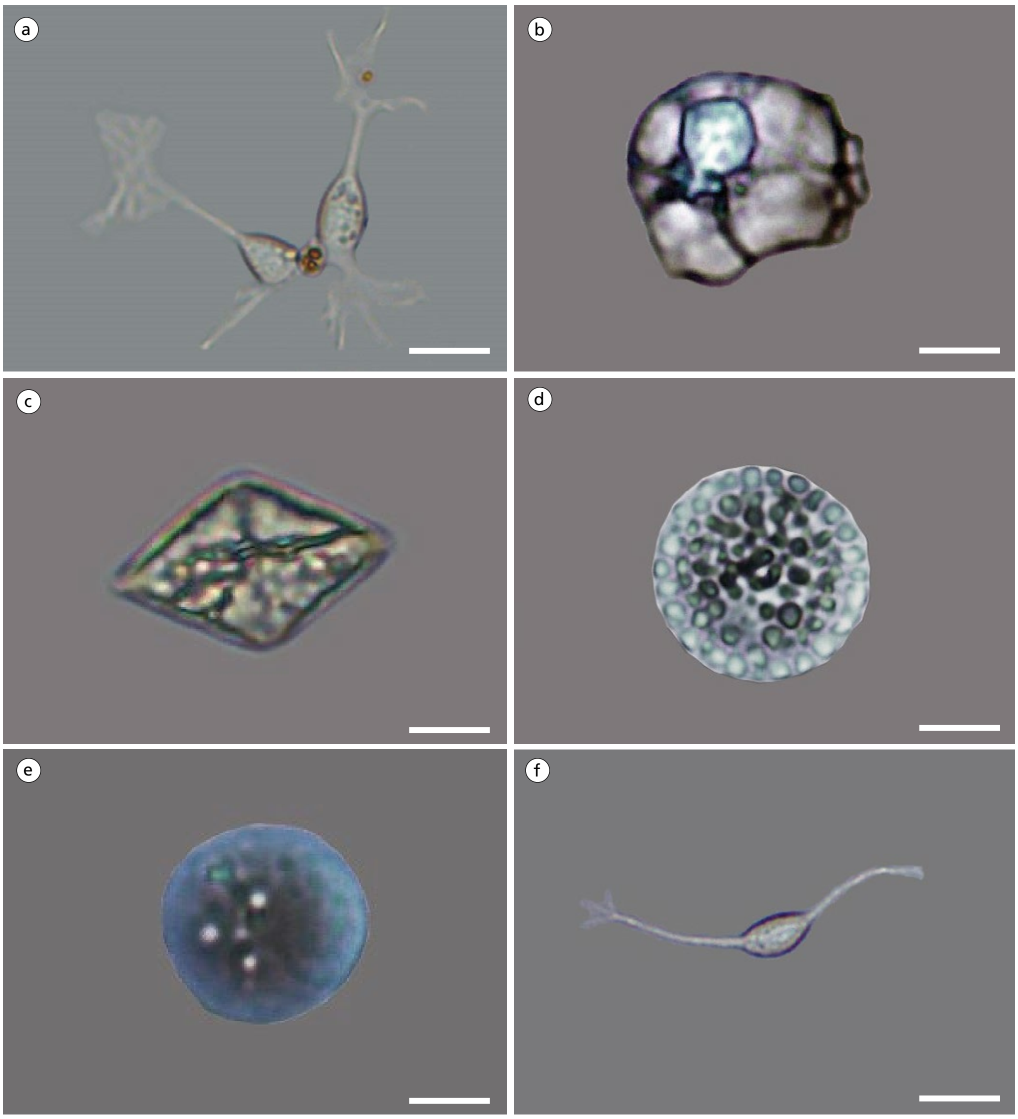


Source: Gianasi, B.L., Hamel, J.-F., Montgomery, E.M., Sun, J. & Mercier, A. 2021. Current knowledge on the biology, ecology, and commercial exploitation of the sea cucumber *Cucumaria frondosa*. *Reviews in Fisheries Science and Aquaculture*, 29(4): 582–653.

2.13 IMMUNE SYSTEM

Like all invertebrates, *Cucumaria frondosa* only possesses an innate immune system (no adaptive immune system) consisting of cellular and humoral factors that help defend the body against infection and diseases (Caulier, Hamel and Mercier, 2020; Jobson *et al.*, 2021; Jobson, Hamel and Mercier, 2022). The primary defence occurs through a suite of immune cells collectively known as "coelomocytes" (Caulier, Hamel and Mercier, 2020; Caulier *et al.*, 2024; Jobson, Hamel and Mercier, 2022). These cells participate in the identification, encapsulation, and removal of foreign particles, such as bacteria and viruses (Caulier, Hamel and Mercier, 2020; Jobson *et al.*, 2021; Smith *et al.*, 2018). Coelomocytes also secrete humoral factors, which are used to recognize different types of foreign bodies (a phenomenon known as cell–cell recognition), and to initiate antimicrobial defences (Chiaramonte and Russo, 2015). Although many coelomocytes are free-floating in the internal body fluids, at least during part of their life, many forms are found attached to the surface of organs like the respiratory tree, Polian vesicle and intestine (Caulier, Hamel and Mercier, 2020; Jobson *et al.*, 2021; Smith *et al.*, 2018). Exposure to stressors like a decrease in salinity or presence of a predator will induce an immune response in *C. frondosa*, translating as an increase in the number of free coelomocytes to help the organism fight against tissue damage and pathogens (Hamel *et al.*, 2021).

FIGURE 11
Free coelomocytes isolated from the perivisceral coelomic cavity of the sea cucumber *Cucumaria frondosa*
(a) Two filopodial phagocytes, (b) petaloid phagocyte, (c) crystal cell, (d) morula cell, (e) progenitor cell, (f) fusiform cell. Scale bar represents 15 μm in panels (a) and (b), 12 μm in panel (c), 20 μm in panel (d), 1 μm in panel (e), and 13 μm in panel (f)



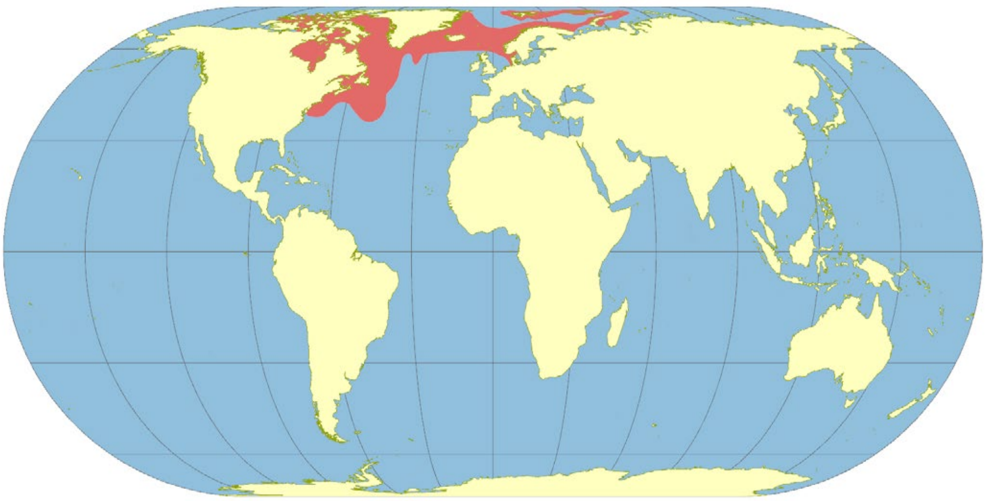
Source: Caulier, G., Hamel, J.-F. & Mercier, A. 2020. From coelomocytes to colored aggregates: cellular components and processes involved in the immune response of the holothuroid *Cucumaria frondosa. The Biological Bulletin*, 239(2): 95–114.

3. Distribution and abundance of *Cucumaria frondosa*

3.1 GEOGRAPHIC DISTRIBUTION

The distributional range of *Cucumaria frondosa* extends from the Arctic Ocean to northern areas of the North Atlantic Ocean (Nelson, MacDonald and Robinson, 2012b). In North America, its geographic range spans from Ellesmere Island in the Canadian Arctic (Hamel and Mercier, 2024) and Greenland to the north, down to Cape Cod (Massachusetts, United States of America) to the south (Figure 12). Sea cucumbers are especially abundant on the Grand Banks, off the coast of insular Newfoundland (Hamel and Mercier, 2008) and in the Hudson Bay around Qikiqtait (traditional name of the Belcher Islands). In Europe, the species is distributed as far north as the Arctic archipelagos of Svalbard (Norway) and Franz Josef Land and Novaya Zemlya (Russian Federation), as far west as Iceland, and as far south as Dogger Bank in the North Sea (Dvoretsky and Dvoretsky, 2021; Hamel and Mercier, 2008). In the Barents Sea, the northern border of the range is registered near Franz Josef Land, while the eastern limit is the Kara Gate (south of Novaya Zemlya). The species also occurs on the Spitsbergen Bank, from the Kharlov Island to Cape Svyatoy Nos, at Murmansk Shallowness, North Kanin Bank and on Goose Bank (Dvoretsky and Dvoretsky, 2021) (Figure 12).

FIGURE 12
Known distribution of the sea cucumber *Cucumaria frondosa*



Source: Purcell, S.W., Lovatelli, A., González-Wangüemert, M., Solís-Marín, F.A., Samyn, Y. & Conand, C. 2023. *Commercially important sea cucumbers of the world – Second edition*. FAO Species Catalogue for Fishery Purposes No. 6, Rev. 1. Rome, FAO.

3.2 ABUNDANCE IN EASTERN CANADA AND THE UNITED STATES OF AMERICA

Cucumaria frondosa is currently regarded as the most abundant commercial species of sea cucumber on the planet, based on density and biomass values. Off the Grand Banks of insular Newfoundland in eastern Canada, *C. frondosa* is fished principally in the region designated by the Northwest Atlantic Fisheries Organization as "NAFO Division 3Ps", which is further partitioned into two areas: the Southeastern and the Northwestern beds. The total weight of sea cucumbers (or biomass) estimated from an area of 130 km^2 was greater in the east (i.e. 56 000 tonnes or 430 tonnes/km^2) than in the west (i.e. 31 000 tonnes or 238 tonnes/km^2) of this fishing division (DFO, 2017a). A subsequent survey estimated a total of 180 million sea cucumbers on the Northwestern bed and 748 million on the Southeastern bed in 2016 (DFO, 2017a).

In the Estuary and Gulf of the St. Lawrence River (Québec, Canada), densities between 0.007 and 1.6 ind/m^2 have been reported (Campagna, Lambert and Archambault, 2005; Hamel, Dallaire and Le Mer, 2013). At some sites, the biomass can reach values as high as 15 kg/m^2, especially in the St. Lawrence Estuary (Hamel and Mercier, 1995).

Densities of *C. frondosa* are also high in the Passamaquoddy Bay in New Brunswick, Canada, ranging from roughly 10 ind/m^2 (DFO, 2009) to 50 ind/m^2 (Singh *et al.*). Further south in waters off the coast of Maine, United States of America, the spatial distribution of sea cucumbers is fairly patchy but some sites support densities of 5 ind/m^2 and other sites support a biomass of about 15 kg/m^2 (Bruckner, 2005; Feindel, Bennett and Kanwit, 2011).

3.3 ABUNDANCE IN NORTHERN CANADA AND GREENLAND

Anecdotally, sea cucumbers seem to be plentiful in many areas of the Canadian Arctic Archipelago (Nunavut, Canada), however, there is little published data in the scientific literature (Hamel and Mercier, 2024). Some researchers noted that *Cucumaria frondosa* was abundant in the waters around Qikiqtait (the traditional name of the Belcher Islands) in Nunavut, Canada (Wein, Freeman and Makus, 1996). Recent studies in the same area identified a shallow nursery habitat, with densities of juveniles 0.9–40 mm in lenght varying between 4 and 104 ind/m^2 and densities of adults up to 22 ind/m^2 in slightly deeper neighbouring areas (Hamel *et al.*, 2023). This species has also been recorded in more northern regions of Nunavut such as near Baffin Island (Grant *et al.*, 2018) and Victoria Island (Hamel and Mercier, 2024), but abundances are not known. In Greenland, *C. frondosa* is abundant in some regions, but densities and biomasses have yet to be published.

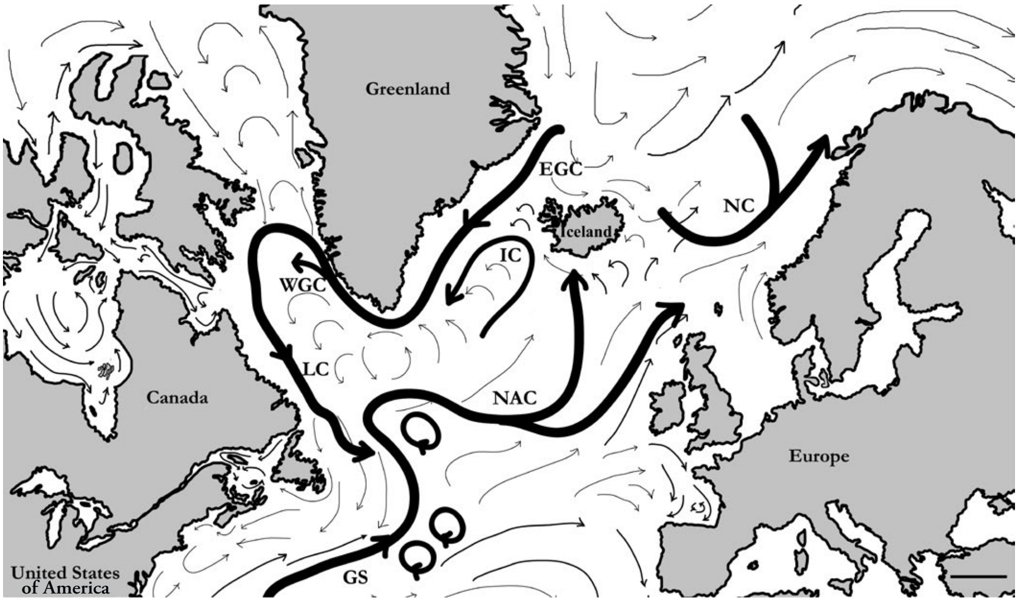
3.4 ABUNDANCE IN NORTHERN EUROPE

In a broad-scale survey conducted in Iceland in 2020, densities estimated by trawl were globally between 0.12 and 0.23 ind/m^2; whereas estimates based on drop camera assessments were 0.6–0.7 ind/m^2. In the Icelandic bay of Faxaflói, the biomass of *Cucumaria frondosa* was about 0.13 kg/m^2 (MFRI, 2017; MFRI, 2021a). Trawl surveys in 2021 caught 1 040–1 757 individuals per nautical mile, or about 560–950 ind/km (MFRI, 2021a; MFRI, 2022). At sampling stations where the species is present in the Spitsbergen Bank in Svalbard, Norway, it was determined that *C. frondosa* could account for about 50–89 percent of the total biomass of organisms inhabiting the sea floor (Anisimova *et al.*, 2010; Jørgensen *et al.*, 2015; Kędra *et al.*, 2013; Wesławski *et al.*, 1997). In another study, *C. frondosa* made up to 20 percent of the total biomass in 15-minute trawls in the Barents Sea (Jørgensen *et al.*, 2016). On Svalbard Bank, off the Russian Federation coast, catches of *C. frondosa* were up to 26 kg (Svalbard Bank), 59 kg (Russia Banks), and 61 kg (Pechora Sea) after 15-minute trawls (Jørgensen *et al.*, 2015; Jørgensen *et al.*, 2016). Dvoretsky and Dvoretsky (2021) described the abundance of *C. frondosa* in the Russian Federation (Barents Sea) where the maximum biomass was between 0.4 and 0.5 kg/m^2. The total stocks were estimated to be between 150 000 tonnes on Spitsbergen Bank and 215 000 tonnes in the south-eastern Barents Sea (Gudimova, 1998a; Gudimova, 1998b).

3.5 POPULATION GENETICS IN THE NORTH ATLANTIC

Population genetic studies on *Cucumaria frondosa* are still rare. The genetic structure of populations from the eastern and western North Atlantic Ocean was studied using a molecular marker called cytochrome c oxidase subunit I (COI). This technique can help scientists establish how independent or linked the various populations of sea cucumbers are across different regions and countries. The study demonstrated that populations of *C. frondosa* are not geographically isolated and are more connected to each other than expected initially (So *et al.*, 2011). Moreover, findings suggest that there exists one large breeding population (called a panmictic population) spanning vast distances across the North Atlantic Ocean. Closer examination of the genetic structure suggests that genetic material is primarily flowing from west to east in the North Atlantic (So *et al.*, 2011). This directional flow is probably a reflection of the long-distance dispersal ability of pelagic larvae that get entrained by the prevailing currents, namely the North Atlantic current, which runs from western to northeastern regions of the North Atlantic (broadly toward Iceland) (Figure 13; Box 3). A recent study confirmed the presence of one metapopulation of *C. frondosa* in the North Atlantic, with at least two subpopulations between North America and Europe, and stressed the need for standardizing methods in future genetic studies (Penney, 2022).

FIGURE 13
Map of oceanic currents in the North Atlantic between April and June, i.e., during the pelagic larval phase of the sea cucumber *Cucumaria frondosa*
Numbers correspond to sites from which samples were collected for the population genetic study of So *et al.* (2011). The boxed area corresponds to eastern Canadian sites. EGC = Eastern Greenland Current, GS = Gulf Stream, IC = Icelandic Current, LC = Labrador Current, NAC = North Atlantic Current, NC = Norwegian Current, WGC = Western Greenland Current. Scale bar represents 500 km



Source: So, J.J., Uthicke, S., Hamel, J.-F. & Mercier, A. 2011. Genetic population structure in a commercial marine invertebrate with long-lived lecithotrophic larvae: *Cucumaria frondosa* (Echinodermata: Holothuroidea). *Marine Biology*, 158(4): 859–870.

BOX 3
Population genetics and management considerations

The putatively high connectivity among populations of *Cucumaria frondosa* in the North Atlantic Ocean has a major impact on stock management. Some local subpopulations may be able to recover from declines resulting from natural or human-driven disturbances and pressures, while others may not. For instance, heavily fished areas could be replenished through larval recruitment coming from more or less distant populations of *C. frondosa* to the west (So *et al.*, 2011). However, as recruitment would likely flow in a northeast direction, fished populations from westernmost areas of the range could be more severely

BOX 3 (CONTINUED)

threatened by overfishing. Populations off New England (United States of America) are already showing low densities and biomasses. Further downturns in fisheries across the central and western Atlantic could eventually impact the stocks in the eastern Atlantic. Fisheries management should thus take a global precautionary approach to managing harvests of *C. frondosa*, despite the initially large biomasses, since the populations are likely to be interdependent.

4. Habitat of *Cucumaria frondosa*

4.1 DEPTH RANGE

Adults of *Cucumaria frondosa* most often live at depths between 3 and 300 metres. Few individuals have been found as deep as 1 450 metres; however it was clear from their poor health and reproductive status that these depths fall outside the ideal range of occurence (Ross, Hamel and Mercier, 2013). Early life stages tend to occur in shallower waters than the adults do. Just-settled larvae or early juveniles were seen at depths of two metres or less in island channels of southern Nunavut, Canada (Hamel *et al.*, 2023), and the St. Lawrence Estuary in Québec (Hamel and Mercier, 1996d), and they were reported in less than 12 metres along the coast of New England, United States of America (Medeiros-Bergen and Miles, 1997).

4.2 HABITAT CHARACTERISTICS

Cucumaria frondosa is most commonly found in rocky habitats, attached to gravel, pebbles, boulders, or the bedrock (Figure 14). Individuals have been occasionally observed on sand, but this is likely a transition as they are dispersing to other areas (Hamel *et al.*, 2019). In contrast to adults, small juveniles are usually found inside rocky crevices and empty bivalve shells, but can also be associated with other complex substrates such as kelp holdfasts, rhodoliths (calcareous habitats formed by red algae), and mussel beds (Hamel and Mercier, 1996d; Hamel *et al*., 2023) (Figure 14). However, the concentration of larger juveniles (between 2–4 cm) in nearby but slightly deeper water allows to suggest the occurance of successive size/age-specific migrations of *C. frondosa*. The finer patterns of ontogenetic (age-related) migrations and the occurrence of movement across habitats remain difficult to ascertain because tagging individuals to follow them is not easy (Box 4).

BOX 4

Tagging and following sea cucumbers

Tagging research provides valuable information on the behaviour, growth patterns, natural rates of mortality, migration, and population sizes of commercial species of fishes and invertebrates. Several types of tags and tagging methods exist; some are attached externally to captured individuals and read when they are recaptured. Others rely on more advanced technologies such as internal implants that can be detected by manual readers or that log and report via satellite. All sea cucumbers, including *Cucumaria frondosa*, are notoriously difficult to tag with any physical devices like T-bars inserted through the skin because they can shed them quickly, whereas chemical pigments may be toxic (Kirshenbaum, Feindel and Chen, 2006). Tags that require physically piercing the skin of the sea cucumber performed the worst: 0 percent retention of the tags after 140 days using double anchor T-bar tags and 65 percent using single anchor T-bar tags (Kirshenbaum, Feindel and Chen, 2006). Chemical tags using visible implant elastomer had a retention rate of about 80 percent after 140 days (Kirshenbaum, Feindel and Chen, 2006). The insertion of a passive integrated transponder (PIT) inside the body emerged as one of the most promising methods since it does not produce any adverse effects and tags are well retained. Tagged individuals consistently recovered from the implant procedure after about 15 hours. PIT tags placed inside the aquapharyngeal bulb had the best retention rate of about 90 percent after 30 days and about 70 percent after 300 days, with no detectable side-effects (Figure 15) (Gianasi *et al.*, 2015).

FIGURE 14
Populations of *Cucumaria frondosa* from in situ photographs
(a) Hudson Bay, Nunavut, northern Canada. (b–c) Grand Banks (NAFO Division 3Ps), southern Newfoundland, eastern Canada. (d) Close-up on individuals attached to pebbles and shells. (d) Picture taken during capture showing a full net (yellow, bottom of picture) and dislodged individuals floating around. Largest sea cucumbers measure 20–25 cm

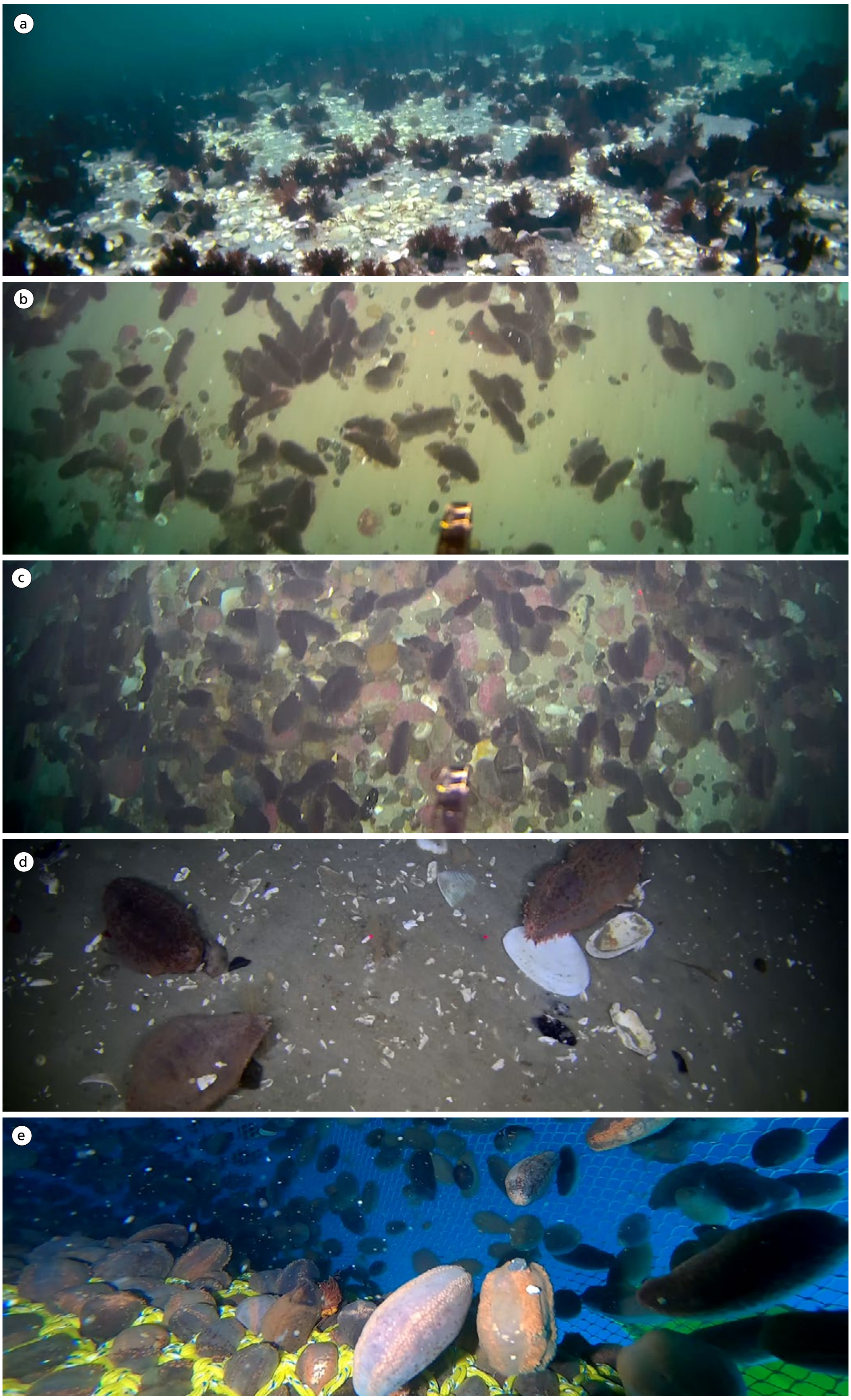


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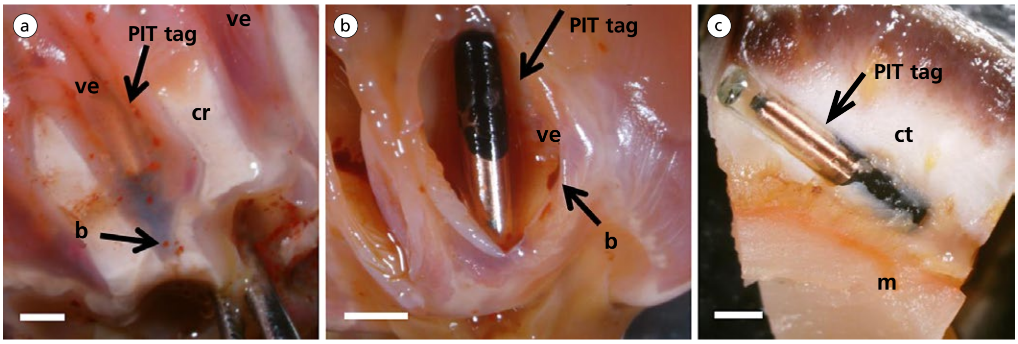
FIGURE 15

Marking individuals of the sea cucumber *Cucumaria frondosa* with PIT tags

(a–b) PIT tags in the vesicle of the tentacle of the aquapharyngeal bulb, and (c) PIT tags in the connective tissue between the epidermis and muscle tissues of the body wall. Labels: b = brown body, cr = calcareous ring, ct = connective tissue, m = longitudinal muscle band, ve = vesicle of the tentacle. Scale bars represent 2 mm



Source: Gianasi, B.L., Verkaik, K., Hamel, J.-F. & Mercier, A. 2015. Novel Use of PIT tags in sea cucumbers: Promising results with the commercial species *Cucumaria frondosa*. PLOS ONE, 10(5): e0127884.

5. Conditions tolerated and preferred by *Cucumaria frondosa*

5.1 TEMPERATURE

Sea cucumbers like *Cucumaria frondosa* do not generate heat or control their own body temperature as humans do; they match the temperature of the environment. Animals with this type of thermal physiology are generally known as ectotherms. Adults of *C. frondosa* normally prefer to stay in areas with seawater temperatures between -1 and 13 °C. Under laboratory conditions, individuals exposed to temperatures above this limit can only survive for short periods (So *et al.*, 2010). The process of fertilization (i.e. when spermatozoa merge with an oocyte) and the subsequent development of embryos and larvae, is also affected by temperature (see Section 7 for details).

5.2 LIGHT INTENSITY

Adults of *Cucumaria frondosa* can tolerate light conditions up to 560 lux (Sun *et al.*, 2020b), which is equivalent to typical room or office illuminance, and do not exhibit any clear preference for either lighted or shaded areas in laboratory trials. Unsurprisingly, they can be found almost everywhere as long as substrate is available to facilitate their anchoring. However, *C. frondosa* actively moves chiefly during the night, which may point to a slightly nocturnal lifestyle, perhaps as a protective strategy against predators, particularly large diurnal hunters, such as seals, walruses (Hamel and Mercier, 2008) and cod (DFO NL, personal communication).

In contrast to adults, newly-settled juveniles tend to avoid direct exposure to light by hiding inside crevices or underneath stones (Hamel and Mercier, 1996d; Hamel *et al.*, 2023; Montgomery, Hamel and Mercier, 2018). Tolerance of light intensity steadily increases as juveniles grow from 1.8 to 4.5 mm in body length between 6 and 21 months old (Gianasi, Hamel and Mercier, 2018a). They remain cryptic (hidden) until they reach a length of approximately 35 mm (when they are roughly 24 months old), after which they will emerge on the surface of the rocks or shells and behave more like adults (Hamel and Mercier, 1996d). More precisely, Gianasi, Hamel and Mercier (2018a) reported that tolerance to light increased with age, from 25 lux in 1-month-old to >50 lux in 6, 12, and 21-month old individuals. The photo-negativity in small juveniles means they seek under surfaces, likely to minimize predatory pressure from sea stars, sea urchins and large polychaetes worms.

5.3 SALINITY

Cucumaria frondosa, like other members of the echinoderm phylum, is a strictly marine species. It usually occurs in areas with salinities between 31–35 psu, which are typical of oceanic conditions. However, *C. frondosa* can tolerate lower salinities down to 26 psu for a short period of time (Hamel and Mercier, 1996d), although it may be detrimental if the exposure is prolonged.

Scientists have shown that the free-swimming embryos and larvae of *C. frondosa* can cope with salinities between 24 and 34 psu. However, the optimal salinity for developmental rate was established at 26 psu, while salinities between 20 and 24 psu were lethal (Hamel and Mercier, 1996d). These results indicate that embryos and larvae have a greater capacity to cope with low salinities than adults.

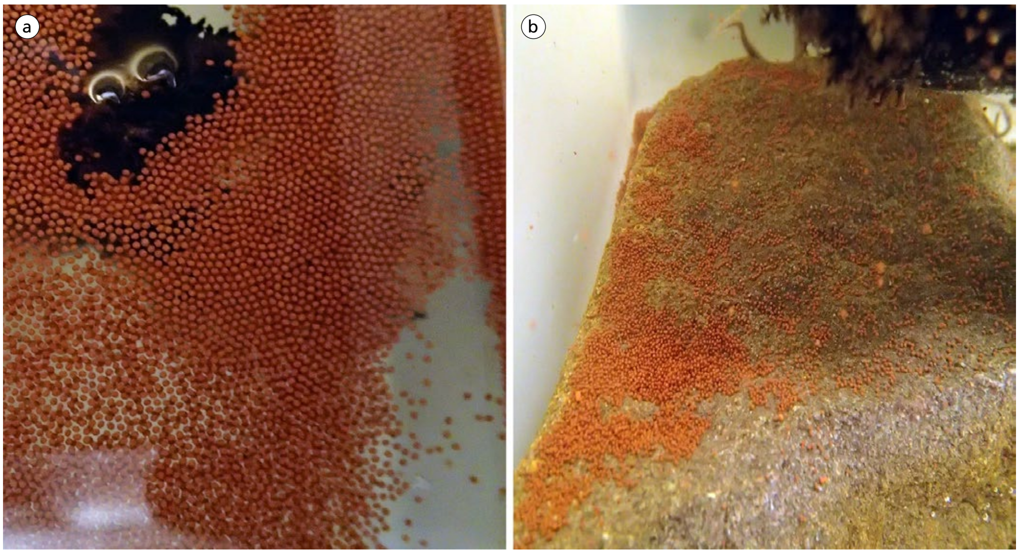
5.4 pH LEVELS

The pH scale is used to measure how acidic or basic a solution is on a scale of 0 to 14, with 7 being neutral, lower values being acidic and higher values being basic. Seawater has a typical pH around 8 (slightly basic) but, depending on local conditions, can vary between 7.5 and 8.5. *Cucumaria frondosa* tends to live in seawater with a pH of 8 (Hamel and Mercier, 1996d). Should the pH of the ocean decrease (ocean acidification) as anticipated in the coming decades, how will *C. frondosa* cope? It is nearly impossible to predict, but exposure of adults of *C. frondosa* to low pH over several months showed that the eggs they produced were abnormal, the embryos sunk and developed poorly, ultimately resulting in 100 percent mortality before the blastula stage (Figure 16) (Verkaik, Hamel and Mercier, 2016). Trans-generational effects are therefore likely to occur. In rearing trials, fertilization and embryonic development did not occur at pH levels below 7.5 (Hamel and Mercier, 1996d). The optimum pH was determined to be 8 and the embryos and larvae were able to survive when exposed to pH between 8.5 and 9, although they grew more slowly than at the optimal pH.

FIGURE 16

Spawning of the sea cucumber *Cucumaria frondosa* under different pH conditions

(a) Positively buoyant oocytes floating at the surface under normal pH conditions.
(b) Negatively buoyant oocytes sinking to the bottom of tank under low pH conditions.
Red-orange oocytes measure 500–600 µm in diameter



Source: Verkaik, K., Hamel, J.-F. & Mercier, A. 2016. Carry-over effects of ocean acidification in a cold-water lecithotrophic holothuroid. *Marine Ecology Progress Series*, 557: 189–206.

5.5 HYDROSTATIC PRESSURE

Pressure level underwater is known as hydrostatic pressure. It can be measured in pascals, bars, or atmospheres and it increases with depth because of the downward force applied by gravity (for instance pressure increases by about 1 atmosphere every 10 metres). Laboratory work has shown that *Cucumaria frondosa* can survive well at a pressure representative of twice its usual depth of occurrence for 24 hours, but such high pressure becomes detrimental or lethal after 3 days (Ammendolia, Hamel and Mercier, 2018). Individuals that were pressurized showed behaviours indicative of stress: reduced feeding activity, slower cloacal movement (respiration), and took longer to anchor on the substrate. However, there did not seem to be lasting side-effects on the survivors once they were brought back to surface pressure or pressures that were more typical for them. This suggests that *C. frondosa* can cope with a broad range of depths, at least for short periods (Ammendolia, Hamel and Mercier, 2018). It may also explain why the species is not common at depths greater than 300 m.

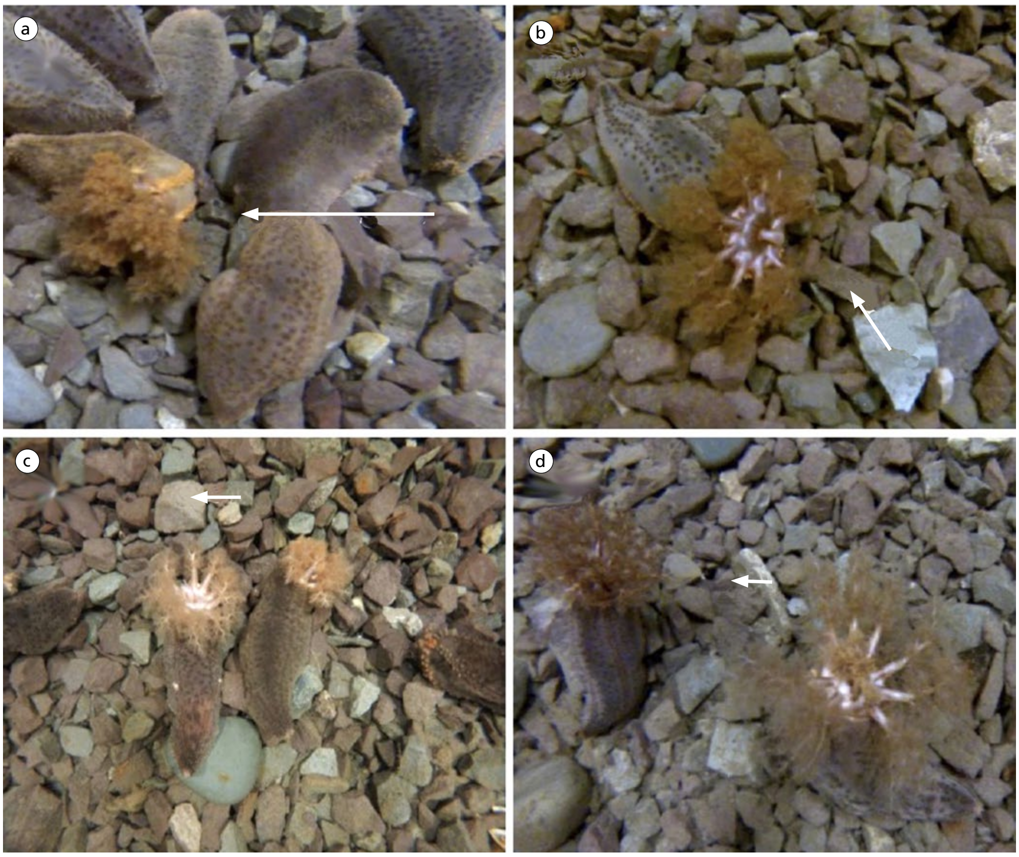
5.6 WATER CURRENT

Adults of *Cucumaria frondosa* are sensitive to water movement. In large-scale mesocosm experiments, they moved away from static conditions or low water current under 20 cm/s and inversely fled the strongest flows (>40 cm/s), preferring in-between values (Sun, Hamel and Mercier, 2018). Moreover, the feeding tentacles of individuals in areas with flows of ≥40 cm/s were aligned with the direction of the current, whereas in flows <40 cm/s, they were typically perpendicular to the direction of flow. In both cases the posture seemed to help particulate food capture. Tentacle deployment and rates of tentacle insertion into the mouth (i.e. feeding) increased with flow, from 0.95 insertion/min in flows of 10 cm/s to 1.13 insertion/mins in flows of 40 cm/s (Figure 17). The settling larvae do not appear to be affected by low water flow, such that settlement rates on different types of surfaces was the same whether in turbulent or static water (Hamel and Mercier, 1996d).

FIGURE 17

Orientation of tentacles in the sea cucumber *Cucumaria frondosa* submitted to different current regimes

Arrows indicate the direction of the flow with arrow length being proportional to flow speed). (a) Tentacles following the direction of the flow when the latter was greater than 40 cm/s. (b) Tentacles facing the direction of the flow when it was 20 cm/s. (c–d) Tentacles perpendicular to the direction of the flow in currents of 10 cm/s or slower. Individuals were the typical size for the species (15.6±2.5 cm in length and a wet body mass of 292.5±35.7 g)

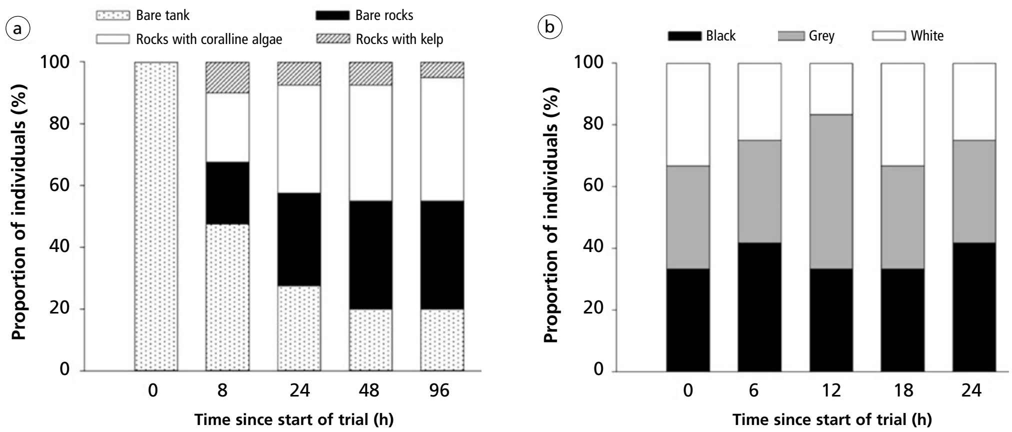


Source: Sun, J., Hamel, J.-F. & Mercier, A. 2018. Influence of flow on locomotion, feeding behaviour and spatial distribution of a suspension-feeding sea cucumber. *Journal of Experimental Biology*, 221(20): jeb 189597.

5.7 COLOUR OF THE SUBSTRATE

The response of *Cucumaria frondosa* to colours present in its environment depends on the life stage. Scientists have found that, when they were given a choice, more adult individuals tended to congregate towards darker substrates (grey and black) than white or pale substrates (Sun *et al.*, 2020b) (Figure 18). Similarly, the just-settled larvae and early juveniles (a few millimetres long) showed a clear preference for backgrounds of darker shades and avoided areas with pale substrates. However, substrate and background colour preferences in juveniles shifted slightly with age. While 1- and 6-month-old juveniles favoured black or red background colours, 12- and 21-month old juveniles showed a clearer preference for red backgrounds. White backgrounds were consistently the least preferred by all sizes of juveniles (Gianasi, Hamel and Mercier, 2018a).

FIGURE 18
Environmental preferences exhibited by the sea cucumber *Cucumaria frondosa* over time
Proportion of individuals found on (a) different types of substrata, and (b) different background colours over time



Source: Sun, J., Hamel, J.-F., Stuckless, B., Small, T. & Mercier, A. 2020b. Effect of light, phytoplankton, substrate types and colour on locomotion, feeding behaviour and microhabitat selection in the sea cucumber *Cucumaria frondosa. Aquaculture*, 526: 735369.

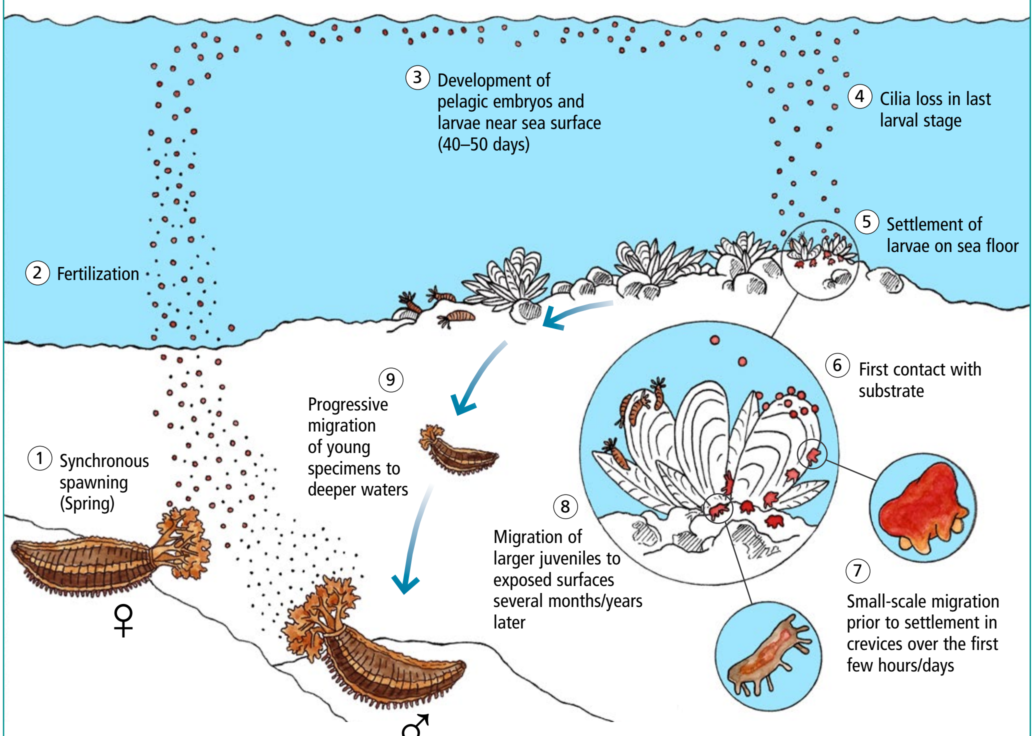
6. Life cycle of *Cucumaria frondosa*

6.1 GAMETES AND FERTILIZATION

Like most other marine animals, the sea cucumber *Cucumaria frondosa* exhibits a complex life cycle involving many different stages (Figure 19). The cycle can be said to begin when adult males and females release their gametes (i.e. spermatozoa and oocytes) in the water column as is typical of broadcast spawners (also called free spawners) (Figure 20). Mature males and females in the same location spawn around the same time (Hamel and Mercier, 1995). However, at the finest scale, males start to spawn first, creating a dense white cloud in the water, and oocytes are released by the females shortly afterwards (Hamel and Mercier, 1996b; Mercier and Hamel, 2010). The entire process of spawning can be as short as 30 minutes or it may last a few hours (Coady, 1973; Hamel and Mercier, 1995; Mercier and Hamel, 2010).

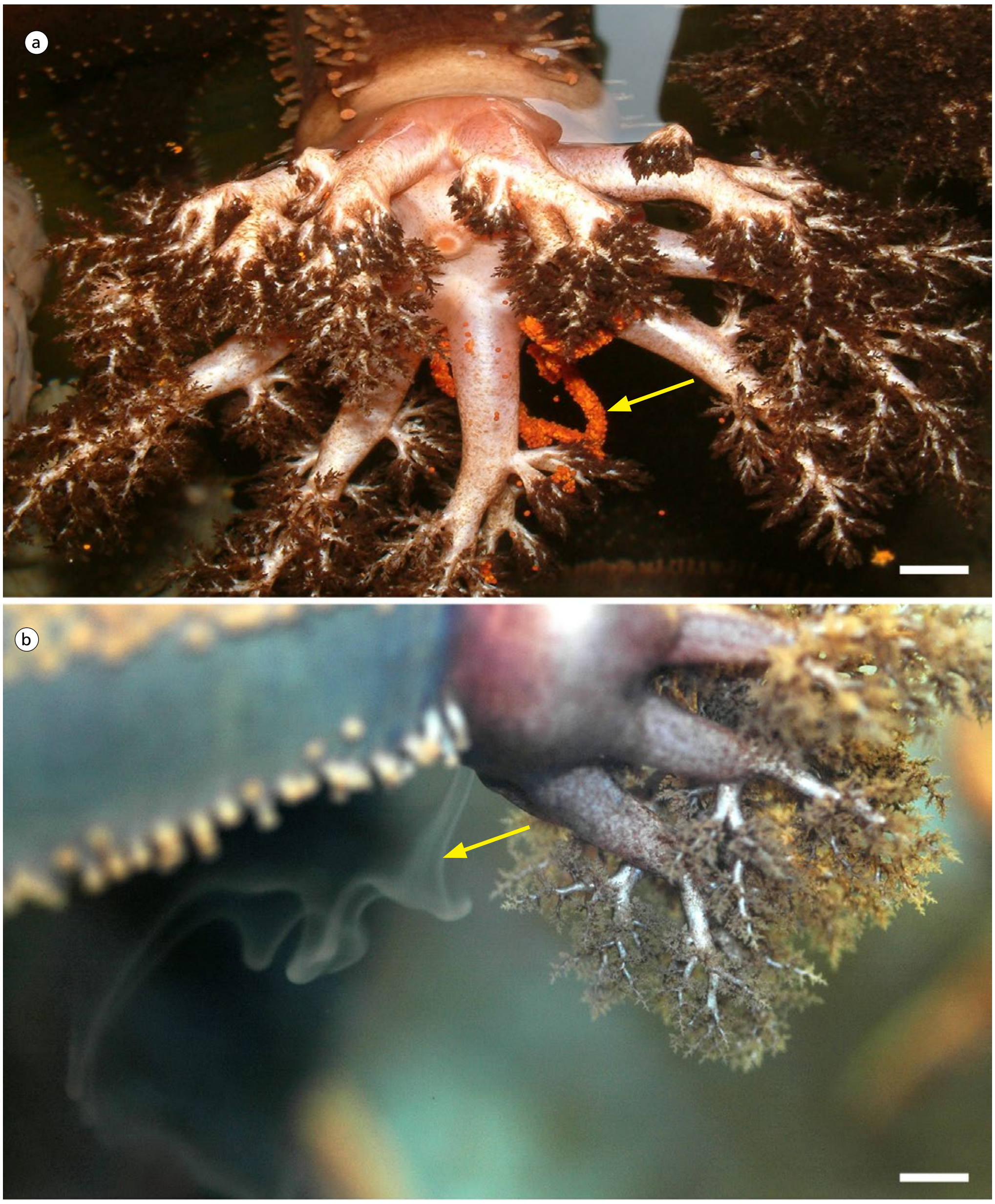
Oocytes and spermatozoa encounter each other and merge together in the open water floating with the current, undergoing a process known as external fertilization. The greater the concentration of spermatozoa, the higher the chances of successful fertilization. However, beyond a certain concentration of spermatozoa (≥25 000/ml), a given oocyte runs greater risks of getting fertilized by multiple spermatozoa, a phenomenon known as polyspermy, which can prevent normal development and lead to mortality. Oocytes and eggs are bright orange or red and they are positively buoyant, which allows them to gather near the surface of the ocean. Scientists discovered that approximately 80–100 percent of the oocytes were fertilized during the monitoring of a natural spawning event in the field (Hamel and Mercier, 1996b).

FIGURE 19
Simplified diagram illustrating the life cycle of the sea cucumber *Cucumaria frondosa*



Source: Authors' own elaboration.

FIGURE 20
Spawning in the sea cucumber *Cucumaria frondosa*
(a) Release of bright red-orange oocytes (arrow) by a female, and (b) release of spermatozoa (arrow) by a male. Scale bars represent 1.5 cm



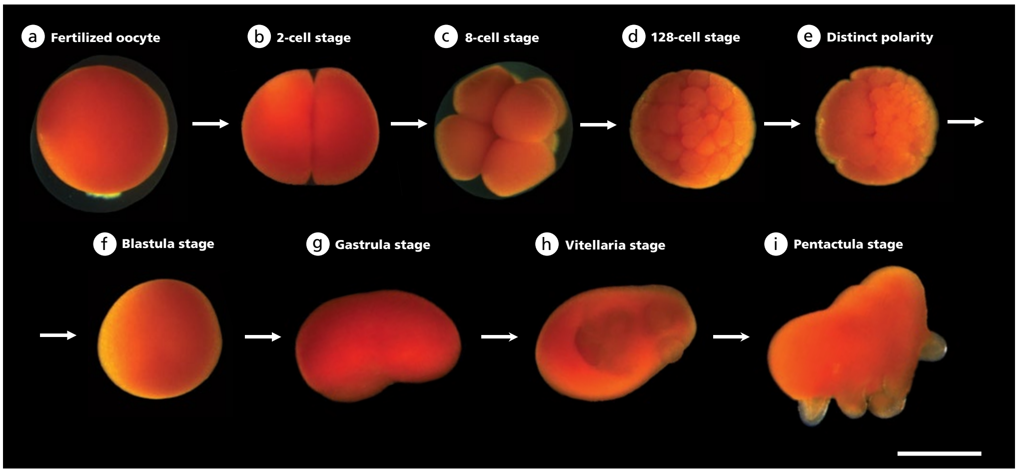
6.2 EMBRYONIC AND LARVAL STAGES

Post fertilization, the eggs of *Cucumaria frondosa* undergo successive cell divisions, going through 2-cell, 4-cell, 8-cell, 16-cell stages, and so on (Figure 21a–d). Within two days post fertilization, they reach the blastula stage (Table 2), which is a dense sphere composed of hundreds of cells, measuring 600–1 350 µm (0.60–1.35 mm) in diametre (Figure 21f). At about 4 to 10 days post-fertilization, the embryo becomes more complex and is called a gastrula (Table 2; Figure 21g), which is bean-shaped and measures 850–1 600 µm (0.85–1.60 mm) in length. Between days 7 and 18 post-fertilization the gastrula develops into the vitellaria/doliolaria (Table 2; Figure 21h), a larval stage measuring 900 and 1 550 µm (0.90–1.55 mm) in length that displays the early features of the tentacles. Around days 10 to 29, the larva reaches a stage called pentactula (Table 2); where "penta" (meaning 5) is in reference to the number of tentacles (Figure 21i). Between days 15 and 32 post-fertilization, the late pentactula also possesses two tube feet. As it develops and grows, the pentactula larva becomes less buoyant and is found closer to the seafloor in preparation for transition from an open-water (or pelagic) to a bottom-dwelling (or benthic) existence. Overall, depending on prevailing environmental conditions, it can take between 5 and 7 weeks for the

FIGURE 21

Development of the sea cucumber *Cucumaria frondosa* from a fertilized oocyte (egg) to a pentactula larva

(a) fertilized oocyte; (b) first cell division; (c) 8-cell stage; (d) 128-cell stage; (e) asynchronous cleavages of the blastomeres; (f) newly-hatched blastula covered with cilia; (g) last gastrula stage covered with cilia and undergoing elongation; (h) vitellaria larval stage with two ambulacral podia and the vestibule; (i) pentactula larval stage with ambulacral podia and rudimentary tentacles. Scale bar represents 500 µm



Source: Gianasi, B.L., Hamel, J.-F., Montgomery, E.M., Sun, J. & Mercier, A. 2021. Current knowledge on the biology, ecology, and commercial exploitation of the sea cucumber *Cucumaria frondosa. Reviews in Fisheries Science and Aquaculture*, 29(4): 582–653.

TABLE 2

Developmental tempo and mean size (± one standard deviation) of embryos and larvae of the sea cucumber *Cucumaria frondosa* under laboratory conditions. Ambient temperatures ranged from 6 to 13 °C in Québec (Canada) and from -1 to 1 °C in Newfoundland (Canada)

	Québec (St. Lawrence Estuary)[1]		Newfoundland (offshore individuals)[2]		Newfoundland (inshore individuals)[3]	
Developmental stage	Size (µm)	Time (h)	Size (µm)	Time (h)	Size (µm)	Time (h)
Spawned oocyte	900 ± 200	0	700 ± 100	0	550 ± 50	0
Fertilized oocyte	1 400 ± 300	0.08 ± 0.03	730 ± 200	0.1 ± 0.03	560 ± 50	0.05 ± 0.01
2-cell	1 300 ± 300	6.1 ± 1.1	800 ± 100	5.1 ± 0.9	560 ± 50	5.0 ± 1.0
4-cell	1 350 ± 400	8.5 ± 1.3	800 ± 100	7.3 ± 1.1	560 ± 50	9.0 ± 3.0
Morula	1 300 ± 500	35.0 ± 2.4	800 ± 100	22.0 ± 2.0	560 ± 50	48.0 ± 8.0
Blastula (fully formed)	1 350 ± 300	48.0 ± 3.6	900 ± 100	41.0 ± 4.2	600 ± 70	72.0 ± 19.0
Early gastrula	1 300 ± 300	72.0 ± 8.5	800 ± 100	65.0 ± 6.0	580 ± 50	192.0 ± 48.0
Elongated gastrula	1 600 ± 500	5.5 ± 0.5 days	1 500 ± 200	4.0 ± 1.0 days	850 ± 60	10.0 ± 3.0 days
Vitellaria (doliolaria)	1 550 ± 300	8.0 ± 1.0 days	1 500 ± 300	7.0 ± 1.0 days	900 ± 80	18.0 ± 4.0 days
Early pentactula (5 tentacles)	1 300 ± 300	11.0 ± 1.5 days	1 200 ± 200	10.0 ± 2.0 days	890 ± 55	29.0 ± 4.0 days
Late pentactula (5 tentacles and 2 podia)	1 400 ± 500	17.0 ± 1.4 days	1 300 ± 200	15.0 ± 1.5 days	950 ± 60	32.0 ± 5.0 days
Newly-settled juvenile	1 400 ± 400	~46 days	1 300 ± 200	~35 days	950 ± 70	49.0 ± 4.0 days

Sources:

[1] Hamel, J.-F. & Mercier, A. 1996b. Gamete dispersion and fertilisation success of the sea cucumber *Cucumaria frondosa. SPC Beche-de-mer Information Bulletin*, 8: 34–40.

[2] So, J.J., Hamel, J.-F. & Mercier, A. 2010. Habitat utilisation, growth and predation of *Cucumaria frondosa*: implications for an emerging sea cucumber fishery. *Fisheries Management and Ecology*, 17: 473–484.

[3] Gianasi, B.L., Hamel, J.-F. & Mercier, A. 2018a. Morphometric and behavioural changes in the early life stages of the sea cucumber *Cucumaria frondosa. Aquaculture*, 490: 5–18.

development of *C. frondosa* to be completed, from fertilization in the water column to settlement onto the seabed (Hamel and Mercier, 1996d; So *et al.*, 2010). Of note is the fact that different embryos can fuse together in the early stages of development in a process called chimerism, which increases their size significantly (Box 5).

BOX 5

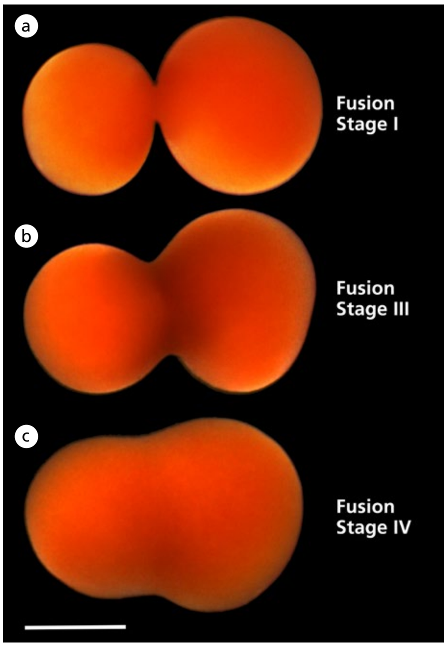
Embryonic fusion and chimaeras

Early life stages of *Cucumaria frondosa* are able to fuse together when held in cultures under laboratory settings. Fusion always occurred at the blastula stage (~5 days post fertilization), not in earlier (unhatched) or later (embryonic or larval) stages (Gianasi, Hamel and Mercier, 2018b). At the onset of this phenomenon, the two embryos are attached to each other but are still visually distinct. Slowly, the fusing embryos assume a bean shape and eventually a normal shape, leaving no trace of being the product of two different embryos (Figure 22). However, these whole-body chimaeras (i.e. individuals composed of genetically distinct cells) are larger, forming what might be considered super embryos, or eventually mega larvae. It is still unclear how frequent this fusion occurs in nature, but it might explain the large variation in size observed in young sea cucumbers belonging to the same cohort.

FIGURE 22

Fusion of embryos at the blastula stage in the sea cucumber *Cucumaria frondosa*

(a) A diffuse bond is present at Stage I. (b) The bond develops into an increasingly solid tissue connection between fused embryos at Stage III. (c) Stage IV shows an almost complete fusion. Full fusion of embryos is attained about 15 d post-fertilization. Scale bar represents 300 µm



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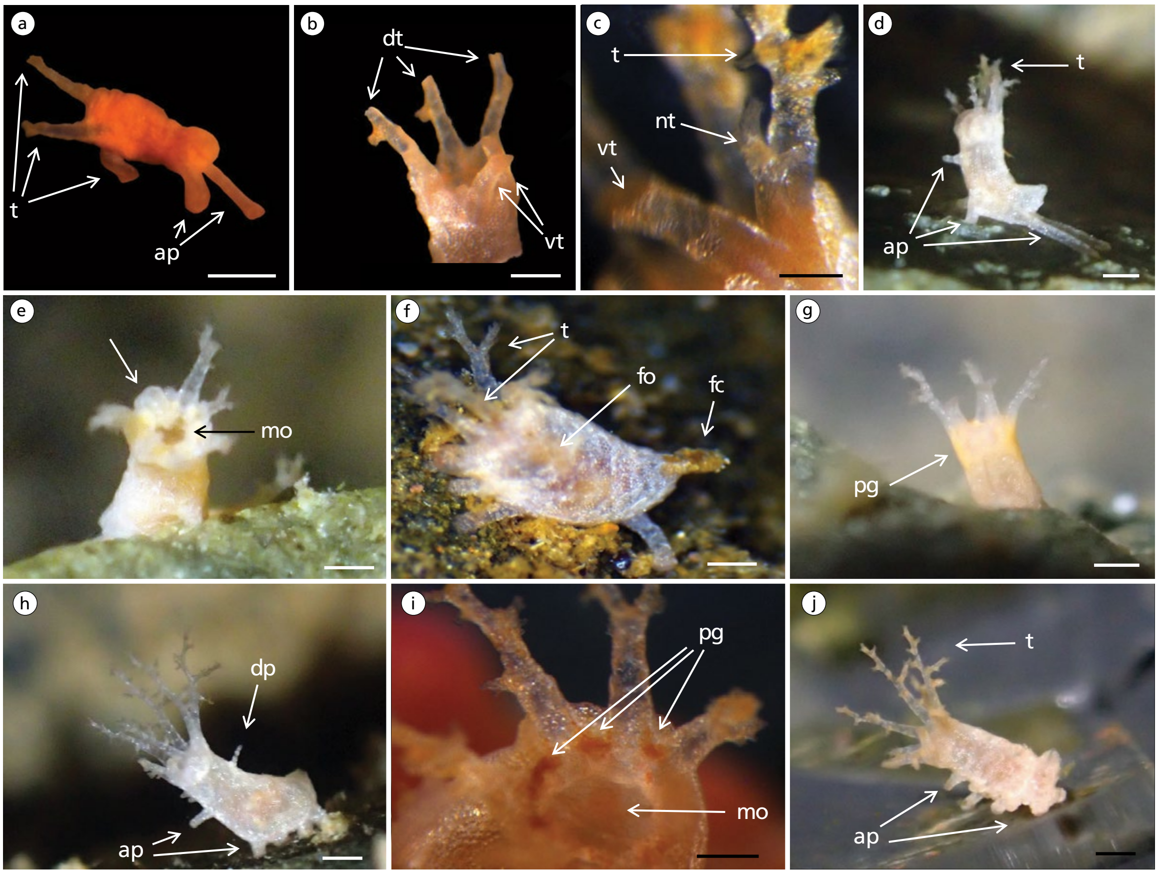
6.3 JUVENILES AND ADULTS

When it is ready to settle on the seafloor, the still-swimming pentactula larva of *Cucumaria frondosa* actively searches for a suitable habitat (Figure 21i). Within the first two days following initial contact with a suitable substrate on the seafloor (generally stones or mussels), the tiny newly-settled sea cucumber seeks a micro-habitat characterized by low light (for example, crevices or under surface of stones or shells). That very early life stage is photo-negative, searching for shaded habitats where it can shelter (Figure 19). As soon as the new recruit begins to feed on its own, it can be called a juvenile. By three months of age, the juvenile has developed five tentacles and two pairs of tube feet; after four months, it will have five pairs or a total of 10 tube feet. The ten buccal tentacles typical of the species can take about 21 months to appear (Figure 23) (Gianasi, Hamel and Mercier, 2018a; Hamel and Mercier, 1996d). The juvenile must grow for at least two years to reach a body length of about 35 mm (Figure 24) (Hamel and Mercier, 1996d; Montgomery, Hamel and Mercier, 2018). Beyond this size, the juvenile can be found relatively exposed on the seafloor like on the surface of pebbles or the shell of mussels (Hamel *et al.*, 2023). Still sexually immature, the young sea cucumber develops into a mature individual after a period that takes at least three years, likely longer (Figure 24). At that stage, it can be called an adult, although it may still be of a small size (between 8–10 cm long), and it will take years still to reach the maximum size of the species (Figure 24) (Hamel and Mercier, 1996d).

FIGURE 23

Development of the sea cucumber *Cucumaria frondosa* from a 1-month-old to a 21-month-old juvenile

(a) 1-month-old with tentacles and ambulacral podia, (b) three ramified dorsally-oriented tentacles for feeding and two non-ramified ventrally-oriented tentacles, (c) development of a new tentacle between a ramified and a non-ramified tentacles, (d) 6-month-old juvenile with seven tentacles and five ambulacral podia, (e) feeding behaviour of a 6-month-old juvenile with a tentacle inserted inside the mouth (arrow without a label), (f) ingested food can be seen through the semi-transparent body wall and discharge of fecal matter through the anus of a 6-month-old juvenile, (g) 8-month-old juvenile with yellow pigmentation on skin around the oral cavity, h) 12-month-old juvenile with the first appearance of a dorsal podium, (i) 16-month-old juvenile with of dark brown pigmentation among its tentacles, (j) 21-month-old juvenile with ten ramified tentacles and nine ambulacral podia. Labels: ap = ambulacral podium, dp = dorsal podium, dt = dorsally-oriented tentacle, fc = discharge of fecal matter, fo = food particles, mo = mouth, nt = new tentacle, pg = pigmentation, t = tentacle, vt = ventrally-oriented tentacle; scale bars represent 0.5 mm

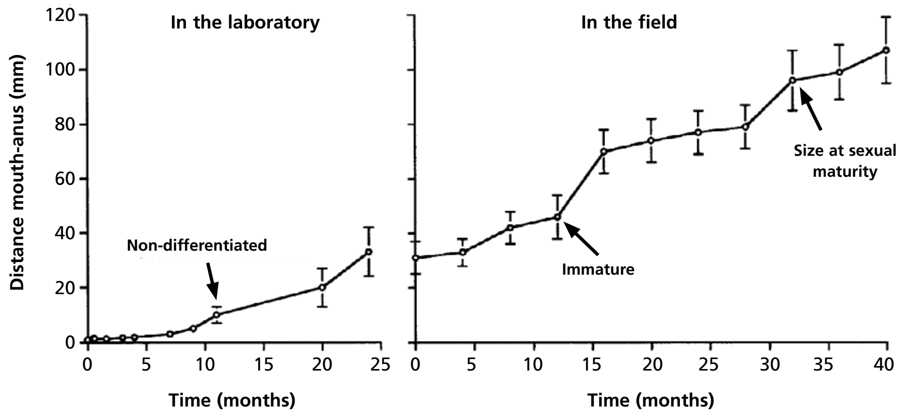


Source: Gianasi, B.L., Hamel, J.-F. & Mercier, A. 2018a. Morphometric and behavioural changes in the early life stages of the sea cucumber *Cucumaria frondosa*. *Aquaculture*, 490: 5–18.

FIGURE 24

Growth in length (distance from mouth to anus) of embryos and juveniles of the sea cucumber *Cucumaria frondosa* in the laboratory (simulating natural environmental conditions) for 24 months and in the field (at 20 m depth) for 40 months

Under laboratory conditions, individuals were monitored from fertilization to a length of ~35 mm (n = 30–40); under field conditions, collected individuals of ~35 mm in length were monitored until a length of ~110 mm (n = 80–90); error bars represent 95% confidence interval



Source: Hamel, J.-F. & Mercier, A. 1996d. Early development, settlement, growth, and spatial distribution of the sea cucumber *Cucumaria frondosa* (Echinodermata: Holothuroidea). *Canadian Journal of Fisheries and Aquatic Sciences*, 53: 253–271.

7. Sexual reproduction in *Cucumaria frondosa*

7.1 SEXUAL MATURITY AND SPAWNING

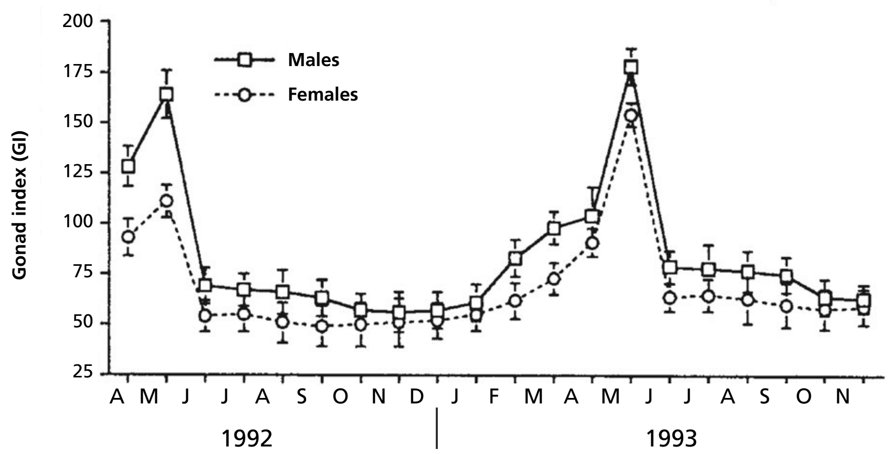
The time needed for *Cucumaria frondosa* to develop the ability to reproduce sexually (reach sexual maturity) has been estimated to be relatively long. In the Estuary and Gulf of St. Lawrence River in Québec, Canada, individuals are generally sexually mature when they reach a body wall weight above 55 g or about 8–10 cm in body length (Figure 24) (Hamel and Mercier, 1996c). Off the coast of insular Newfoundland, Canada, sexual maturity is attained when individuals reached a body length of around 9–11 cm (Grant, Squire and Keats, 2006). In the Barents Sea of northern Europe, sexual maturity reportedly begins at around 47–60 g (Gudimova and Antsiferova, 2006) and it was established to be reached at a lenght of ≥13 cm in the Canadian Artic (Hamel *et al*., 2023). Based on the current knowledge, it may take at least three years, possibly longer, to reach these sexually mature sizes (Hamel and Mercier, 1996d; So *et al*., 2010). Such knowledge forms a crucial part of science-based management strategies (Box 6).

Photoperiod (the length of daylight) and water temperature are the factors associated the most strongly with reproduction in *C. frondosa*. For example, in Québec (Canada), the reproductive cycle is triggered when water temperature is around 0 °C and photoperiod begins to increase in January. Adults begin the process of gamete synthesis, termed gametogenesis, which will ensure they have mature gametes (oocytes in females and spermatozoa in males) ready for the spawning season several months later. As described in the reproductive system in Section 2.11, the gonad of *C. frondosa* is composed of many tubules that evoke noodles. The sea cucumbers found on the east coast of New Brunswick down south to the Isles of Shoals (New Hampshire, United States of America), and southern Newfoundland, exhibit gonad tubules that develop homogeneously; they develop mature gametes inside a single year. However, the gonad of individuals sampled at high latitudes (Labrador Coast) and down to the Chaleur Bay (Québec), including the north shore of Newfoundland, are divided in two classes of tubules (small and large). This is because it takes two full years rather than one to synthesize mature gametes in populations from these locations, presumably as a result of environmental conditions (Hamel and Mercier, 1996c).

Irrespective of how long it takes to develop mature gametes, the ripe gonad (or gonad section) of adult sea cucumbers at the time of spawning is visually larger and more colourful (pinkish in males and reddish in females). The ratio of gonad weight to sea cucumber body weight, known as the gonad index or GI, is one of the most common indices used to approximate the reproductive state and the time of spawning for a given population (Mercier and Hamel, 2009). Correspondingly, a sudden drop in the gonad index value can be detected in a population immediately following a spawning event because the spent gonad would have a decreased size and weight (Figure 25) (Hamel and Mercier, 1996c; Singh *et al.*, 2001).

From a management perspective, it is important to gain a good understanding of local spawning seasons (Box 6). *Cucumaria frondosa* spawns once a year between February and July, depending on the region, when a majority of mature adults within an area undergo what is referred to as synchronous or mass spawning. For instance, in eastern Canada, spawning occurs on or around a full moon between February and May in Newfoundland waters (Mercier and Hamel, 2010), between March and April in Maine (United States of America), between April and May in New Brunswick, and

FIGURE 25
Seasonal variation in gonad index in males and females of the sea cucumber *Cucumaria frondosa* from April 1992 to November 1993; error bars represent 95% confidence intervals



Source: Hamel, J.-F. & Mercier, A. 1996c. Gonad morphology and gametogenesis of the sea cucumber *Cucumaria frondosa. SPC Beche-de-mer Information Bulletin*, 8: 22–33.

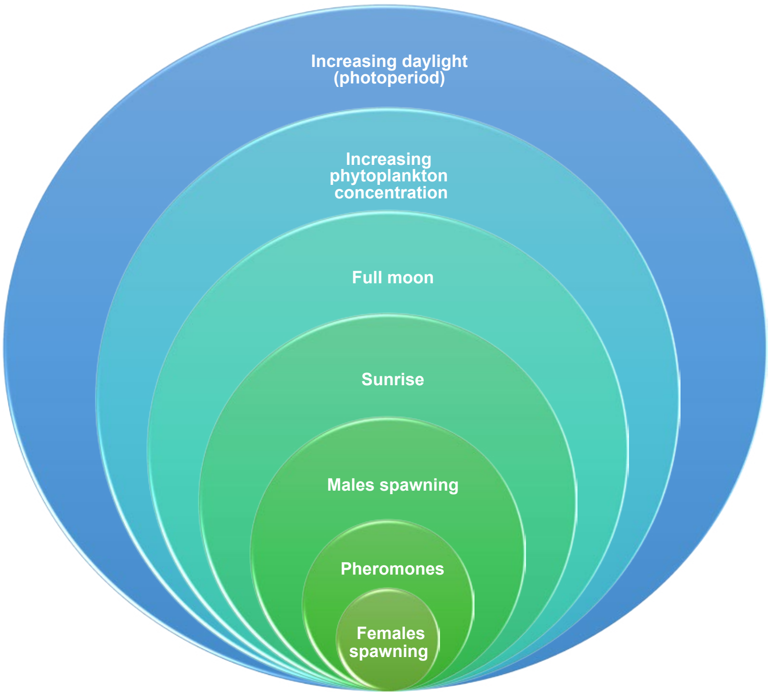
BOX 6
Science-based recommendations for harvesting size and season

The management of fisheries for *Cucumaria frondosa* is currently fairly permissive in most regions. Québec is the only province in Canada with legally mandated size restrictions on harvested sea cucumbers, which must be larger than 11.4 cm (just above the size at sexual maturity). Based on the estimated size at maturity (Grant, Squire and Keats, 2006; Hamel and Mercier, 1996d), the recommended minimum body length should be above 10–11 cm in all regions. Efforts to design fishing gear that reduce the probability of harvesting undersized individuals should be carried out. Returning undersized individuals to the sea post-harvest would only be recommended if the survival rate is sufficiently high. As for the fishing season, it should ideally not overlap with the peak of the reproductive season. The development of spermatozoa and oocytes (or gametogenesis) in *C. frondosa* begins in January and spawning ensues at some point between February and July, depending on the region (Gianasi *et al*., 2021). The conservative seasonal window for harvest would thus be from August (safely in the post-spawning period) to October-November, before the next onset of vitellogenesis, which corresponds to the final phase of gamete maturation when the female sexual cells are becoming larger and full of yolk.

in June in Québec waters (DFO, 2021d; Gianasi, Hamel and Mercier, 2019c; Hamel and Mercier, 1995; Hamel and Mercier, 1996b). Elsewhere such as in the waters off the coast of Iceland, the species spawns between the months of May and July (MFRI, 2022).

What tells sea cucumbers that it is time to spawn their gametes all together at the same time? The simplified answer to this complex question is environmental conditions combined with inter-individual communication through pheromones (Figure 26). Scientists have determined that throughout the long months of gamete synthesis, males and females continuously exchange chemical messages to make sure that gamete maturation, and ultimately spawning, is well synchronized (Hamel and Mercier, 1996a; Hamel and Mercier, 1999). When sea cucumbers have nearly completed gametogenesis and all individuals are reaching the mature stage, at least some of them become very sensitive to their environment. The increase in phytoplankton concentrations at the onset or peak of the spring bloom identifies the month(s) in which to spawn (Hamel and Mercier, 1995; Jordan, 1972). The telltale factor is probably the concentration of pigment (chlorophyll-α) that reaches its annual maximum, around 3 mg/m^3 (Hamel and Mercier 1995). Once that is determined, the monthly lunar phase establishes the day(s) during which the spawning event could happen (Hamel and Mercier, 1995; Mercier and Hamel, 2010). Finally, individuals will typically spawn during a specific time of day determined by finer light and temperature cues; morning is typical for *C. frondosa*.

FIGURE 26
Schematic view of layered abiotic and biotic cues that seem to drive gametogenesis and spawning in the sea cucumber *Cucumaria frondosa*



Source: Authors' own elaboration.

Spawning in *C. frondosa* was shown to reliably occur around the first spring full moon, indicating that lunar periodicity plays an important role in synchronizing the release of gametes (Mercier and Hamel, 2010). For instance, synchronized spawning in the wild was observed in Bar Harbor, Maine (United States of America), when individuals released gametes around the full moon in 2009 and 2010 (Ross, 2011). Interestingly, Mercier and Hamel (2010) observed that many boreal marine invertebrates (across six phyla), including *C. frondosa*, can respond to the same spawning cues and release gametes within the same period (e.g. same-day multi-species spawning). Observation of spawning events in mesocosms containing several species of echinoderms, molluscs, cnidarians, and ascidians suggested that *C. frondosa* has a species-specific spawning window set apart from that of other species by a few hours. These results suggest that spawning of one species might act as an interspecific cue on *C. frondosa* and help regulate the optimal time of spawning (Hamel and Mercier, 1995; Mercier and Hamel, 2010). On a daily scale, data on tidal oscillation in the St. Lawrence Estuary (eastern Québec) indicated that the first isolated spawning of males and females coincided with the slack tide. Generally, males began to spawn at sunrise. Females began to spawn soon after, when the spermatozoa concentration in the water column was already high (Hamel and Mercier, 1995). Spawning generally began with a few individuals, spreading and intensifying like a wave. Spawning became epidemic in males following the direct influence of sperm from their neighbours, presumably as pheromones or other chemical cues were emitted by other spawning individuals (Figure 26). The female spawning also began with a few isolated events before becoming epidemic. It is now clear that various elements work synergistically at various levels to orchestrate the spawning of *C. frondosa*.

7.2 SEX RATIO

In Canada, the sex ratio is roughly equal between males and females for populations of *Cucumaria frondosa* examined in waters off the coast of Québec (Hamel and Mercier, 1996c), New Brunswick (Singh *et al.*, 2001), Newfoundland (E. Montgomery, unpublished data) and Nunavut (Hamel *et al*., 2923a). The sex ratio was also reportedly equal in the Barents Sea (Gudimova and Antsiferova, 2006). In contrast, the ratio was slightly skewed in a study conducted off Nova Scotia, eastern Canada, which found values of 1.7 females for each male (Gianasi *et al.*, 2021).

7.3 POTENTIAL REPRODUCTIVE OUTPUT

Fecundity is a measure of how many offspring an individual (usually female) can have either in a season or over its lifetime. In turn, fecundity is an important biological factor to predict recruitment levels and any changes in population size. The fecundity of females in *Cucumaria frondosa* tends to increase with body size. For instance, one study showed that small-sized females have about 300 mature oocytes ready to be spawned, compared to about 8 100 mature oocytes in large-sized females (Hamel and Mercier, 1996c). Another estimate counted between 200 000–300 000 oocytes of all sizes, both immature and mature, in the gonad of a typical adult female (Gudimova, Gudimov and Collin, 2004). However, this latter value is an overestimation of fecundity because only fully mature oocytes are susceptible to contribute to recruitment, and even this conservative estimate is an exaggeration since not all eggs will develop into viable young due to the vagaries of life in the ocean.

Laboratory studies have shown that factors such as the type and quantity of food can have impacts on the production of oocytes, or fecundity, in *C. frondosa*. Both males and females that consumed fish eggs had the highest fecundity per centimetre of gonad tubule (180 million spermatozoa; 310 000 mature and immature oocytes). Fasted sea cucumbers produced the least (30 million spermatozoa; 125 000 oocytes), whereas individuals collected from the wild and those fed on a diet of phytoplankton had intermediate fecundities (Gianasi *et al.*, 2017).

Observations from the field show that the reproductive output, as ripeness or fecundity, may vary with depth. Individuals inhabiting shallow waters at depths of around 10 m tend to have higher gonad indices than those living in deeper waters at depths of 80–100 m (Singh *et al.*, 2001). Additionally there is no evidence of mature gonads in any of the individuals collected deeper (1 200–1 450 m) which may be due to suboptimal environmental factors and limited food availability at such depths (Ross, Hamel and Mercier, 2013). This notion is supported by other experimental evidence, which demonstrated that a poor diet can delay or inhibit reproduction (Sun *et al.*, 2020a) and that individuals of *C. frondosa* react negatively to increased pressure (Ammendolia, Hamel and Mercier, 2018).

8. Growth in *Cucumaria frondosa*

8.1 GROWTH RATES IN JUVENILES

Under laboratory settings mimicking natural conditions, newly-recruited juveniles of *Cucumaria frondosa* were found to exhibit a growth rate of about 1.4 mm in body length per month (Hamel and Mercier, 1996d). A study from another region obtained lower growth rates (0.14–0.21 mm per month) suggesting that there may be differences in food supply or environmental factors among regions (Gianasi, Hamel and Mercier, 2018a; So *et al.*, 2010). In the field, older juveniles (starting body length of 35 mm) placed in experimental cages grew about 0.25 mm per month at a depth of 10 m and about 2 mm per month at a depth of 20 m (Hamel and Mercier, 1996d). These reported differences in juvenile growth between depths may again be due to differing levels and types of food supply, with or without the contribution of other environmental conditions (Figure 24).

8.2 GROWTH RATES IN ADULTS

The growth rates of small-sized adults of *Cucumaria frondosa*, with a starting body length of about 10 cm, ranged between 0.5–4 mm per month, depending on their diet under laboratory conditions (Gianasi *et al.*, 2017). Sea cucumbers experience the greatest rate of growth during the spring and summer when planktonic food is typically abundant (Gianasi, Hamel and Mercier, 2018a). Yet, under sub-optimal conditions, individuals can lose body weight and, consequently, decrease in size (So *et al.*, 2010). For instance, the body lengths of starved individuals shrunk by about 1.2 mm per month (Gianasi *et al.*, 2017). This makes the determination of size-at-age very complex, and largely speculative (Box 7).

BOX 7

The challenge of linking size and age

At present, there are no techniques to age wild-caught individuals of *Cucumaria frondosa*. In the case of cultivated or reared individuals, their age may be known by monitoring them from settlement over their first years of life. The fact that sea cucumbers in nature can grow and shrink at different rates (So, Hamel and Mercier, 2010), depending on season and food availability, means that the relationship between size and age may be highly unreliable. Surprisingly, even a cohort of individuals born in the same season and reared at the same time can have substantially differently growth rates. Although the age of another closely related species of sea cucumber can be determined using their ossicles (Sun *et al.*, 2019), the same cannot as easily be done with *C. frondosa* for the time being.

In lieu of methods to age sea cucumbers, stock assessments currently rely on body lengths, body circumference (or girth), total wet weights, and similar types of indirect measurements to monitor the populations structures and manage stocks. However, measuring size and weight also comes with a host of challenges. Live individuals can quickly contract and relax their bodies, which drastically alters their shape and renders any arbitrarily measured body length and girth inaccurate. With respect to weight, the amount of seawater held within a sea cucumber can change over a matter of seconds or minutes. Some researchers surmise that the dry weight of the body wall is probably the most reliable estimate of relative age in sea cucumbers. Optimistically, other non-lethal types of measurements, such as underwater weight (or immersed weight), indices that combine more than one measurements, and image analysis, may help establish relative age until a method to determine true age is identified (Harper *et al.*, 2020; Trenholm *et al.*, 2024).

9. Ecology of *Cucumaria frondosa*

9.1 MOVEMENT OF EMBRYOS AND LARVAE

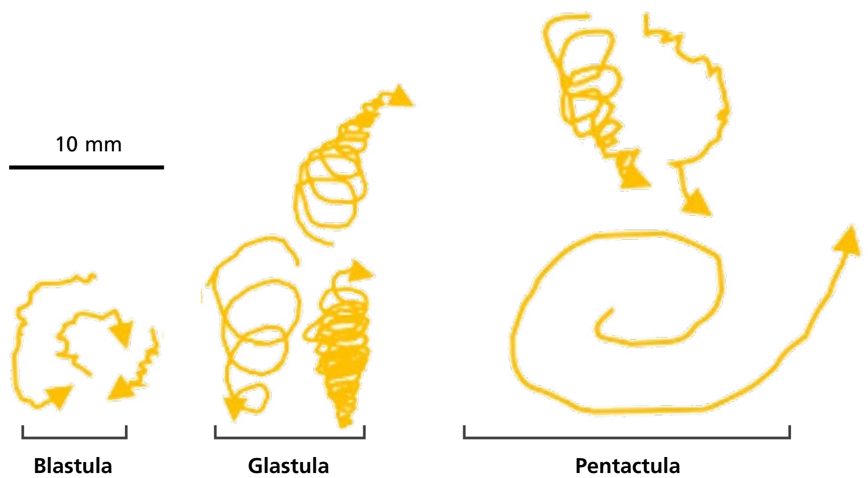
After about a week of cell divisions and growth, the embryos of *Cucumaria frondosa* develop hairlike projections called cilia, which enable them to move around (Hamel and Mercier, 1996d) The blastula and gastrula embryos move in a circular motion (Figure 27) at absolute speeds up to 0.21 mm/s (Montgomery, Hamel and Mercier, 2017; Montgomery, Hamel and Mercier, 2019), which helps them stay near the surface of the water column (i.e. prevent them from sinking) and facilitate gas exchange by continually renewing the water surrounding them. Later on, the vitellaria/doliolaria larvae actively swim in a more linear fashion at speeds of about 12 cm/h (Hamel and Mercier, 1996d). At the last larval stage, the pentactula loses its buoyancy and its cilia, and passively sinks to the seafloor. At the fastest, sinking speeds can be up to 32 cm/h (Hamel and Mercier, 1996d).

9.2 BEHAVIOUR DURING LARVAL SETTLEMENT

At or near the seafloor, the pentactula larva of *Cucumaria frondosa* searches for a place to settle, moving about in a straighter fashion compared to earlier stages (Figure 27) (Montgomery, Hamel and Mercier, 2017). The larva usually makes multiple, temporary contacts with the seafloor until it finds a suitable habitat. During this exploration phase, between 12–15 of such temporary contacts lasting about one hour can occur each day until final settlement (Hamel and Mercier, 1996d). The larva tends to settle in areas that are sufficiently lit and on hard surfaces (e.g. in rocky crevices, on gravel bottoms, or on stones or mussel shells), and avoids habitats that consist of sand or mud. Unlit conditions usually prevent final settlement indefinitely, which indicates that light is a prerequisite for the initiation of larval settlement. At the moment of definitive settlement, the larva moves towards dark or shaded areas of the seafloor, with preference for narrow crevices or other tight spaces (Hamel and Mercier, 1996d; Hamel *et al.*, 2023).

FIGURE 27

Typical swimming trajectories of the early life stages (blastula, gastrula, and pentactula) of the sea cucumber *Cucumaria frondosa* at temperatures between 1 and 3 °C and at a light intensity of 300 lux. Scale bar represents 10 mm



Source: Modified from Montgomery, E.M., Hamel, J.-F. & Mercier, A. 2017. Ontogenetic shifts in swimming capacity of echinoderm propagules: a comparison of species with planktotrophic and lecithotrophic larvae. *Marine Biology*, 164: 43.

9.3 MOVEMENT OF JUVENILES AND ADULTS

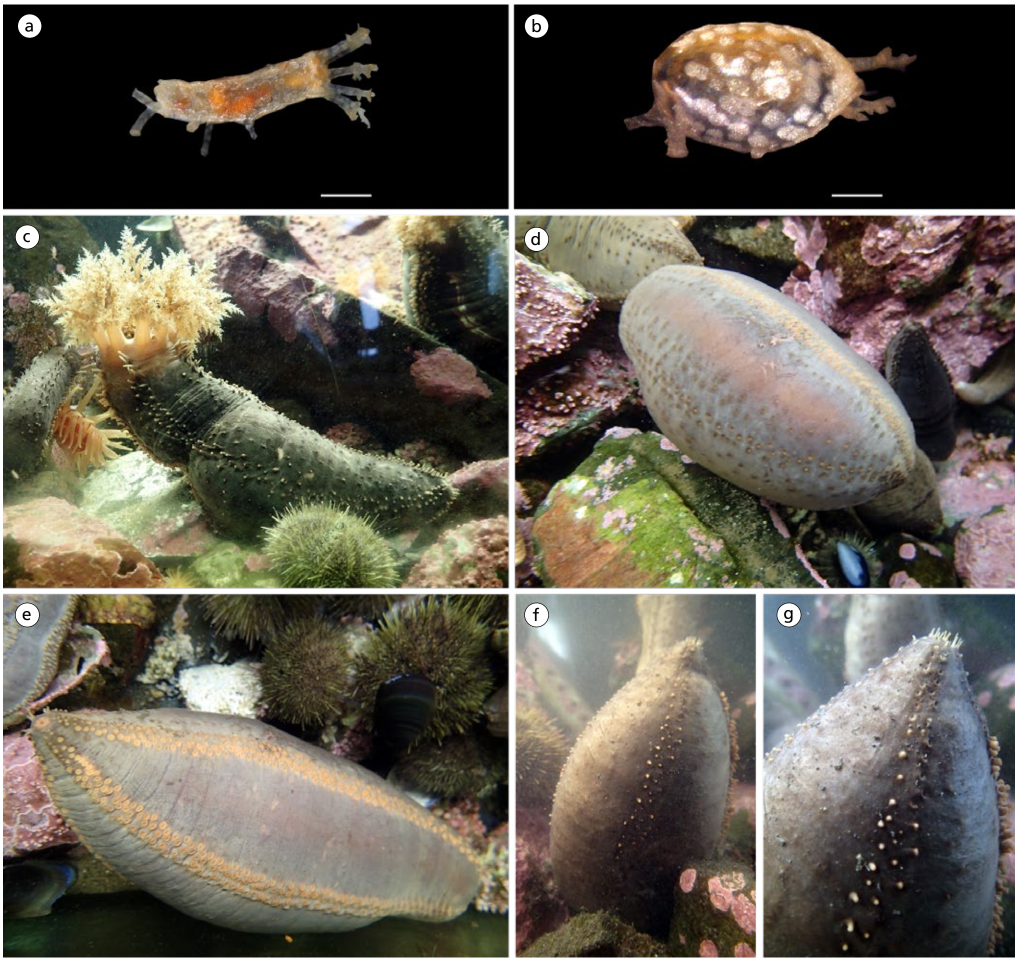
Juveniles and adults of *Cucumaria frondosa* have a so-called sedentary lifestyle, for the most part, which does not mean they do not move around. They have three main locomotion behaviours: crawling, active rolling and passive rolling (Sun, Hamel and Mercier, 2018; Sun *et al.*, 2020b). Forward crawling relies on the movement of the tube feet and contractions of the longitudinal and circular muscles, producing worm-like or peristaltic movement patterns (Edwards, 1910). Active rolling involves purposeful rolling on the longest body axis while passive rolling occurs when the sea cucumbers are neutrally buoyant and get carried by the water current. In general, their crawling speed is estimated at approximately 0.2–0.9 m/h (Sun, Hamel and Mercier, 2018; Sun *et al.*, 2020b).

It was only recently discovered that adults and juveniles of *C. frondosa* (and other species) have the ability to intentionally fill with water to increase their buoyancy and allow themselves to be moved with the currents (Hamel *et al.*, 2019). Known as active buoyancy adjustment (ABA), this behaviour increases their water to flesh ratio by up to 740 percent, essentially making them float as they let go of the substrate (Figure 28).

FIGURE 28

Comparisons of normal states and typical displays associated with active buoyancy adjustment (ABA) in the sea cucumber *Cucumaria frondosa*

(a) Normal state of a juvenile with extended tentacles, and (b) balloon-shaped juvenile undergoing ABA. (c) Normal state of an adult with anterior end in an upright position and extended tentacles, and (d) adult in the process of detaching itself from the substratum at the early stages of ABA. (e–g) Adult undergoing ABA with its posterior end shifting upwards as it becomes neutrally buoyant. Scale bars represent 0.5 mm in panels (a–b); individuals of standard adult size in (c–g)



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Source: Modified from Hamel *et al.* (2019). Hamel, J.-F., Sun, J., Gianasi, B.L., Montgomery, E.M., Kenchington, E.L., Burel, B., Rowe, S., Winger, P.D. & Mercier, A. 2019. Active buoyancy adjustment increases dispersal potential in benthic marine animals. *Journal of Animal Ecology*, 88: 820–832.

This allows currents to carry them at speeds ~1 000 times faster than those associated with forward crawling. It can be roughly estimated that their maximum movement rate could be as high as 90 km a day under the right conditions, which is up to 7 500 times further than previously thought (roughly 12 m/day) (Hamel *et al.*, 2019). In the laboratory, ABA has been triggered by high sea cucumber density, and changes in environmental conditions like lower salinity or higher turbidity (Hamel *et al.*, 2019). The presence of predators triggers a similar escape behaviour that involves an increase in body size and the onset of strong peristaltic contractions (So *et al.*, 2010).

9.4 DIET AND FEEDING BEHAVIOUR

The larvae of *Cucumaria frondosa* do not receive any nutrition through feeding. Instead, they rely on energy reserves (yolk), provided by the mother and stored in the oocytes before they are spawned, to grow and develop (Hamel and Mercier, 1996d). This type of developmental strategy is known as lecithotrophy. It is presumed to be complemented by direct (transmembrane) absorption of nutrients from the environment, although this remains largely speculative.

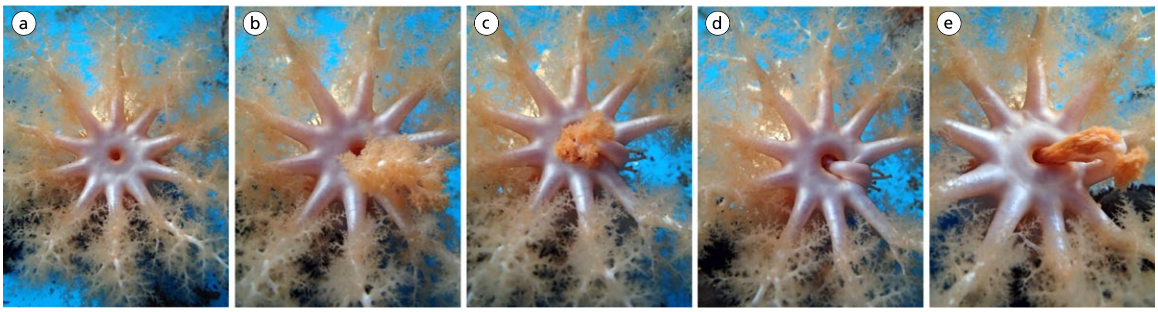
As their tentacles develop, small juveniles (under 6 months of age and 2 mm in length) can collect and assimilate organic matter that is present on the seafloor (Figure 23). Older juveniles with more developed tentacles can extend them into the water column to capture tiny, floating food particles; this feeding strategy is known as suspension feeding. The particles are trapped by the mucus on tentacles and then the particle-encased tentacles are inserted into the mouth, one tentacle at a time (Gianasi, Hamel and Mercier, 2018a) (Figure 29).

The adults are also suspension feeders, indiscriminately capturing suspended food particles that usually measure between <0.005–1.5 mm in diametre, although they may be able to ingest larger food items. Their diet primarily consists of phytoplankton, zooplankton (including eggs, embryos, and larvae of various species), and non-living organic particles (Gianasi *et al.*, 2017; Hamel and Mercier, 1998). Larger fragments of algae can occasionally be found in the digestive system of wild-caught individuals (R. Morrison, personal communication). The suspension-feeding lifestyle and chiefly vegetal diet of *C. frondosa* have a major incidence on its dietary value (Box 8).

FIGURE 29

Feeding behaviour of the sea cucumber *Cucumaria frondosa*

(a) Tentacles are fully deployed in the water column to capture particulate food. (b–c) A tentacle with its load of food gets inserted inside the mouth, and (d–e) the mouth contracts around it to remove the particles. The process is repeated successively with the other tentacles



BOX 8

Nutritional and pharmaceutical value of *Cucumaria frondosa*

The fact that, as a suspension feeder, *Cucumaria frondosa* primarily ingests fresh vegetal matter, which consists mainly of live phytoplankton, makes it a unique source of nutrients and bioactive molecules. Almost all other commercially-exploited species of sea cucumbers sold on the market today are deposit feeders that sift through the sediment to collect more or less degraded organic matter accumulated on the seafloor (i.e. in the sand or mud).

Globally, *C. frondosa* has been shown to contain a broad range of compounds like collagen, chondroitin sulphate, saponins, phenols, and mucopolysaccharides (Hossain, Dave and Shahidi, 2020), which possess unique biological and pharmacological properties (e.g. anticancer, antihypertensive, anti-inflammatory, antidiabetic, anticoagulation, antimicrobial). Particular forms of triterpene glycosides (for instance the one called “frondoside A” after the name of the species) are being extensively researched due to their potential anticancer activity. The distinct biochemical make-up of *C. frondosa* also includes novel, and possibly more abundant, phenolic compounds with strong antioxidant properties, shown to help prevent cell damage and potentially find use in the treatment of diseases (Hossain *et al*., 2023). In addition, remarkable levels of the pigment astaxanthin (a type of carotenoid) were recently detected in *C. frondosa*, along with the presence of vitamin A (Morrison *et al*., 2023), both of which come from the phytoplankton diet and are powerful antioxidants with roles in vision, growth, cell division, reproduction and immunity. The same study identified a suite of beneficial fatty acids such as omega-3 fatty acids and amino acids such as proline (Morrison *et al*., 2023), making representatives of the species, particularly those living in the northernmost section of the distribution range, a promising source of nutraceuticals and pharmaceuticals (see Section 14.2).

9.5 RESPONSE TO PREDATORS

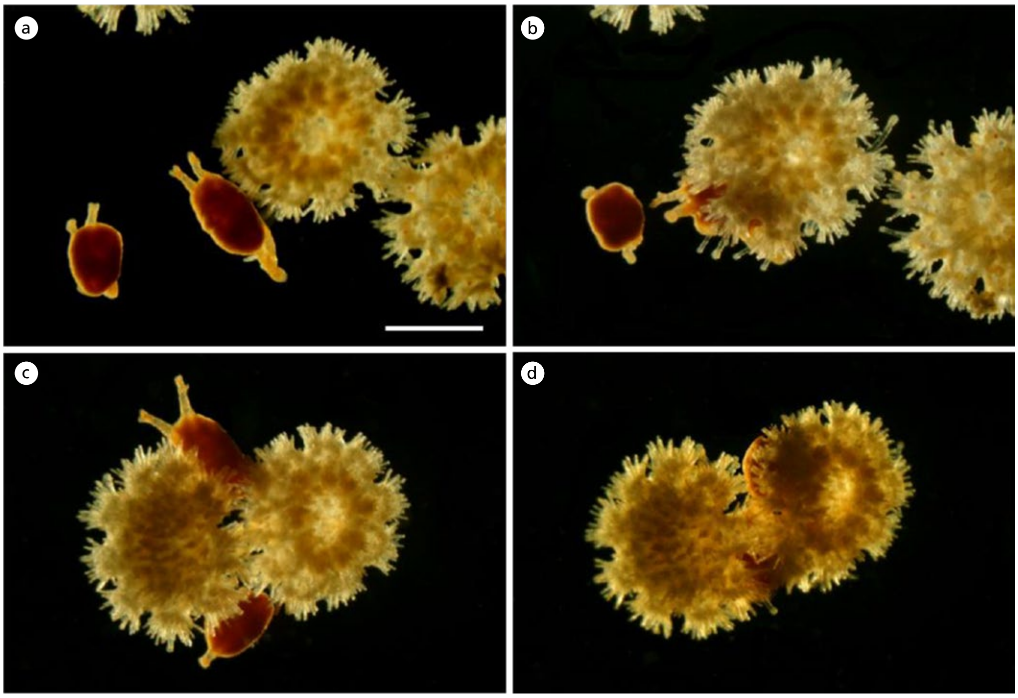
The eggs, embryos, and larvae of *Cucumaria frondosa*, which float around in the water column, are presumably at risk from pelagic predators like fishes and carnivorous zooplankton. In addition, they may get carried close to the coast by currents and tides, where larvae preparing to settle onto the seafloor may be eaten by suspension and filter feeders such as brittle stars, tunicates, mussels (Mercier, Doncaster and Hamel, 2013), and polychaete worms (Medeiros-Bergen and Miles, 1997).

Once they are settled on the seafloor, juveniles may be preyed upon by small sea stars, especially the purple sunstar *Solaster endeca*, that have access to crevices in which they are found (Figure 30) (So *et al.*, 2010). Besides humans, one of the most well-known predators of adult sea cucumbers is *S. endeca* (Figure 31; Box 9) (Francour, 1997; Legault and Himmelman, 1993; So *et al.*, 2010). Other species that have been documented to ingest sea cucumbers include the walrus, *Odobenus rosmarus* (Fay, 1982), the bearded seal, *Erignathus barbatus* (Government of Nunavut, 2012), the common eider, *Somateria mollissima* (Bustnes and Erikstad, 1988), the Greenland shark, *Somniosus microcephalus* (Nielsen *et al.*, 2019), the Atlantic wolffish, *Anarhichas lupus* (Hamel and Mercier, 2008) and, Atlantic cod, *Gadus morhua* (DFO NL, personal communication) (Figure 32).

FIGURE 30

Interaction between juveniles of the sea cucumber *Cucumaria frondosa* (prey) and juveniles of the sea star *Solaster endeca* (predator)

(a) Sea stars (right) converging towards the sea cucumbers (left), and (b–c) eventually engulfing sea cucumbers. (d) Sea stars feeding on sea cucumbers. Scale bar represents 1 mm and applies to all panels



BOX 9

Potential impact of the fishery on predation risk

Bottom-trawling gear used to harvest *Cucumaria frondosa* (see Section 11.5) can cause injuries to sea cucumbers, which may range from blemishes and tears on the skin to the forcible insertion of a relatively large stone inside the body cavity (Ma *et al*., 2023). Although most individuals damaged by the trawl are eventually landed, some may escape the net and avoid capture. It is also possible that sea cucumbers thrown back at sea by harvesters might be injured or unhealthy. However, there is presently no legal minimum landing size in most jurisdictions, so it is not common practice to reject any of the fished sea cucumbers. Irrespective of how it might happen, the uptick of injured sea cucumbers in fished populations may have an undesirable side-effect. Local populations of predators, such as the purple sunstar *Solaster endeca* (Figure 31), may increase in abundance and density as the predators are attracted to these vulnerable sea cucumbers (So *et al*., 2010). The influx of more predators to the fishing grounds is especially concerning, given that the baseline rate of predation may be considerably high. For example, So *et al.* (2010) gathered experimental data in the laboratory and extrapolated that up to two percent of the sea cucumber stocks (0.012 ind/m^2) might be consumed annually by the purple sunstar. Efforts to minimize injuries to sea cucumbers during harvest by improving gear design and prohibiting discards are recommended to mitigate against any potential cascading impacts on sea cucumber populations.

FIGURE 31

Interaction between an adult of the sea cucumber *Cucumaria frondosa* (prey) and an adult of the sea star *Solaster endeca* (predator)

(a–d) Successful predation, and (e–h) unsuccessful predation. (a) The sea star roaming the tank, (b) converging toward a sea cucumber, (c) taking hold, (d) and feeding on a sea cucumber. (e) A swollen sea cucumber, exhibiting slight active buoyancy adjustment or ABA, in physical contact with a sea star, (f–g) escaping the arms of the sea star, and (h) successfully evading capture. Scale bars represent 10 cm

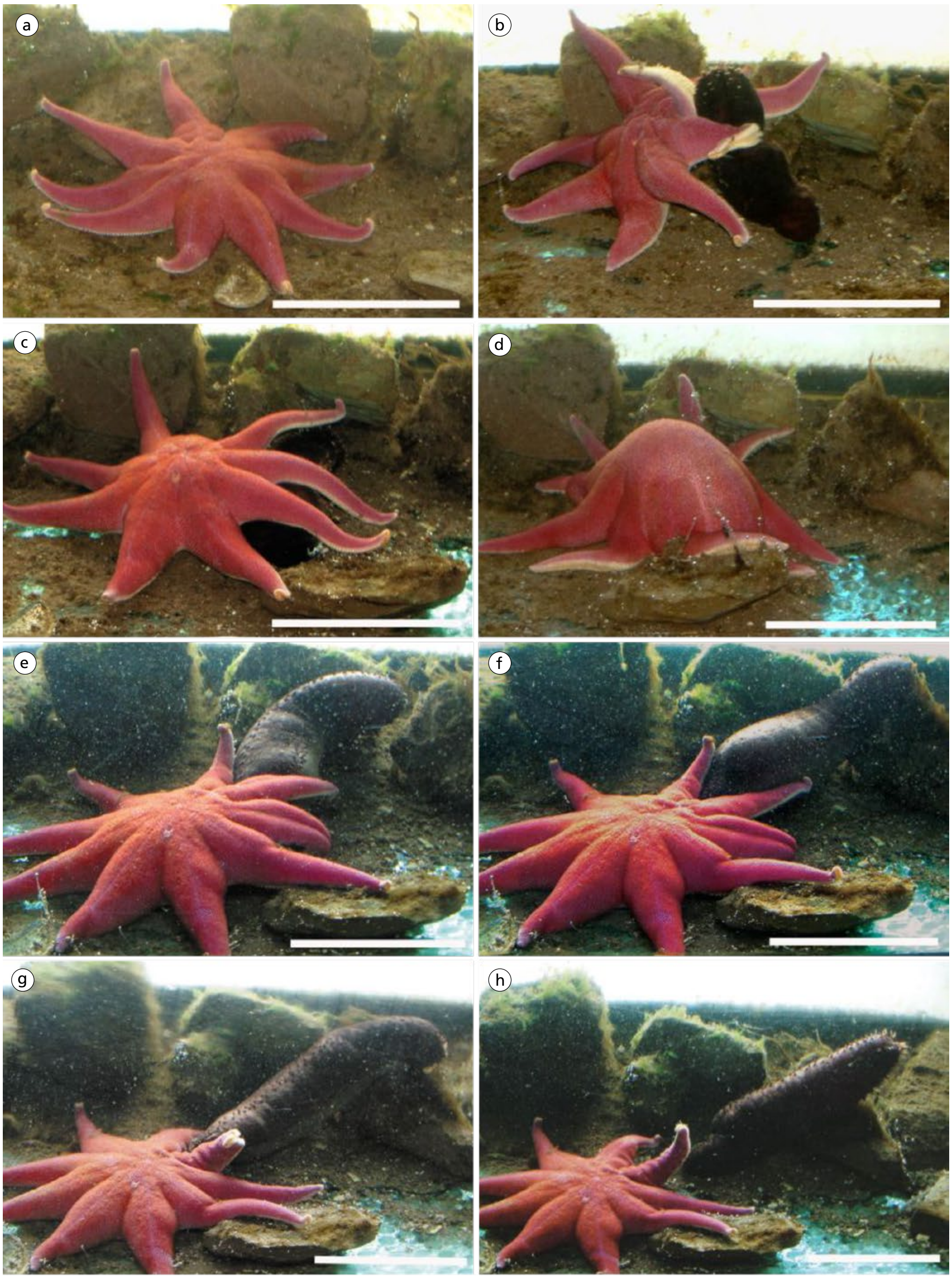
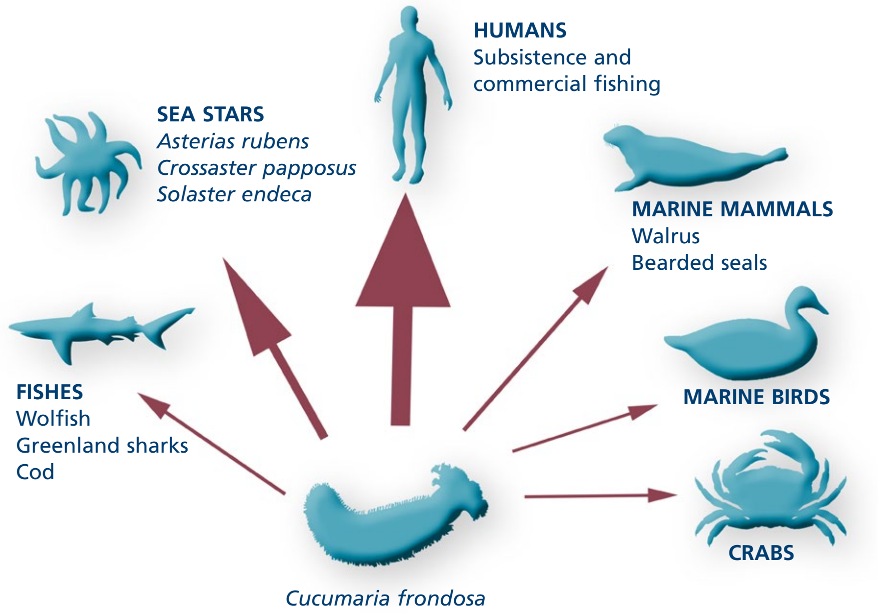


FIGURE 32

Main predators of adults of the sea cucumber *Cucumaria frondosa* include humans, sea stars, fishes, marine birds, marine mammals and decapod crustaceans (crabs). The width of the arrow approximates the relative strength of the relationship



Source: Authors' own elaboration. Shapes from Openclipart.org

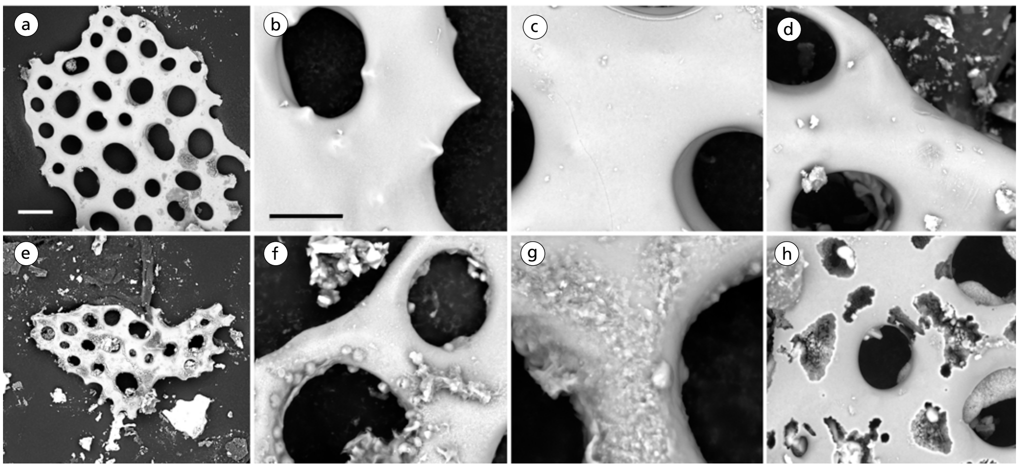
10. Threats faced by *Cucumaria frondosa*

10.1 OCEAN ACIDIFICATION

Since the advent of the industrial revolution circa 1750, human activities have steadily increased the amount of carbon dioxide (CO_2) released into the atmosphere, much of which eventually gets absorbed by the ocean. The chemical reaction of water combining with carbon dioxide produces an excess of hydrogen ions. Both dissolved carbon dioxide and free hydrogen ions in the ocean contribute to the decrease of its pH in a process known as ocean acidification. The sensitivity of early life stages of *Cucumaria frondosa* to lower than normal pH levels is particularly concerning as the ocean turns more acidic. It has been shown that spawning and embryonic development may be negatively impacted when adults are exposed to low pH conditions during the period of gamete production (Verkaik, Hamel and Mercier, 2016) (Figure 16b, c).

Another effect of ocean acidification is the depletion of free carbonate ions in the environment. Carbonate ions freely available in the ocean are required for calcifying organisms to construct and maintain their calcium carbonate structures such as shells and skeletons (including the ossicles in sea cucumbers). Therefore, once pH gets too low, calcified structures begin to dissolve away. Laboratory work has shown that the ossicles of *C. frondosa* are altered, becoming more brittle and pitted, when the sea cucumbers were exposed to lower pH conditions over a number of months (Figure 33) (Verkaik, Hamel and Mercier, 2016).

FIGURE 33
Effects of ocean acidification on the ossicles of the sea cucumber *Cucumaria frondosa*
(a–d) Ossicles under ambient pH conditions, compared to (e–h) ossicles under low pH conditions. Abnormalities include calcified bumps and thinning centers, and etched, textured or eroded surface. Scale bar represent 40 μm in panel (a), also applying to (e), and 5 μm in panel (b), also applying to (b–d) and (f–h)



Source: Modified from Verkaik, K., Hamel, J.-F. & Mercier, A. 2016. Carry-over effects of ocean acidification in a cold-water lecithotrophic holothuroid. *Marine Ecology Progress Series*, 557: 189–206.

10.2 PLASTIC POLLUTION

Experimentally, *Cucumaria frondosa* was found to ingest various types of suspended micro-plastic fragments, generally <1.5 mm in maximum length (Graham and

Thompson, 2009). Individuals may mistake these plastic fragments for food particles, possibly when the plastic becomes coated with a microbial layer known as a biofilm, giving it an organic signature. Additionally, sea cucumbers showed a preference for plastic fragments over sediment particles, despite both particle types are not being considered true food, which could lead to malnourishment or starvation. Most importantly, toxic chemicals such as polychlorinated biphenyls (PCBs) may adhere to the surface of the plastic, exposing organisms that consume it to toxins in concentrations that they otherwise would not face. Together, these findings suggest that, as a suspension feeder, *C. frondosa* is susceptible to the ever increasing threat of micro-plastic pollution in the marine environment (Graham and Thompson, 2009).

10.3 OIL CONTAMINATION

Oil is a type of fossil fuel derived from ancient plants and animals. While oil can be naturally found in the marine environment in trace amounts, massive oil contamination can occur through oil spills during drilling activities, or the transportation and use of petroleum products. *Cucumaria frondosa* was one of the first species used to explore the impacts of oil contamination on cold-water subarctic echinoderms (Osse, Hamel and Mercier, 2018). Males and females were exposed to two concentrations of water-associated used lubricating oil at three seasonal time points, and common enzyme biomarkers were measured in their digestive and reproductive tissues. One of the biomarkers (glutathione peroxidase) showed greater activity levels in the female gonad than in the male gonad. Activity was also greater in the post-spawning than the pre-spawning period for both sexes (Osse, Hamel and Mercier, 2018). Much more work will be needed to assess and fully understand the potential impacts of oil contamination on *C. frondosa*.

10.4 HEAVY METAL POLLUTION

Heavy metals are naturally found in the marine environment at low doses. However, human activities have dramatically increased their concentrations, which can become toxic above certain levels. Heavy metals are not biodegradable and can persist in the environment for long periods of time. They tend to be stored in increasing amounts inside the bodies of living organisms, a phenomenon known as bioaccumulation. In eastern Canada, wild individuals of *Cucumaria frondosa* were found to contain arsenic in the form of arsenosugars at average levels ranging from 5.2–8.7 mg/kg of dry weight, depending on the body part examined (Gajdosechova *et al.*, 2020). Although arsenosugars are not considered acutely toxic compared to other forms of arsenic, *C. frondosa* in the study contained arsenic levels that are higher than those of scallops and seaweeds (Taylor *et al.*, 2017), but comparable to those of fishes (DeBlois *et al.*, 2014).

11. Commercial harvesting of *Cucumaria frondosa*

11.1 OVERVIEW OF THE FISHERIES

Today, commercial fishing for the sea cucumber *Cucumaria frondosa* mainly occurs in the eastern provinces of Canada, including Québec, New Brunswick, Nova Scotia, and Newfoundland and Labrador (DFO, 2017c; DFO, 2019; DFO, 2021d; DFO, 2021c). Additional fishing activities at commercial and exploratory scales are also occurring in Maine (United States of America), Saint-Pierre and Miquelon (a territory of France in North America), Iceland, Greenland, Norway and possibly in the Russian Federation. Subsistence fisheries for *C. frondosa* by Indigenous communities have been ongoing for generations around parts of northern Québec and the territory of Nunavut, in the Canadian Arctic.

Commercial interests around *C. frondosa* first emerged in the 1980s, starting in eastern United States of America (Maine), with the eastern provinces of Canada following suit. The commercial fishery in Maine began in 1994, but it has remained small relative to established fisheries, with about 4 500 tonnes landed at the peak of the activities in the early 2000s (Feindel, Bennett and Kanwit, 2011), down to about 225 tonnes in 2014, the last year for which data are available (Maine Department of Marine Resources, 2022). As of 2019, the Maine fishery was described as a very limited, closed-access drag fishery with a handful of licenced boats (Maine Department of Marine Resources, 2022). The exploratory fishery that started in the Canadian province of Québec in the 1980s (Desrosiers, Lavallée and Michaud, 1989) never transitioned into commercial status; annual harvests remain at ~1 000 tonnes (DFO, 2017b). An exploratory (Phase I) fishery started in New Brunswick in 1999; in 2009 it moved into a small (Phase II) commercial fishery of ~760 tonnes/year (Rowe *et al.*, 2009) that remains active to date. In Newfoundland and Labrador, an emerging fishery in NAFO Division 3Ps began in 2003 and it transitioned to a commercial fishery in 2012 (DFO, 2019); around 7 000 tonnes are currently harvested every year by a growing number of licensees (DFO, 2023). The Nova Scotia fishery began in 2004 in two areas, and a third area opened in 2005; harvests now reach ~2 000 tonnes/year.

Iceland is the only European country with a targeted commercial fishery for *C. frondosa* (Christophersen, Jonasson and Sunde, 2024). An experimental fishery started in 2003 but landings remained minimal until 2008, when they started to progressively increase, from about 1 000 tonnes to a maximum around 5 500–6 000 tonnes in 2018 and 2019 (Christophersen, Jonasson and Sunde, 2024). In Greenland, a trial fishery for *C. frondosa* began in 2019, with landings of approximately 106 tonnes in that year, reportedly down to just two tonnes in 2021 (Nygaard, Nogueira and Burmeister, 2022). Other northern European countries do not collate any specific landings for sea cucumber, either because there is no fishery or the captures are very minimal; e.g. in Norway, they get grouped with various other "invertebrates" (Christophersen, Jonasson and Sunde, 2024). Although interest was identified around the exploitation of *C. frondosa* in the Barents Sea two decade ago (Gudimova, Gudimov and Collin, 2004), later developments and the current situation in the Russian Federation remain undocumented.

11.2 STOCK ASSESSMENTS

Cucumaria frondosa is not evenly distributed and its abundance can vary regionally. Overall, local biomasses of *C. frondosa* tend to be quite large by sea cucumber standards (see abundance data in Section 3), but the lack of monitoring remains a serious concern (see Box 3). Stock assessments and therefore stock size estimates are lacking or incomplete for most regions where the species is fished. Where assessments occur, they do so at irregular and infrequent intervals, likely because they necessitate complex logistics to conduct offshore trawl or video surveys under the harsh conditions of the North Atlantic. For this reason, the biomass of *C. frondosa* has not been assessed with equal celerity and precision across the four eastern provinces of Canada: despite early attempts, no systematic assessment of the sea cucumber stock in waters off New Brunswick seems to have been conducted; in Québec, stock data were collected in 2016 and 2020; off the Scotian Shelf in Nova Scotia, the last survey was carried out more than a decade ago; on the Grand Banks of Newfoundland, partial assessments occurred in 2016 and 2017, and a more complete survey took place in 2022. In the United States of America, available data on the sea cucumber stocks in the state of Maine date back to 2005. Stocks of *C. frondosa* have apparently not been assessed for the trial fishery in Greenland. In Icelandic waters, regional stocks are known to have been estimated in 2008 and in 2012, but the first broad scale survey using beam trawl and drop cameras was carried out in 2020 (Christophersen, Jonasson and Sunde, 2024). The only data available on the stocks in Norway and northern Russian Federation were published in the 1990s.

11.3 FISHING SEASON

In eastern Canada, the fishing season for *Cucumaria frondosa* varies from province to province. With one regional exception (Gaspé Peninsula, Québec), provinces do not allow fishing during the anticipated spawning season (~March–May). In New Brunswick and Nova Scotia, the fishery is open in the months that lead up to the spawning season, while in Québec (Units B & C) and Newfoundland and Labrador fishing is only permitted after the spawning season is over, from July to October. Sea cucumber fishing in Iceland occurs nearly year round, with closures during the spawning period, i.e. May–June in western areas and June–July in eastern areas (Christophersen, Jonasson and Sunde, 2024).

11.4 MANAGEMENT OF THE FISHERY

In Canada, the commercial fishery for *Cucumaria frondosa* is managed by the Department of Fisheries and Oceans (or DFO) at the federal level by limiting the number of fishing licences (a process known as "limited entry") and by determining the total allowable catch (TAC) per season. Stocks are separately assessed and managed for each of the four provinces that are engaged in commercial fishery. The TAC for *C. frondosa* in Canada has increased progressively over the years (DFO, 2021a; DFO, 2021b). It is currently set at 2 242 tonnes in the Northwestern bed and 4 717 tonnes in the Southeastern bed, with corresponding 2022 landings totalling 2 065 tonnes in the Northwestern bed and 4 019 tonnes in the Southeastern bed (DFO, 2023).

There is a mandatory 100 percent dockside monitoring program that observes and records offloading of catches and a Vessel Monitoring System (tracking vessel location to ensure fishing is occurring in the licenced areas) is required on all boats for all provinces. Additionally, there are often at-sea observers in the fishery, although the coverage is partial. Since 2013, Québec is the only province that has a minimum sea cucumber size requirement of 11.4 cm in body length (DFO, 2021d). The stocks in all four provinces are managed through TAC quotas, save the fishing grounds off the coast of Gaspé Peninsula in Québec (limited by number of fishing days instead). In practice, most managed areas in Canada do not go above the TAC allocated for a given season, but if catches surpass the TAC then the difference is taken off the next season's quota. It is obvious from the TAC values that commercial harvesting of *C. frondosa* in North America occurs on a different scale than the sea cucumber fisheries typical of the Indo-Pacific, which is not necessarily positive or desirable (Box 10).

In Iceland, the commercial fishery for *C. frondosa* is also managed via limited entry and a regional TAC. The total TAC in all areas for the fishing year 2021/2022 was 2 307 tonnes (Christophersen, Jonasson and Sunde, 2024). Intense unregulated fishing on virgin grounds and late closures in recent years have resulted in increased effort and catches that have surpassed the recommended TAC (MFRI, 2021a). In Norway, the fishery has remained relatively small, non-targeted, and unregulated. Although the amount of landed sea cucumbers is not known, the total landing for shellfish (not counting shrimps and crabs), molluscs (a group that includes species such as scallops), and echinoderms (including sea cucumbers) was 1 200 tonnes in 2020 (Directorate of Fisheries, 2020). Data on the management of sea cucumbers in the waters of the Russian Federation are not available. Greenland's fishery for *C. frondosa* is still in the experimental phase so their landings are low, under 100 tonnes, and no specific regulations are in place (Nygaard, Nogueira and Burmeister, 2022).

BOX 10

From high-volume to high-value fishery

A majority of sea cucumber fisheries around the world have been over-exploited. Populations that are overfished can shrink past the point of recovery, which can put the species at risk of extinction. At present, the method used in the commercial fisheries for *Cucumaria frondosa* in the North Atlantic has been bottom-trawling with a modified drag net. Not only is this method relatively destructive for life inhabiting the seafloor, but it has also inadvertently entrenched a high volume–low value model for this fishery. Because sea cucumbers in northern Canada are known to have different biochemical properties compared to those found further south (Morrison *et al*., 2023), it is recommended that the development of the sea cucumber fishery in Nunavut and other northern jurisdictions adopt a low volume–high value model instead. This would entail small-scale harvests while marketing the unique biochemical properties of *C. frondosa* from pristine polar waters. Overall, with guidance from local Indigenous knowledge and wisdom, this model can better protect the sea cucumbers from overfishing and favour the use of less-destructive gear to limit collateral damage to the seafloor habitat.

11.5 HARVESTING METHODS

Commercial fisheries in the western North Atlantic Ocean has been primarily conducted by bottom trawling using a "sea cucumber drag" that was developed by modifying a green sea urchin drag (Figure 34) (Barrett, Way and Winger, 2007). The shoe or cutting bar remains in contact with the seafloor and most of the sea cucumbers within the swept area are dislodged by the cutting bar or the chain grid and then collected in the net bag (Figure 34) (Barrett, Way and Winger, 2007). A similar trawling gear is used in Iceland, with boats sometimes operating one on each side (Christophersen, Jonasson and Sunde, 2024).

Much smaller trawls are towed behind non-commercial boats to supply the localized subsistence fishery in Nunavut, northern Canada. Hand collections, sometimes using nets, at the ice edge or via an opening through the ice, is another common practice for harvesting sea cucumbers in the Canadian Arctic (Hamel and Mercier, 2024). Commercial diving for sea cucumbers once operated in waters off the coast of Gaspé Peninsula in Québec, Canada. This harvesting method has not been pursued since 2018 due to low yields (DFO, 2021d).

FIGURE 34

A sea cucumber bottom trawl (also known as a sea cucumber drag) used in Newfoundland, Canada

(a) Front view of the trawl, (b) schematic of the steel front end (ironwork), chain grid, and chaffing mat, and (c) side view of the trawl. (d) A drag suspended in air from a fishing vessel. Braided polyethylene net bag is orange in panels (a) and (b) and green in panel (d)

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Sources:

Barrett, L., Way, E. & Winger, P.D. 2007. Newfoundland sea cucumber drag reference manual. Canadian technical report of fisheries and aquatic science 2736. Fisheries and Oceans Canada. 22 pp, Canada.

Ma, K.C.K., Trenholm, R., Hamel, J.-F. & Mercier, A. 2023. The enigma of stones found in the body cavities of sea cucumbers. *SPC Beche-de-mer Information Bulletin*, 43: 32–38.

11.5.1 Bycatch associated with the sea cucumber fishery

Bottom-trawling for *Cucumaria frondosa* may be associated with the collection of non-target species in a process known as bycatch. Between 2004–2008 and 2016–2017 bycatch increased from about two percent of the total harvested biomass (DFO, 2017a) to as much as 33 percent (DFO, 2018) in Newfoundland waters. The most common species caught as bycatch are sea stars and sea urchins, including sand dollars (70–80 percent of bycatch). Other recorded bycatch species include scallops, whelks, crabs, lobsters, and groundfish (DFO, 2017a). In waters off of New Brunswick, sea urchins are by far the most common bycatch, followed by sea stars, crabs, hermit crabs, scallops, lobsters, octopuses, and flatfishes (DFO, 2009). In eastern Canada, bycatch associated with the sea cucumber fishery is typically returned to sea when the catch is sorted on board a fishing vessel, however it is unknown what the survival rates of these species are post-release (Gianasi *et al.*, 2021). In Iceland, bycatch reportedly forms a low percentage of the total weight, but comprises species like sponges and soft corals that are indicators of vulnerable marine ecosystems, warranting further investigation (Christophersen, Jonasson and Sunde, 2024).

11.5.2 Sea cucumbers as bycatch in other fisheries

The fishery for the North Atlantic scallop *Chlamys islandica* in western Iceland frequently involves bycatch of the sea cucumber *Cucumaria frondosa*. On average, sea cucumbers accounted for 24.6 tonnes or 25 percent of the benthic bycatch in tows conducted between 1993 and 2001 (Garcia, Ragnarsson and Eiríksson, 2006). In the Barents Sea, northern Europe, sea cucumbers reportedly constitute a substantial portion (up to 66 percent) of the bycatch associated with the fishery for the northern shrimp *Pandalus borealis* (Anisimova *et al.*, 2010).

11.6 HOLDING POST CAPTURE AND HANDLING AT DOCKSIDE

After the sea cucumber drag is brought on board the fishing vessel, the catch is sorted. The crew opportunistically removes large rocks and bycatch before the sea cucumbers are put in the hold with seawater. Some small rocks and pebbles may remain in the catch because the sea cucumbers hold onto them with their tube feet, or more rarely because stones are forced inside their body cavities (Ma *et al.*, 2023). Once the hold is full (Figure 35a), the sea cucumbers are transported from the fishing grounds to the landing site. In Newfoundland waters, sea cucumbers can remain in the hold of the vessel between 12 and 24 hours from the moment they are harvested to the dockside where they are landed.

Sea cucumbers are transferred from the fishing vessel to large, insulated containers (900 litres in volume) manually using a shovel and a bucket (Figure 35b, c) or mechanically using a vacuum. Unloading sea cucumbers manually can take 4–8 hours to complete (R. Trenholm, personal communication). Using this method, harvested sea cucumbers are passed over a sorting grid, which removes some of the debris and bycatch (Figure 35d, e). In comparison, the mechanical method using a vacuum takes approximately 45 minutes (R. Trenholm, personal communication). Since the vacuum does not readily pick up heavy objects such as rocks, a sorting grid is not used in association with this method, so any bycatch is removed at the processing plant.

After processing at the dockside, the sea cucumbers stored in fish bins (Figure 35f) are moved using a forklift (Figure 35g) onto refrigerated vehicles and transported over land to the processing plants. Typically, a mix of seawater and freshwater ice is added to the containers holding the catch, which has been shown to be the best method for short-term storage (Gianasi, Hamel and Mercier, 2016). The industry aims to process the catch at the plant within three days of harvesting *Cucumaria frondosa* to minimize damages and maximize yield and quality (Box 11).

BOX 11

Physical handling of sea cucumbers

Blemishes on the skin can affect the marketability of both the frozen and dried forms of the sea cucumber product. For instance, forced removal of pebbles and rocks attached to individuals can cause perforations on the skin. Also, impact with hard objects (especially blunt objects such as large rocks or shovels) during transport and processing can inflict severe bruises (Figure 36). Therefore, care is recommended during handling of post-harvested *Cucumaria frondosa* to minimize damage to the skin. Sea cucumbers under physical or thermal stress can eviscerate their guts (Figure 36i; Box 2).

Experiments have shown that acceptable results can be obtained as long as the temperature inside holding containers remains cold (<4 °C). However, one of the most common method currently in use (freshwater ice slurry with direct salting) yielded the highest rates of mortality and skin necrosis, whereas iced seawater emerged as the best storage condition (Gianasi, Hamel and Mercier, 2016). Above all, care should be taken to avoid direct contact of ice on the skin of *C. frondosa* because it has been linked to freezer burns, affecting the quality of the product (Gianasi, Hamel and Mercier, 2016). In the future, the implementation of flow-through seawater in the boat holds and dockside holding containers is recommended to minimize thermal shock and to flush away any waste produced by sea cucumbers over time. Given that sea stars are one of the main predators of *C. frondosa*, priority should be placed on separating sea star bycatch from the catch as early as possible during processing to reduce stress levels in sea cucumbers.

FIGURE 35

Dockside processing of harvested sea cucumbers *Cucumaria frondosa*

(a–c) Offloading catch using buckets. (d) Manual sorting of catch and bycatch. (e) Collection of stones and other bycatch into a black container. (f) Catch in an insulated container. (g) 1 000-L insulated container with catch topped with ice

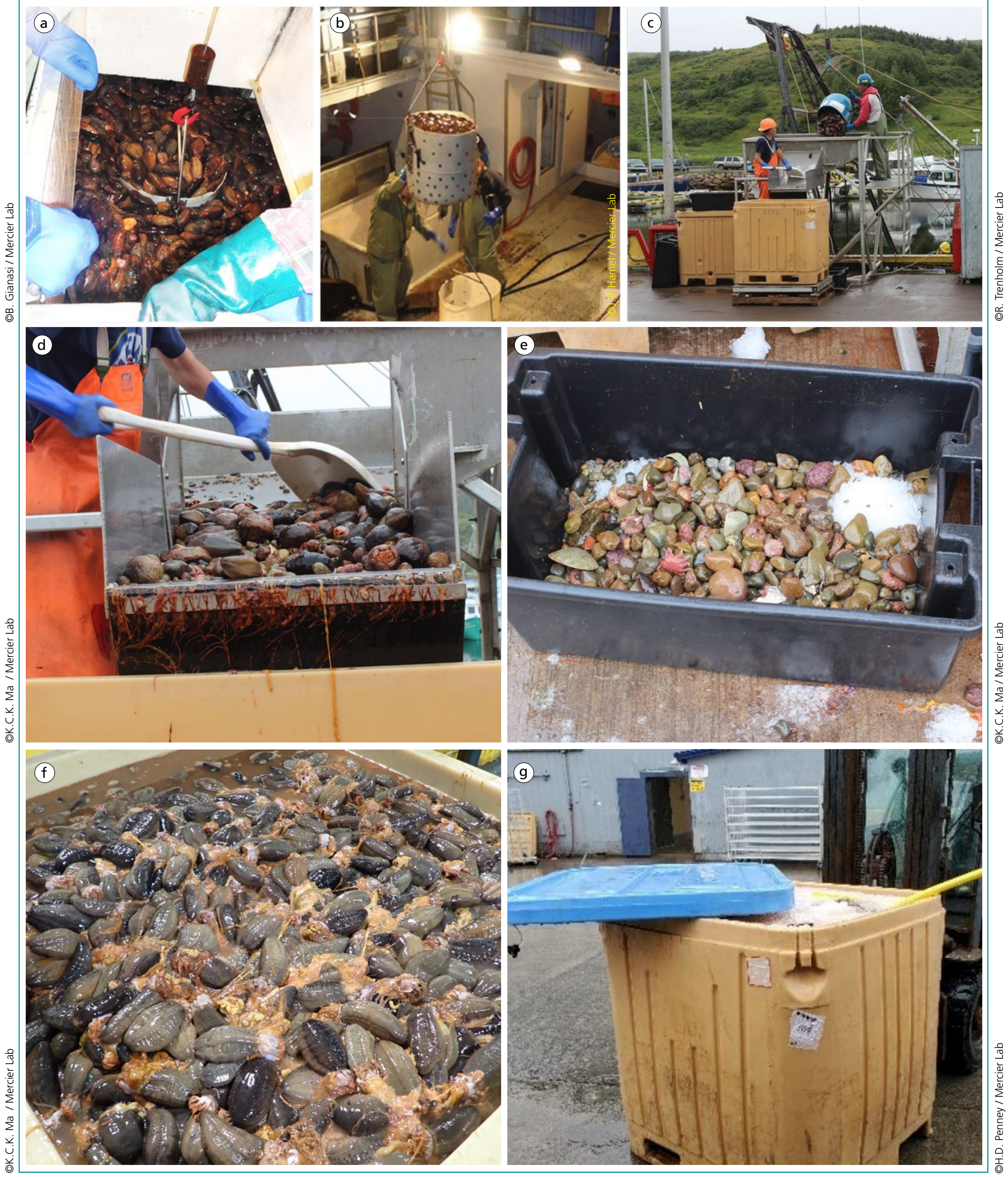
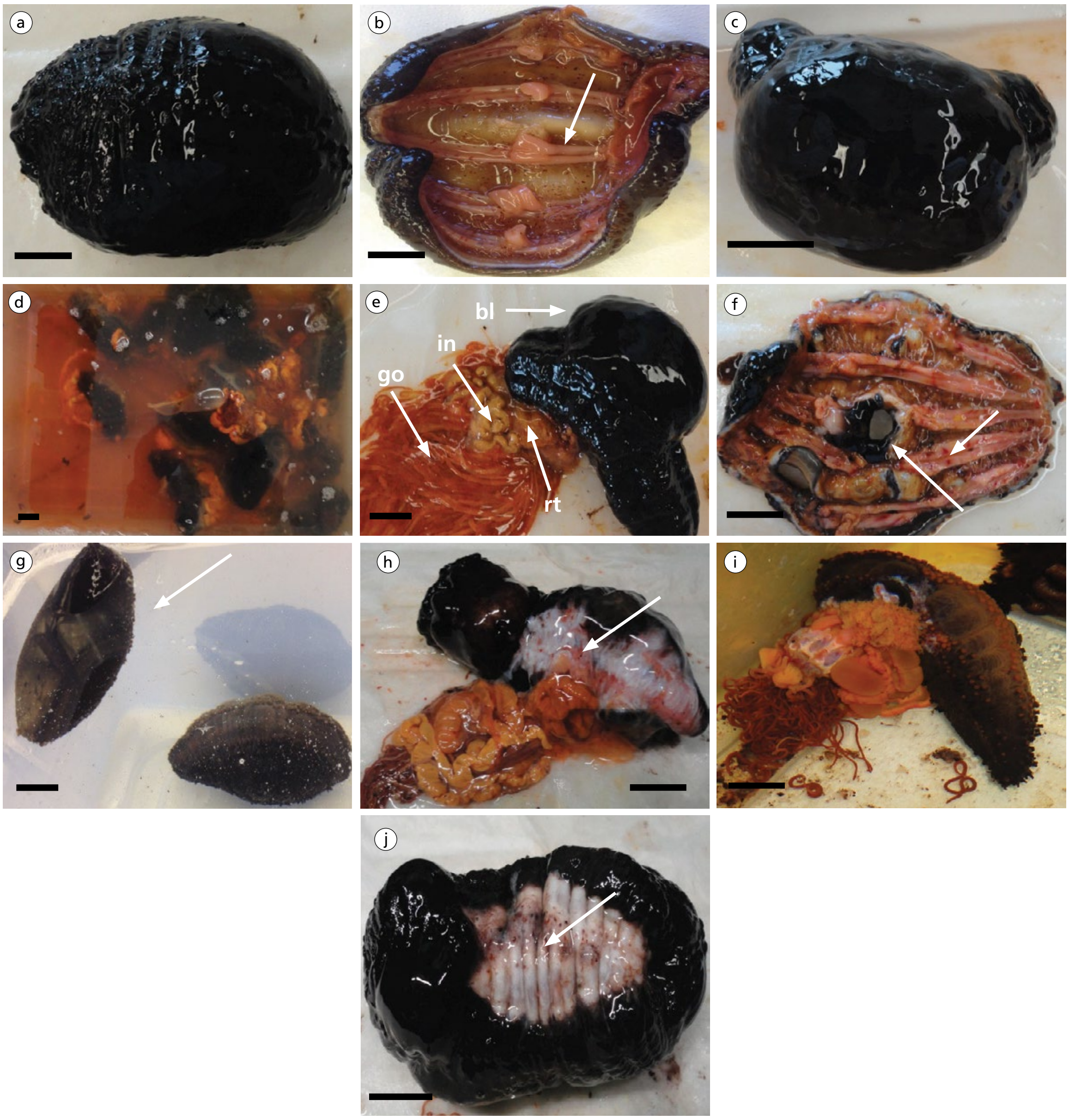


FIGURE 36

State of post-harvested individuals of the sea cucumber *Cucumaria frondosa*

(a) External view of an individual in very good condition with firm body wall and no visible skin damage. (b) Interval view of an individuals in very good condition with healthy pinkish longitudinal muscle bands (arrow). (c) External view of a slightly deteriorated individual with blemishes on the body wall. (d) Dead or moribund individuals, non-responsive to stimuli and exhibiting signs of evisceration. (e) Deteriorated individual with a blister on the body wall (bl) and eviscerated gonad (go), intestine (in), and respiratory tree (rt). (f) Internal view of a deteriorated individual with a tear in the body wall (arrow) and red spots on longitudinal muscle bands (arrow). (g) Positively buoyant individual (arrow) after being transferred from freshwater ice storage to a recovery tank. (h) Skin necrosis and evisceration of internal organs through a hole (arrow) in the body wall of deteriorated individual. (i) Dead individual exhibiting evisceration of internal organs. (j) External view of a deteriorated individual with signs of skin necrosis such that the connective white tissue is exposed (arrow). Scale bars represent 2 cm



Source: Gianasi, B.L., Hamel, J.-F. & Mercier, A. 2016. Experimental test of optimal holding conditions for live transport of temperate sea cucumbers. *Fisheries Research*, 174: 298–308.

12. Aquaculture potential of *Cucumaria frondosa*

12.1 AQUACULTURE OF SEA CUCUMBERS

To meet global demand for their consumption, various ways of cultivating and farming different commonly-traded sea cucumbers have been explored (Lovatelli *et al.*, 2004; Mercier and Hamel, 2013). Larval and juvenile rearing of *Cucumaria frondosa* has been studied under laboratory settings with an aim to assess the potential of eventually developing aquaculture operations at larger scales (Hamel and Mercier, 1996d; Gianasi, Hamel and Mercier, 2016; Gianasi *et al.*, 2017; Gianasi, Hamel and Mercier, 2018a, 2019a, 2019c). Investigation of its potential inside multitrophic aquaculture systems has also been examined (Sun *et al.*, 2020a).

There are three major factors that make *C. frondosa* a good aquaculture candidate: first, the species has a non-feeding larval form (Figure 21) and, therefore, requires less management during early developmental stages when mortality is often highest. This differs from the larval forms of the vast majority of commercially-exploited sea cucumbers, which need to be fed and frequently monitored. Second, *C. frondosa* occurs in dense populations (Figure 14). This allows easy collection of broodstock and their maintenance under relatively crowded conditions provided there is enough planktonic food. Lastly, *C. frondosa* has a high nutritional value, due in part to its diet of fresh plankton, which is more nutritive than the deposited organic matter that other commercially-exploited sea cucumbers typically eat.

Two of the biggest challenges with the culture of *C. frondosa* include the annual spawning (Figure 25), which limits the procurement of seedlings, and the slow rate of growth (Figure 24), which is typical of cold-water species. Food availability and other prevailing conditions can have important impacts on the conditioning of broodstock (Gianasi *et al.*, 2017; Gianasi, Hamel and Mercier, 2019b), and on the subsequent growth rates of juveniles under captive conditions. For instance, it took about 24 months for individuals to reach a body length of 35 mm in conditions associated with Québec waters (Hamel and Mercier, 1996d), while it took 21–24 months to reach a length of 4–6 mm under naturally fluctuating conditions found in Newfoundland waters (Gianasi, Hamel and Mercier, 2018a; So *et al.*, 2010). Based on the latter, it could take 8–25 years to grow *C. frondosa* to maturity or market size under ambient conditions (So *et al.*, 2010), which is markedly longer than values established for temperate and tropical sea cucumbers. For instance, *Apostichopus japonicus* or *Holothuria scabra* can reach a length of 10 mm inside 2–3 months, and may even reach market sizes in 12–24 months under optimal conditions, even though yields can be low (Mercier and Hamel, 2013). However, there may still be ways or approaches to make aquaculture of *C. frondosa* worthwhile (see below and Box 12).

12.2 INTEGRATED MULTITROPHIC AQUACULTURE

Integrated multitrophic aquaculture (IMTA) involves co-culturing multiple complementary species in one aquaculture setting. The by-products from one species can be considered fertilizer or food for another species. For example, farming simultaneously filter-feeding species near fish cages can somewhat reduce wastes. Bivalves may ingest faeces and excess feed, while seaweeds would absorb excess nutrients. The implementation of IMTA can thus minimize the environmental footprint and organic loading of fish farming in comparison to monocultures (Chopin *et al.*, 2004).

BOX 12

Prospects for the aquaculture of *Cucumaria frondosa*

The body of knowledge gathered to date indicates that the biology of *Cucumaria frondosa* is somewhat incompatible with traditional aquaculture for the purpose of developing food products. The annual spawning and slow growth are not entirely offset by the absence of feeding larvae and the rich nutritional profile of the species. It would realistically take too many years to grow adults of marketable size in captivity to market them as seafood. While broodstock can be conditioned and juvenile grown out, the best results would likely be obtained using lipid-rich ingredients (e.g. fish eggs, formulated feeds) in combination with the necessary fresh or frozen phytoplankton diet (Gianasi *et al*., 2017; Gianasi, Hamel and Mercier, 2019b). Cost-effectiveness is therefore unlikely to be reached.

The use of *C. frondosa* as an extractive species in IMTA systems certainly holds greater promise, since it has been shown to ingest and assimilate aquaculture waste materials (Nelson, MacDonald and Robinson, 2012a; Sun *et al*., 2020a). However, many aspects remain to be confirmed under real conditions. One unknown is whether the sea cucumbers would continue to extract the fish or shellfish wastes in the presence of their preferred planktonic food. Another question is whether a combination with filter feeders such as bivalves would be beneficial (complementary) or detrimental (competitive) to each species.

Alternatively, aquaculture could be considered with an aim to develop non-food products, such as pharmaceuticals and nutraceuticals. Under this scenario, growth to the full adult size may not be necessary, making the venture more cost-effective. In addition, the diet can be modulated to promote the concentration of the desired biomolecules. In favour of this, *C. frondosa* already shows great potential as a source of nutritional extracts and active biocompounds (see Section 14.2).

Cucumaria frondosa has been investigated for the purpose of IMTA. As a suspension feeder, it could be used around salmon cages to fulfill the same role as bivalves that have been tested in other settings. Laboratory experiments have shown that *C. frondosa* is capable of ingesting salmon feed and faeces and absorb these particles in an IMTA situation (Nelson, MacDonald and Robinson, 2012b). However, another study showed that the sea cucumbers were left in poor physical condition and exhibited signs of atrophy (i.e. shrinkage in body size, poor gonad condition) when feeding exclusively on salmon wastes for several years (Sun *et al.*, 2020a). This suggests that the effluent from a salmon culture alone did not provide suitable nutrients to support growth and reproduction. The natural diet of *C. frondosa* includes phytoplankton and other suspended particulate organic matter, which may be important to maintain health and maximize reproductive output. In addition, the biochemical profile of individuals fed salmon waste was modified (Sun *et al.*, 2020a), suggesting that further studies must be conducted to determine if *C. frondosa* can be used in any land-based IMTA system, both as an extractive species and a seafood species.

13. Processing of *Cucumaria frondosa*

In eastern Canada, sea cucumbers are typically transported in large containers placed inside refrigerated trucks (Figure 37a). Once at the plant, they may be sorted by size, with those under about four inches (10 cm) in body length being processed differently than larger ones. Individuals scored as undersized are sold to buyers without further processing. Generally, bigger sea cucumbers are cut, gutted and cleaned. Two types of processing methods are used in the industry: butterfly cut or cocoon cut. For the butterfly cut, the sea cucumber body is sliced lengthwise producing a rolled body wall either with or without the "flower" (i.e. aquapharyngeal bulb). A patent was filed by Singleton *et al.* (2016) for a machine that can semi-automatically eviscerate the sea cucumber *Cucumaria frondosa*, resulting in a butterfly cut. The evisceration machine aligns the individual sea cucumber, cuts and flattens it, removes internal organs, and cleans the remaining body wall (Figure 37). This allows plants to process high volumes of sea cucumbers quickly; however, a possible downside of mechanical processing is the increased health risks associated with high concentrations of aerosols (see Box 13). For the cocoon cut (sometimes known as the "round cut" or "football cut"), the anterior end of the body is sliced transversally, and the viscera removed using a vacuum-like tool. This method simultaneously removes internal organs and the "flower" while the sea cucumber retains its elongated, cylindrical shape intact (Figure 37). The majority of processing plants in eastern Canada transform *C. frondosa* using the butterfly cut; however, sea cucumbers prepared using the cocoon cut tend to fetch higher prices (Hossain, Dave and Shahidi, 2020). Following a more artisanal approach, beche-de-mer from *C. frondosa* can be produced by eviscerating, boiling, and drying the sea cucumbers (Figure 38).

At present, beche-de-mer (body wall either with or with muscle bands) is the main commercial product (Figure 39a, b), and internal organs are generally discarded

BOX 13

Sea cucumber asthma

Workers at a plant may be vulnerable to injuries via repetitive actions related to processing sea cucumbers by hand. The adoption of the vacuum and evisceration machines has greatly reduced the human labour required to process large volumes of catch. However, intensive processing over several days can generate other problems, like eye, skin, throat, and lung irritation. Despite wearing face masks and other protective gear, some workers have been experiencing respiratory difficulties commonly referred to as "sea cucumber asthma". The exact nature of this condition remains a mystery. It has been proposed to be favoured by underlying factors like smoking and asthma, and suggested to be the consequence of allergies. However, it is more likely to be due to high concentrations of aerosols carrying natural toxins of sea cucumbers (saponins), which may build close to and around evisceration lines. Aside from closing off certain portions of the chain to avoid splashing, and implementing the use of personal protective equipment, many work areas in a plant are now better ventilated to mitigate against this potential health hazard. Highly predisposed or vulnerable workers are sometimes removed from the sea cucumber production line.

BOX 14

Potential commercial uses of internal organs

During post-harvest processing, some of the individuals of *Cucumaria frondosa* may display full or partial protrusion of the oral complex, chiefly the aquapharyngeal bulb with associated buccal tentacles, which is dubbed the "flower" (Figure 39d). Before processing using the evisceration machines, the "flower" from these individuals can be isolated without damaging the body wall. Also, instead of being discarded, the internal organs can be transformed into nutraceutical capsules or other forms of supplements (Figure 40). Among the discard organs, the gonads of *C. frondosa* may be sold dried, or fresh, similar to sea urchin roe, especially in Japan. However, the fishery currently aims to avoid the spawning period (when gametes are fully ripe), so a separate market for the gonad may need to be explored under specific fishing regulations.

(Hossain, Dave and Shahidi, 2020), which is perhaps a major waste (see Box 14). Occasionally, the gonad, muscles, and "flower" of *C. frondosa* can be marketed separately (Figure 39c, d). The bulk of the beche-de-mer is exported frozen to buyers, who then prepare the product for sale by freezing, cooking, or dehydrating. Other types of processing, perhaps using undersized individuals, include pulverising sea cucumbers into powder or extracting active ingredients into supplements.

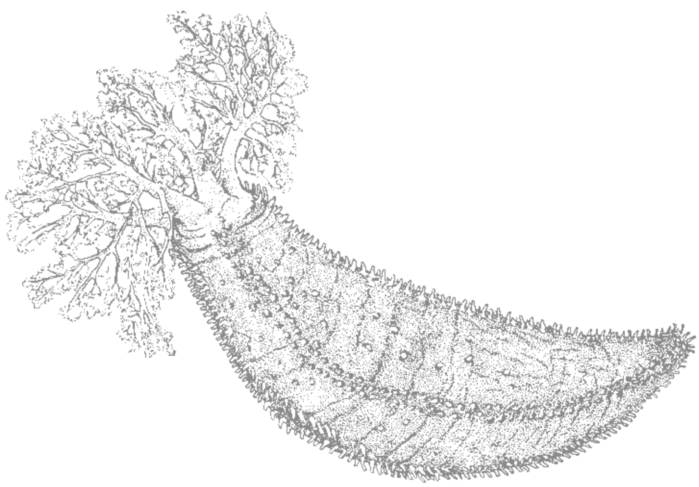


FIGURE 37

Post-harvest processing of the sea cucumber *Cucumaria frondosa* at an industrial plant

(a) Transport of sea cucumbers in large insulated containers to the plant. (b) Conveyer belt used to move sea cucumbers into the plant. C) Size-sorting of sea cucumbers and feeding of market-sized into the evisceration machine to produce butterfly cuts. (d) View of an evisceration machine. (e–f) Cleaning of eviscerated sea cucumbers with water in a rotating apparatus to remove any remaining internal organs. (g) Packaging and weighing boxes of sea cucumbers after evisceration and cleaning. (h) Storage of packaged boxes on racks in a walk-in coldroom

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FIGURE 38
Artisanal processing of the sea cucumber *Cucumaria frondosa* into beche-de-mer
(a–b) Body walls are placed in boiling water, where they will start to coil after 2–3 minutes. (c) Boiled body walls are placed in a dehydrator. (d) Dried body walls after 24 hours in a dehydrator

FIGURE 39

Dried products of the sea cucumber *Cucumaria frondosa*

(a) Beche-de-mer with a butterfly cut. (b) Beche-de-mer with cocoon, round, or football cut. (c) Dried muscle bands. (d) Dried "flower" consisting mainly of the aquapharyngeal bulb and tentacles

Source: Figures (a) and (b) from Hossain, A., Dave, D. & Shahidi, F. 2020. Northern sea cucumber (*Cucumaria frondosa*): a potential candidate for functional food, nutraceutical, and pharmaceutical sector. *Marine Drugs*, 18(5): 274.

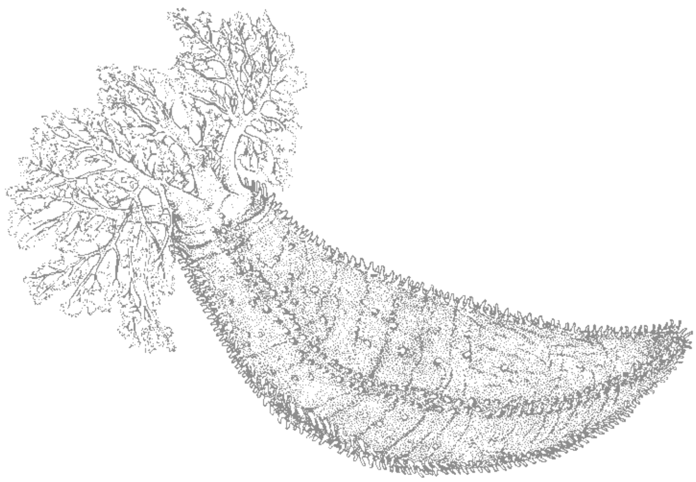

FIGURE 40
Examples of marketed products of the sea cucumber *Cucumaria frondosa*
(a) Beche-de-mer produced in Newfoundland, Canada. (b) Packaged beche-de-mer on sale in Guangzhou, China. (c) Beche-de-mer on sale at a Chinese-owned store in Newfoundland. (d–f) Nutraceutical products from Atlantic Canada, for humans and pets

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14. Markets for *Cucumaria frondosa*

14.1 SEAFOOD

Canadian and Icelandic processors of *Cucumaria frondosa* are making mostly frozen and dried bulk products, rather than retail products aimed at consumers. In Canada, buyers typically sell the frozen sea cucumbers to secondary processors who convert them into a beche-de-mer (dried product) sold in bulk to Chinese distributors based in Toronto and Montreal (Figures 39, 40a, b, c). Most of the sea cucumbers are then shipped to Asia for packaging and sale, with only some being packaged before being exported to mainland China and Hong Kong markets (C. Bonnell, personal communication). Beche-de-mer of *C. frondosa* can also be found on domestic markets in Canada and the United States of America, alongside other species of sea cucumbers mainly marketed to the Asian diasporas. Increasingly, beche-de-mer products are packaged by North American retail companies at one pound (about 0.45 kg) per bag under the label "dried sea cucumber" (Figure 40c). This packaged and loose sea cucumber products can be found in major urban centres, such as Vancouver, Los Angeles, Chicago, Toronto, and New York (C. Bonnell, personal communication). The main market of *C. frondosa* from Iceland is China, where 98.1 percent was exported as a frozen product in 2019 (Christophersen, Jonasson and Sunde, 2024). The official export value from Iceland in 2019 was USD 14.1 million for 4 233 tonnes, chiefly as whole frozen products (4 209 tonnes), with an average export value of USD 3.06/kg. The remaining 24 tonnes of other products (not fresh, frozen, or smoked) were exported with a higher value of USD 48.8/kg.

Compared to other species of sea cucumbers, *C. frondosa* has a medium retail value; as is typical, quality, and price of the products can vary with size (Song *et al.*, 2020). In Canadian cities, loose beche-de-mer of *C. frondosa* is sold about USD 210–350/kg and packaged products are about USD 100–130/kg. In comparison, dried "flowers" (aquapharyngeal bulbs) are sold for about USD 110/kg. Dried *C. frondosa* from Iceland was recently reported to sell direct online for about USD 200/kg (Christophersen, Jonasson and Sunde, 2024).

Frozen body wall or beche-de-mer products from *C. frondosa* (Figure 40a, b, c) can be prepared raw, pickled, steamed, boiled, braised, in soup/consommé, stir-fried, or fried for human consumption. In the Chinese cuisine tradition, dried beche-de-mer is first soaked in water to rehydrate the body wall and to remove the slight smell associated with dried seafood. The soaking process can take a substantial amount of time, easily more than a day, with water changes from time to time. Some recipes add ginger or spring onion to the water during the soaking process. Once the beche-de-mer has been rehydrated, the soft and chewy meat of *C. frondosa* is then customarily braised or made into consommé with other ingredients (Figure 41).

14.2 NUTRACEUTICALS AND PHARMACEUTICALS

Powdered extracts of *Cucumaria frondosa* are marketed in the form of capsules (generally 500 mg) retailing at about USD 1/capsule. They are purported to contain bioactive ingredients with antioxidant and other beneficial properties. Extracts of active ingredients derived from sea cucumbers, including *C. frondosa*, have been associated with antimicrobial, anticoagulant, anticancer, and anti-inflammatory properties (Figure 40) (Bordbar, Anwar and Saari, 2011; Hamel, Phelps Bondaroff and Mercier, 2024; Hossain, Dave and Shahidi, 2020; Kamyab *et al.*, 2020; Zhao *et al.*, 2008). Traditional Chinese medicine use sea cucumbers to treat a variety of health issues,

FIGURE 41
Examples of dishes made from the sea cucumber *Cucumaria frondosa*
(a) Braised sea cucumber, and (b) braised sea cucumber (front right) served alongside other dishes

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but it is unknown whether *C. frondosa* is explicitly used in the same way. The wide availability of health supplements made from *C. frondosa* suggests that there is some demand for these products as nutraceuticals and pharmaceuticals (Hamel, Phelps Bondaroff and Mercier, 2024). Indeed, oils extracted from *C. frondosa* are known to contain a compound called frondoside A (a type of triterpenoid glycoside), which is proposed to have anticancer properties (Adrian and Collin, 2018). Studies have also discovered that powdered extracts from *C. frondosa* had cardio-protective properties, and acted against insulin resistance and obesity (Gangadaran and Cheema, 2017; Vaidya and Cheema, 2014).

Liquid extracts of *C. frondosa* are either alcohol- or non-alcohol-based extracts and branded as "sea cucumber glycerite" or "sea cucumber tincture". These extracts are priced about USD 15–40/120 ml. In the past, Canadian processors of *C. frondosa* have made attempts to market viscera as a bulk product but the market value was relatively low for this product and efforts were abandoned.

15. Comparing *Cucumaria frondosa* to other commercial sea cucumbers

Between 80 and 90 species of sea cucumbers are harvested and traded around the world (Allison *et al.*, 2017; Purcell *et al.*, 2023). Among these species, the most common and highly valued is the Japanese sea cucumber, *Apostichopus japonicus.* Other well-known commercial species include the brown sea cucumber *Isostichopus fuscus* and the sandfish *Holothuria scabra*.

15.1 DIFFERENCES IN THE BIOLOGY AND ECOLOGY

The suspension-feeding habits and phytoplankton-based diet of *Cucumaria frondosa* differ from the deposit-feeding lifestyles of almost all other commercially exploited species of sea cucumbers. Where *C. frondosa* ingests fresh vegetal matter, other species rely on largely degraded organic matter, leading to different nutritional profiles.

Other fundamental differences relate to reproduction. *C. frondosa* reproduces only once annually, whereas many other sea cucumbers display multiple spawning events every year, with some of them spawning monthly. Furthermore, *C. frondosa* is a lecithotrophic species, meaning it develops via a non-feeding larva that draws energy from nutritive reserves (yolk) provided by the mother. Nearly all other commercially important species are planktotrophic, with larvae that must actively feed in the plankton to complete their development. The concrete outcome of this difference is that *C. frondosa* produces fewer much larger oocytes/eggs than the other species, and its larvae do not require food when they are reared.

The growth rate of the cold-water *C. frondosa* is quite slow compared to tropical or even warm-temperate species of sea cucumbers that can be commonly found on the markets. For example, the sandfish *H. scabra* and Japanese sea cucumber *A. japonicus* can reach sexual maturity within a few months post settlement and be grown to full marketable size inside 1–3 years under optimum conditions (Mercier and Hamel, 2013). By comparison, *C. frondosa* barely grows to 1–5 cm in length over the same interval. The species is estimated to take several years to reach sexual maturity and has therefore never been grown to market size in captivity, a process that would likely require 8–25 years (Hamel and Mercier, 1996d; So *et al.*, 2010).

15.2 DIFFERENCES IN HARVEST VOLUMES AND METHODS

The global capture fisheries for *Apostichopus japonicus* peaked around 2000–2005 at an estimated 26 000 tonnes/year. During this period, Japan and Indonesia produced 8 100 and 4 200 tonnes/year, respectively (Choo, 2008). Today, wild stocks are essentially gone and *A. japonicus* is almost exclusively farmed. Comparatively, about 17 000 tonnes of *Cucumaria frondosa* are being harvested annually worldwide, based on reports from 2020/21 (DFO, 2021a; DFO, 2021b; Directorate of Fisheries, 2020; MFRI, 2021b). Therefore, *C. frondosa* is currently considered the number one wild-caught sea cucumber.

Commercial sea cucumbers are generally hand-picked or captured one at a time by net, usually at low tide via wading, or in shallow water via free, hookah, or SCUBA diving. Harvests of *C. frondosa* are typically focused on much deeper waters that are not accessible by divers. Therefore, *C. frondosa* is the only species to be almost exclusively harvested by bottom trawling, from medium to large vessels, using a specially designed drag. At smaller scales, the subsistence fishery for *C. frondosa* conducted by Indigenous communities in northern Canada relies either on much smaller trawlnets towed by small boats or, in shallower regions, on long-pole nets used to reach down from holes cut into the sea ice (Hamel and Mercier, 2024).

15.3 DIFFERENCES IN PROCESSING AND MARKETING

In small-scale fisheries, sea cucumbers are traditionally eviscerated by hand, then boiled over an open fire and dried in the sun (Brown *et al.*, 2010; Li *et al.*, 2019). This can be scaled up by selling sea cucumbers to companies for further industrial processing such as drying them via gas stoves or larger drying ovens (Purcell *et al.*, 2013). Although industrial processing tends to yield a more consistent product, local and small-scale processors can be negatively affected by this industrialization of the supply chain (Friedman *et al.*, 2008).

The handling of *Cucumaria frondosa* differs both with respect to the small-scale and industrialized fisheries. Indigenous communities in northern Canada that traditionally harvest *C. frondosa* for subsistence tend to eat it whole, fresh, and uncooked, often right out of the water (which means half or fully frozen in winter); they may also pound them with rocks or roast them lightly over a fire. In the commercial fishery typical of the eastern North American seaboard and northern Europe, harvested sea cucumbers are processed at industrial plants. Automated processing is often used to cut the sea cucumbers and remove their internal organs. Typically, only the first steps are carried out at the initial plant and the product is sold in bulk for further processing into beche-de-mer; sometimes whole fresh or frozen sea cucumbers are sold to intermediate buyers. Another particularity of *C. frondosa* is the separate marketing of the prominent oral complex or aquapharyngeal bulb in a dried form called the "flower". Finally, both the muscle bands and the gonad of *C. frondosa* are distinctively large and brightly coloured; they can sometimes be sold separately, usually frozen.

While the exploration of its nutritional and bioactive properties is still in its infancy, the cold-water habitat and plankton-based diet of *C. frondosa* give it a different dietary profile than that of deposit-feeding sea cucumbers which dominate the markets (see Box 8). The general health benefits ascribed to sea cucumbers are present, but key elements also stand out (see Section 14.2). One of them is the compound "frondoside A", which has been determined to possess strong anticancer and immunomodulatory properties; other promising avenues include bioactivity related to the treatment of diabetes and obesity disorders (Gangadaran and Cheema, 2017; Hossain, Dave and Shahidi, 2020; Vaidya and Cheema, 2014). Interistingly, non-negligible regional variations in the biochemical profile of *C. frondosa* are also emerging, for instance with respect to amino acids, fatty acids, vitamins, and pigments (Morrison *et al*., 2023).

16. Recommendations for the management of *Cucumaria frondosa*

16.1 PRECAUTIONARY APPROACH

The precautionary approach in fisheries is a management strategy that aims to ensure sustainable use of the marine resource, especially in situations where there is uncertainty about the stock size and the impact of the harvesting activities. This approach considers known risks, but also potential ones that may arise in the future. Typically, this management approach involves setting conservative limits on the amount that can be harvested, based on the best available scientific information and adjusting those limits as new data becomes available. For instance, biological and ecological aspects of *Cucumaria frondosa* that have remained problematic include the ageing of captured individuals that would allow reliable population metrics to be obtained, the location of nursery grounds where protection efforts could be focused (currently only known for southern Hudson Bay; Hamel *et al*., 2023) and the natural mortality rates and population turnovers that would inform on sustainable capture rates.

The precautionary approach can be applied at the ecosystem level to manage the fishery for sea cucumbers, which takes into account the interactions of sea cucumbers with the environment and with other species. In the case of *C. frondosa* off the coast of Newfoundland, Canada, there appear to be differences in the population structure between two main beds in the fishing ground, namely the Northwestern and Southeastern beds of NAFO Division 3Ps (DFO, 2023). At present, the biological and oceanographic factors that may explain these differences and whether long-term harvesting of sea cucumbers can exacerbate this phenomenon, potentially leading to overfishing, are largely unknown. At the ecosystem level, setting quotas that reduce the risk of overexploitation for *C. frondosa*, and consideration of the impact that the fishery has on non-target species, is an important part of implementing the precautionary principle for long-term sustainability.

Despite the key differences outlined earlier, industry best practices available for other sea cucumber fisheries (Friedman *et al.*, 2008; Purcell *et al.*, 2010) may be transferrable to *C. frondosa*. These universal recommendations comprise four major themes: (i) communication among stakeholders, (ii) protection of spawning adults, (iii) promotion of high-quality processing methods, and (iv) development and implementation of management plans (Friedman *et al.*, 2008; Purcell *et al.*, 2010). They are further discussed below.

16.2 COMMUNICATION AMONG STAKEHOLDERS

Successful management of any fishery critically depends on the co-operation among all stakeholders, including harvesters, processors, buyers, scientists, government managers and policymakers, and Indigenous communities (Friedman *et al.*, 2008). This co-operation can be maintained by creating frequent opportunities for all stakeholders to communicate and exchange information. Communication should go beyond informing stakeholders of fishery regulations to include the dissemination of the latest scientific information and stock assessments (Purcell *et al.*, 2010). The establishment of different lines of communication and regular interactions among stakeholders is key to building and maintaining co-operation and understanding. Crucially, the capacity for the different stakeholders to self-advocate for their own interests and to negotiate how the fishery should be managed requires everyone to understand the science underpinning management decisions. Social acceptability is also highly desirable (Box 15).

BOX 15

Public awareness of the fishery for sea cucumbers

Public awareness of the fishery for *Cucumaria frondosa* has grown over the past two decades, but it remains limited outside of consumers of the beche-de-mer and the rare Indigenous communities that integrate the species to their diet. This is true even in countries where the species is commercially harvested. Efforts to increase awareness and support for the fishery and how it is managed can include public education programs targeting youths and adults, publications in local newspapers, and television broadcastings of news and public interest. Recent examples include efforts by an Indigenous community in northern Canada to manage their subsistence fishery and to collaborate with scientists that were featured in the Nunatsiaq News in a 2019 piece titled "Meet the marvellous sea cucumber" (Rhoner, 2019). Also, the 12th episode of season 19 of a major television show (Land and Sea) produced by the Canadian Broadcasting Corporation showcased the Newfoundland sea cucumber fishery and ongoing academic research. This show was titled "The creatures called sea cucumbers" and aired in January 2020 (https://gem.cbc.ca/land-and-sea-nfld/s55e08).

In the Canadian context, where the exploitation of *C. frondosa* is currently concentrated, industry stakeholders, and partners of the commercial fishery work closely with scientists and government managers and policymakers. At the sub-national (provincial) level, fisheries scientists inside the government often invite industry and academic partners to attend regional stock assessments of *C. frondosa*. In eastern Canada, many industry stakeholders participate in fisheries other than that of sea cucumbers. They are well-versed in how fisheries are regulated and managed but are just coming to understand that sea cucumbers differ fundamentally from all the traditional products such as groundfish, shrimp, lobster, and crab. Members of Indigenous communities in northern Canada have only recently started exploring the development of a commercial fishery for *C. frondosa* in Nunavut.

16.3 PROTECTION OF IMMATURE INDIVIDUALS AND SPAWNING ADULTS

A key factor for the majority of sustainable fisheries is to protect spawning adults to sustain a healthy demographic structure of the stocks. This can be achieved through the establishment of no-take zones, implementation of minimum size limits, improvements to the fishing gear design, and closure of the fishery during the spawning season (Friedman *et al.*, 2008; Purcell *et al.*, 2010). Protection of known nursery grounds should also be considered (Hamel *et al.*, 2023).

In Canada, marine protected areas (MPAs) effectively serve as no-take zones. For example, the Laurentian Channel MPA is a relatively large one in eastern Canada with an area of about 11 580 km^2. This MPA intersects with the fishing area for *Cucumaria frondosa* in the NAFO Division 3Ps such that it may help replenish stocks in the neighbouring areas. Species-specific no-take zones for *C. frondosa*, however, have not been established. Yet, a nursey habitat was recently identified in northern Canada, which makes it a good candidate for formal protection to ensure long-term sustainability of the local subsistence fishery for *C. frondosa* (Hamel *et al*., 2023).

The fishery in the province of Québec is the only one to enforce a minimum size limit for *C. frondosa*. There, the minimum size is 11.4 cm in body length, which is above the estimated size range of 8–10 cm associated with sexually mature individuals (see Section 7.1). Other jurisdictions in Canada have not yet imposed a minimum size limit to protect spawning adults from being harvested. Due to the slow growth rate of *C. frondosa* and its other unique biological traits, the minimum size limit should ideally be set at 12 cm (fully contracted length) to give the recruiting individuals additional time to mature and spawn over one or two seasons before being removed from the population. This precaution would also help maintain suitable densities of mature adults during the breeding season, as *C. frondosa* is known to rely on inter-individual chemical communication to coordinate gamete production (Hamel and Mercier, 1996a; Hamel and Mercier, 1999).

The fishery for *C. frondosa* in eastern Canada is generally closed during the spawning season. However, two provinces (Nova Scotia and New Brunswick) still allow fishing in spring during a period that is likely to overlap with spawning. A closer examination of region-specific timing of spawning (i.e. reproductive phenology; see Section 7.1) could better inform when to close the fishery to protect spawning sea cucumbers.

Improvements should be made to the fishing gear design, not only to increase the efficiency of capturing sea cucumbers, but also to restrict capture to those individuals over a certain size. Gear restrictions for the commercial fishery in eastern Canada currently entails a mesh size requirement of 80 mm (inside knot) on the sea cucumber drag (DFO, 2019). Because current catches still comprise undersized individuals, along with some bycatch species, increasing the mesh size on the drag is strongly recommended (for example to 100 or 120 mm).

16.4 PROMOTION OF HIGH-QUALITY PROCESSING METHODS

Beche-de-mer is graded according to its quality, with grade A being the highest (Friedman *et al.*, 2008). Hence, the promotion of high-quality processing and value-added products is essential to maintaining and, ideally, to increasing the value of the beche-de-mer. This is especially relevant in fisheries where a quota is in place. There are several ways to promote better processing of sea cucumbers, including that of *Cucumaria frondosa*. By understanding how market prices are affected by product quality, harvesters and processors can modify how sea cucumbers are handled and processed (Friedman *et al.*, 2008). Ultimately, this can promote the negotiation of fair prices.

Chiefly, the best practices in handling and processing sea cucumbers during and after harvesting is to treat the sea cucumbers gently to minimize bruising and damage to their skin and body wall. On fishing vessels and at the dockside, harvested individuals of *C. frondosa* are sometimes treated roughly; they are dropped from the nets onto the deck, and then shovelled or poured in and out of larger containers. In lieu of refrigeration, ice is often used to reduce thermal shock while sea cucumbers are transported overland for processing. However, direct contact of the sea cucumber skin with ice can negatively affect their quality (Gianasi, Hamel and Mercier, 2016). Concerted effort to treat sea cucumbers with utmost care throughout the entire supply chain to ensure optimal quality of end products is highly recommended.

The promotion of proper handling at sea can also empower harvesters to negotiate fair prices for products of higher quality. Harvesters in Canada are commonly organized into unions. For example, in the province of Newfoundland and Labrador, the roughly 15 000 inshore harvesters and plant workers (all seafood species combined) are represented by the Fish, Food & Allied Workers Union (FFAW-UNIFOR). In addition to wages, the union is also involved in negotiating prices of sea cucumbers through collective bargaining. Moreover, it is not uncommon to have union representatives participating in federal stock assessments of sea cucumbers.

The knock-on effect of high-quality processing at the plant can translate to more valuable beche-de-mer products and, in turn, to higher prices on the market. Increasing product value may incentivize harvesters and processors alike to shift the industry focus from producing high volumes of low-value products to producing less of high-value products (see Box 10). Should this incentive be strong enough, an industry-wide effort to reduce the total volume of the catch can be an earnest step towards a sustainable fishery for *C. frondosa*. However, economic pressure on government policymakers to increase the quotas (including the total allowable catch) and the number of licences constitutes a key obstacle towards volume reduction and, indirectly, the built-in incentives towards high-quality high-value processing. Along with increasing the grade of the final products, thoughts should be given to fully processing sea cucumbers locally and developing value-added products, such as nutraceutical capsules produced from the organs that are currently discarded (see Box 14). Overall, a more fully optimized exploitation of the resource would lead to a healthier industry, whereby the same incomes could be generated through lower capture volumes that would ensure the perennity of the wild stocks.

16.5 DEVELOPMENT AND IMPLEMENTATION OF MANAGEMENT PLANS

A comprehensive plan to manage *Cucumaria frondosa* is essential to regulate access to this resource and to respond to changes in its stock status, especially under the anticipated impacts of climate change. Recommendations that can be made to government managers and policymakers for developing a management plan for sea cucumber involve three main themes: access to the fishery, monitoring the fishery, and outlining triggers for intervention by management (Friedman *et al.*, 2008; Purcell *et al.*, 2010).

Managing access to a fishery can involve place-based or user-based access (Purcell *et al.*, 2010). In eastern Canada, entry to the commercial (and exploratory) fishery for *C. frondosa* has been limited through licences which is a user-based model adhering to the precautionary principle. Because of the potential inter-connectedness of the populations of *C. frondosa* across eastern Canada (So *et al.*, 2011), harvesting from one area can affect the population dynamics in a neighbouring fishing area. Hence, good management in one stock can have an overall positive effect on nearby populations and, inversely, poor management can have far-reaching negative outcomes (see Box 3).

In eastern Canada, the management of *C. frondosa* involves monitoring the effect of activities on both catches and stocks. Catch statistics mainly come from four sources: (i) obligatory dockside monitoring, (ii) a Vessel Monitoring System (VMS) on all fishing vessels, (iii) at-sea observers tasked with monitoring some fishing trips, and (iv) logbooks obtained from harvesters. Catch records ensure that harvesters comply with quotas and fish in areas where they are licenced to do so. For monitoring of stocks, Purcell *et al.* (2010) recommended conducting fishery-independent stock assessments. As an example of a fishery-independent survey, government scientists carry out directed surveys of *C. frondosa* in the waters south of insular Newfoundland, Canada. To add to this, incidental records of *C. frondosa* from directed surveys of scallops in these waters are all used in assessments of sea cucumber stocks.

To mitigate against unfavourable changes in the status of the fishery, management plans should define thresholds levels for key indicators and prescribe actionable measures when these levels are reached (i.e. triggers for management intervention; Friedman *et al.*, 2008). The development and implementation of management plans that monitor ecologically important indicators, such as densities and biomasses, and that clearly outline intervention strategies are strongly recommended in the case of *C. frondosa* (Box 16).

BOX 16

Key recommendations for improved management

While our understanding of *Cucumaria frondosa* has grown substantially over the past three decades, and information exists on most aspects of its biology and ecology, future research should strive to address some of the most pressing uncertainties. In addition, new and improved practices should be considered to favour sustainable fisheries across the species distribution range. Some key recommendations are listed below:

- Additional research at the organismal and population level should include the development of an ageing method, characterization of nursery habitats, confirmation of larval and adult dispersal potential and migration patterns, and determination of population genetics, to help manage stocks at regional and global geographic scales.
- Stock and capture assessments and price settings should all move away from weight-based metrics, given the difficulty associated with accurately weighing sea cucumbers that may hold or release large amounts of seawater. Length and girth measurements are only marginally better and should not be considered either. Instead, stocks, captures and prices should all be based on the sea cucumber unit, ideally for individuals above a certain size.
- Ideally, and in line with the above recommendation, non-destructive stock assessments using video transects should be held on a regular basis (e.g. annually), minimally every three years for all regions where commercial harvests occur.
- To favour cross-jurisdiction exchanges and the flow of crucial information, stakeholders should consider holding a national conference or workshop involving industry, managers, policymakers, and academia, at least on a decadal basis.
- In addition to more frequent and better designed regional and global stock assessments, triggers for management intervention such as limit reference points (biomass or CPUE levels below a certain threshold) should be developed.

17. General conclusion

This document summarizes and distils available information on *Cucumaria frondosa*, drawing heavily on previous efforts to synthesize the scientific knowledge base by Gianasi *et al.* (2021). Given that most capture fisheries for other species of sea cucumbers have been overexploited elsewhere in the world, there is an opportunity to avoid this outcome for *C. frondosa*. However, this window of opportunity is closing rapidly. The current reality is that enormous quantities of *C. frondosa* have been and continue to be harvested and that this species is probably greatly undervalued as beche-de-mer. Despite the often cited precautionary principle in managing sea cucumber stocks, the earliest fishery for *C. frondosa* that started in Maine (United States of America) in the 1990s appears to have already gone over the threshold of profitability and is now very limited. If left unchecked, the fisheries in Canada and elsewhere in the North Atlantic may soon follow the same trajectory. A beacon of hope may be offered by sea cucumber products of greater value sold at higher prices. The potential development of a new fishery for *C. frondosa* in northern Canada is a prime opportunity to further demonstrate the benefits of a low-volume high-value model.

Transitioning from the current finfish-inspired high-volume low-value model, which is both destructive and irresponsible, toward a more sustainable low-volume high-value model comes with daunting challenges. A shift in harvesting and processing methods is required to ensure consistent high-quality products. Emphasis should be placed on handling sea cucumbers with care since their body wall is unprotected and easily damaged, yet it is at present the most valuable commercial asset. The high-volume (trawlnet) methods employed for the capture *C. frondosa* go against the reverence that their main consumers bestow to sea cucumbers. Other species of sea cucumbers are usually harvested by hand and carefully handle throughout the processing chain.

On the basic research side, habitat requirements for newly-settled recruits and juveniles and the location of these nursery habitats are largely unknown for *C. frondosa* (and most other species), severely hampering efforts to protect stocks through spatial planning. However, during the process of examining the feasibility of an Arctic fishery for *C. frondosa* in Nunavut, Canada, a major nursery habitat was identified (Hamel *et al.*, 2023). This discovery will hopefully support the establishment of a marine protected area and development of a management plan for a sustainable fishery, whether it remains a subsistence fishery and/or becomes a commercial one. Efforts should be undertaken to identify and protect nursery grounds of *C. frondosa* elsewhere in the North Atlantic to increase sustainability in the most heavily fished areas.

The lack of knowledge on sustainable exploitation rates and the inability to age wild-caught individuals of *C. frondosa* are serious impediments to the proper management of stocks. Without knowing population age structures and sustainable exploitation rates, it is difficult to both determine and intervene when the population is not self-sustaining. The next best option to tackle questions of age structure is to rely on indirect indicators and relative age, as opposed to true age. Various measurements of size and weight have been used, but these values are intrinsically highly variable and inaccurate. In the context of harvesting and processing, this variability, however, depends mostly on stress levels. Notably, freshly captured individuals of *C. frondosa* tend to be swollen in shape (colloquially known as "footballs" in eastern Canada) as a response to the disturbance associated with bottom trawling. After having been stored in the hold of a fishing vessel for several hours or days, sea cucumbers at the dockside appear to be flattened, limp, with some displaying partly extruded tentacles and partial evisceration. Therefore, measurements of size and weight can vary greatly, depending on how much water is retained inside the body cavity in response to stress (e.g. active buoyancy adjustment or ABA), how much time has elapsed since capture, and how much pressure the sea cucumbers have sustained (i.e. maximum at the bottom of the hold or vats). Work towards establishing better measurements standards is under way (Trenholm *et al.*, 2024).

Trawl-induced ABA behaviour in *C. frondosa* (Hamel *et al.*, 2019) can additionally have wide-reaching implication for catchability. Speculatively, this may suggest that successive attempts to catch sea cucumbers in a given area may require increased effort over time. Disturbed individuals exhibiting ABA may even disperse into deeper depths outside their preferred range. On the bright side, sea cucumbers are known to occur in certain regions where bottom trawling does not occur as frequently, which may inadvertently provide a sanctuary for the species to thrive and replenish stocks of nearby fishing grounds.

Advocating for the low-volume high-value model for the commercial fishery of *C. frondosa* worldwide cannot be emphasised enough. Humankind has been interacting with sea cucumbers since time immemorial, especially in Asia and in northern Canada where there is a culture of consuming them. Scientific studies of the taxonomy, biology, and ecology of sea cucumbers, including that of *C. frondosa*, have expanded our understanding of this group of animals. Yet, among the commercially exploited sea cucumbers, *C. frondosa* exhibits major biological differences related to reproduction, feeding, and growth, which set it apart from other species.

The potential to market beche-de-mer and other derivatives of *C. frondosa* as high-quality products exists and should be realized to transition away from the current mass fishery model. In addition to folk beliefs with respect to the nutritional and healing properties of *C. frondosa*, a suite of biochemical analyses have already demonstrated beneficial effects of extracts on human health, such as antimicrobial, anticoagulant, anticancer, antiobesity, and anti-inflammatory responses. As consumers become more familiar with this species from the North Atlantic and the Arctic, strategic marketing, high-quality processing, and sustainable fishery management will be required to help position *C. frondosa* and products derived from this species as highly prized items with exceptional health benefits.

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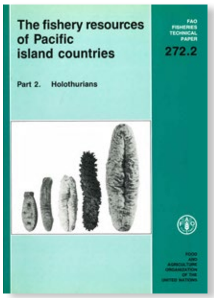

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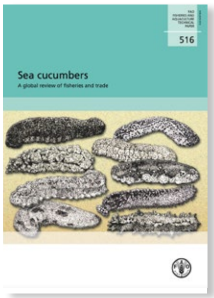

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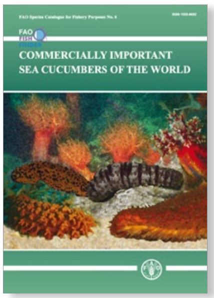

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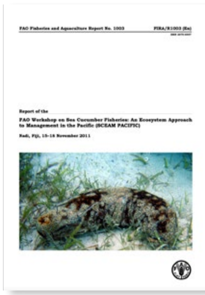

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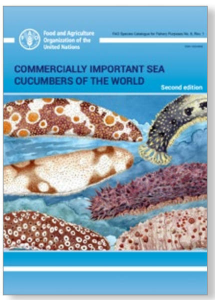

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Notes and observations

This technical guide provides an introduction to northern sea cucumbers, focusing on the biology, ecology, and commercial exploitation of the dominant species, *Cucumaria frondosa*, also known as the orange-footed or the Atlantic sea cucumber. A vast scientific knowledge base, gathered over some 40 years of research, is being made accessible to a non-scientific audience, including the major stakeholders in the industry, with an aim to guide the management of the species across its broad Arctic, North American and North European range. Following a basic introduction to the unique anatomy and appearance of *C. frondosa*, the guide goes on to cover the distribution and habitat, environmental tolerance, life cycle and sexual reproduction, growth patterns, movement ecology, and main threats faced by the species. Additional sections present an overview of the wild stocks, commercial harvesting practices, aquaculture potential, processing chain, and diversified marketing strategies. Finally, the key elements that fundamentally distinguish *C. frondosa* from all major sea cucumber species on the market today are summarized, and perspectives on its conservation and management are offered.

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