A predator´s diet
– prey composition analysis of Atlantic bluefin tuna in Skagerrak and Kattegat

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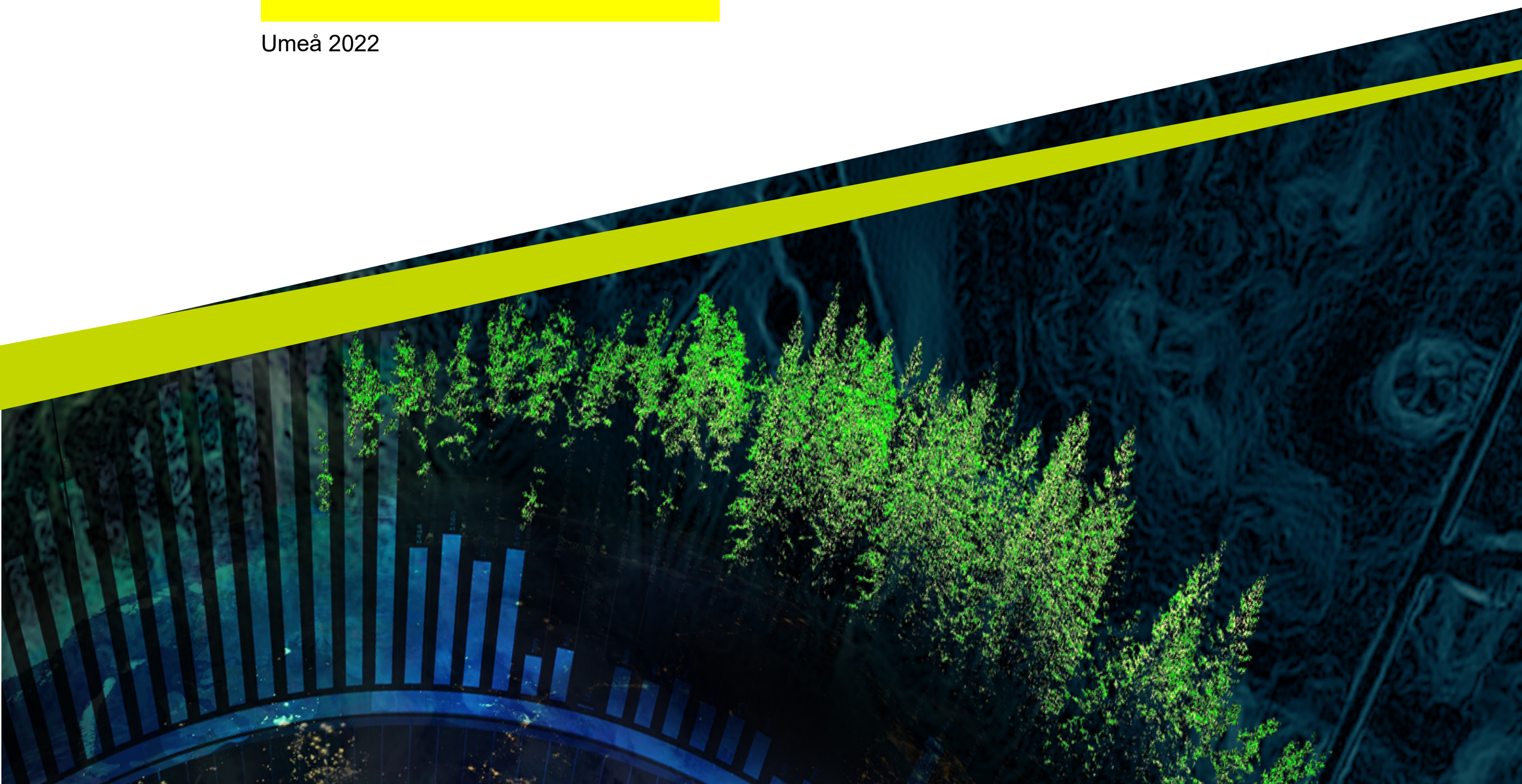

Atlantic bluefin tuna feeding in north-eastern Europe – A study on Atlantic bluefin tuna stomach content in Skagerrak and Kattegat seas

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Abstract

Atlantic bluefin tuna is an efficient predator and was a common pelagic species in the north-east Atlantic, including the North Sea and the areas of Skagerrak and Kattegat, in the first half of the 20th century. Following a population collapse in the 1960s, the tuna disappeared from Skagerrak and Kattegatt, however in recent years the tuna has returned to these waters following successful management. Little is known about this returning population, and research is conducted to get a better understanding of their origin and ecological impact. In this study, stomach content analysis was made for 19 tunas caught in Skagerrak/Kattegat to gather insights into tuna feeding habits and prey preferences in the area. The stomach content analysis revealed 17 prey species. Garfish was the most prominent prey by weight and abundance, followed by mackerel, cod and herring. Total prey consumption was calculated for four possible population sizes of Bluefin tuna in Skagerrak/Kattegatt (500, 1500, 15 000 and 25 000 individuals) over a visiting season of 90 days. The results of these calculations showed predation on cod and mackerel may be significant given high populations size scenarios of tuna, in relation to Swedish commercial harvest. The study is the first to report feeding habits of Bluefin tuna in Skagerrak/Kattegat and results are discussed from a resource conflict management perspective.

Keywords: Atlantic bluefin tuna, stomach content analysis, fisheries.

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Abbreviations

ABFT	Atlantic bluefin tuna
SCF	Size correction factor

1. Introduction

Atlantic bluefin tuna, *Thunnus thynnus* (Linnaeus, 1758) (hereby referred to as ABFT), is an efficient predator and was a common pelagic species in the north-east Atlantic, including the north sea and the areas of Skagerrak, Kattegat and Öresund in the first half of the 20th century (MacKenzie & Myers 2007; ICCAT 2017a; Bennema 2018). The fish was believed to migrate from the Mediterranean and North/Central American spawning grounds to the North Sea, presumably for feeding (Fromentin 2009; Cort & Abaunza 2015).

Developed commercial fisheries for ABFT and its primary prey species put great pressure on the population after the second world war (1940-1960) (Tiews 1978; MacKenzie & Myers 2007) causing a population collapse in the North Sea in 1963 (Figure 1), resulting in a complete disappearance of the species in Skagerrak and Kattegat (Tiews 1978; Mather et al. 1995; Fromentin & Powers 2005; Bjørndal & Brasão 2006; MacKenzie & Myers 2007; Fromentin 2009). Stock assessments made by the International Commission for the Conservation of Atlantic Tunas, or ICAAT, estimated that 40% of historical viable ABFT spawning stock remained in 2009 (ICCAT 2009).

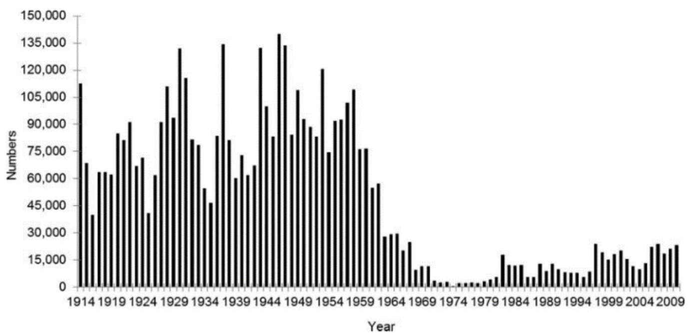

Figure 1 Spawning ABFT catches in traps by Morocco, Portugal and Spain in the Strait of Gibraltar between 1914 and 2010 visualizing the population collapse in early 1960s (Cort & Abaunza 2015).

Since the collapse, improved management, mainly through restricted harvest, have succeeded in increasing the stock, and ABFT have recently reappeared in Skagerrak and Kattegat (Bennema 2018), raising questions on how they may affect local ecosystems as a top predator. Studying feeding habits and prey composition is one piece of the puzzle in understanding the impact of returning ABFT and developing proper management.

1.1. Management

1.1.1. Fisheries

Following WW2, northern European commercial fisheries expanded greatly in capacity. Fisheries on ABFT intensified from under 1000 tonnes combined between Norway, Germany, Sweden and Denmark in the 1930s, to almost 18 000 tonnes between the same countries in the early 1950s as a result of effectivization in methods and a corresponding development of processing facilities (Tiews 1978; MacKenzie & Myers 2007; Figure 1; 2).

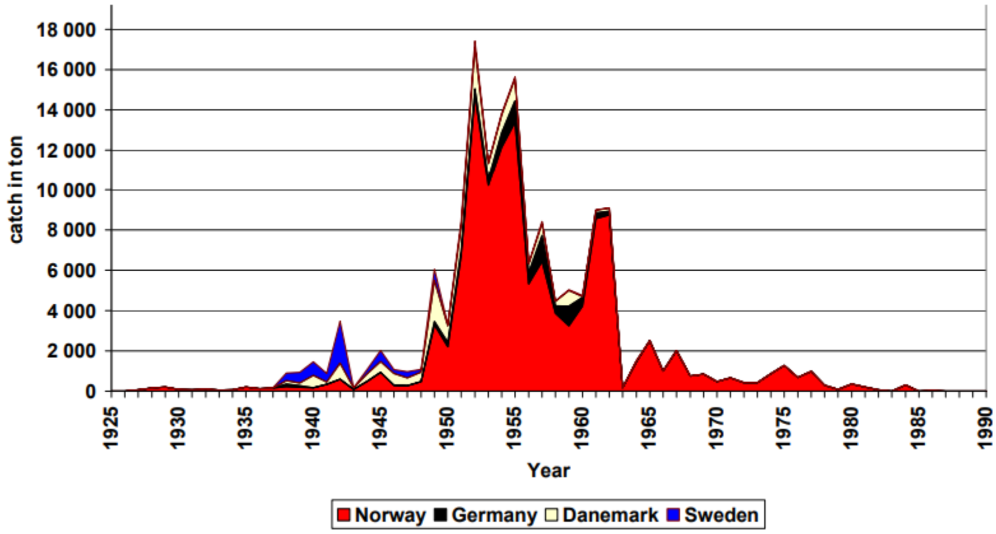

Figure 2 Atlantic bluefin tuna harvest in metric tonnes in the North Sea by country with Norway (red), Germany (black), Denmark (white) and Sweden (blue) represented between 1925 and 1990 (Fonteneau 2009)

In 1978, central North Sea Norwegian fishing grounds had reportedly only held substantial stocks of ABFT from the 1952 year-class since an assessment just prior to the 1963 collapse. All other year classes had been lacking in stock numbers (Tiews 1978). Abundances have been deemed too low for commercial or recreational fisheries in northern European waters since the population collapse in the 1960s (MacKenzie & Myers 2007; Figure 1; 2), but great interest from commercial fisheries puts high pressure on stakeholders and legislators, with ABFT being one of the most valuable fish species on the market (Porch 2005). Although, in 2006, agencies and NGOs clearly stated the population of ABFT were too small to be resilient and withstand commercial and recreational fishing pressures (ATRT, S.L. & WWF 2006).

Harvest quotas are allocated to several European and non-European countries (Korman 2010; ICCAT 2021). In 2011, Juan-Jordá et al. (2011) estimated both western and eastern ABFT populations to be overexploited, meaning that biomass of spawning stock (adult) fish is insufficient and limits reproduction (MacKenzie et al. 2009). With an exploitation rate surpassing the maximum sustainable yield (MSY), the eastern ABFT population were the most overexploited of the populations of tunas and their relatives covered in an analysis by Juan-Jordá et al. (2011). In the 2020 stock assessment by ICCAT, recruitment of the western ABFT stock were lower than those estimated in the 2017 stock assessment. Between 2018 and 2020, the stock biomass declined by 11,7% (ICCAT 2021). Hence, during the ICCAT 2021 assembly, WWF stated that maintaining harvest quotas would risk negative population trends and overfishing (ICCAT 2021).

Researchers have tried to find the reasons for the northern European ABFT collapse in the 1960s, and it is now established that fisheries on important ABFT prey species in northern Europe and fisheries on juvenile ABFT were the main causes for the collapse (Tiews 1978; Mather et al. 1995; Fromentin & Powers 2005; Bjørndal & Brasão 2006; MacKenzie & Myers 2007; Fromentin 2009). Fisheries in north European feeding grounds have developed dramatically and high-energy prey species (mackerel, herring etc.) fisheries have affected prey populations greatly (Hornborg et al. 2020). This lack of prey species in conjunction with local overfishing of ABFT in the northern feeding grounds (Fromentin 2009) caused low abundances in these waters. Fisheries on spawning individuals in southern Europe also greatly affected the species (Figure 1). Fisheries on juveniles is a common way of decreasing a population as it reduces future yield and recruitment (Najmudeen & Sathiadhas 2008). Juvenile fisheries on ABFT in the Bay of Biscay is thought to have resulted in just that with intensive fishing on individuals that had not yet had the time to spawn (Fromentin 2009; Cort & Abaunza 2015).

1.1.2. International Commission for the Conservation of Atlantic Tunas

As ABFT is a migratory species affecting fisheries in multiple countries, international management is needed. Multi-national ABFT management initiatives started in 1966 with the establishment of a management authority, the International Commission for the Conservation of Atlantic Tunas, or ICCAT, and through this, the adoption of the Convention for the Conservation of Atlantic Tunas (Battaglia et al. 2013; ICCAT 2017a; FAO 2022; EFCA n.d.; *Dartmouth SESMAD. Atlantic Bluefin Tuna (ICCAT)* n.d.). ICCAT is an intergovernmental fishery organisation consisting, as of 2022, of 53 contracting parties and 6 cooperating states (FAO 2022) working for the conservation and management of tuna and similar species in the Atlantic and adjacent waters (EFCA n.d.). ICCAT works with fish management both at a legislative level and at a practical level with research programmes and management development (ICCAT 2021).

1.1.3. Reappearance

Likely as a result of management actions tuna have returned to previously inhabited areas (Cort & Abaunza 2019). In 2006, ICCAT adopted a ABFT recovery plan. Spanning from 2007-2022. Management measurements were to include lowered total allowable catches (TACs), shorter fishing season, restrictions in fishing areas and fishing times, and increased minimum size limits to protect juveniles (ICCAT 2006). This, in conjunction with requirements for all entities fishing for ABFT to develop management plans for their respective areas, have assisted population preservation and growth (Cort & Abaunza 2019; ICCAT 2021).

Complementing this have been implementation of successful management actions for mackerel and herring, presumably important ABFT prey species in Skagerrak, Kattegat and Öresund. This has resulted in ABFT having returned to the area, where the species has been reported since the early- to mid-2010s (MacKenzie et al. 2009). Following ABFTs return to previously inhabited ecosystems, impact on these ecosystems is resumed with potentially unknown new effects.

1.2. Aim and research question

As a reappearing species with reoccurring migrations into Skagerrak, Kattegat and Öresund, a multitude of issues and questions regarding ABFTs presence and possible ecosystem impact as a top predator has emerged. Fisheries, ecosystem changes and other anthropologically induced ecological and environmental changes have affected these waters since ABFT was last present (Kadin 2008; Klima- of Forurensningsdirektoratet 2012). ABFT are opportunistic feeders (Battaglia et al., 2013), but detailed feeding habits as well as ecological consequences of their feeding in Skagerrak, Kattegat and Öresund is unknown.

Changes in abundance of top predators have the potential to alter complete ecosystems with impacts throughout the trophic chain (Logan et al. 2011) Large and abundant piscivore predators may have an effect on prey fish population, and may act as a catalyst for increased conflicts within a fishery. On Sweden's Baltic coast, commercial fisheries have been affected by seal feeding on commercially valuable fish species and affecting fishing gear, causing conflict between seal and fisheries (Bruckmeier & Höj Larsen 2008; Bruckmeier et al. 2013; Tverin et al. 2019; Waldo et al. 2020). Potentially, ABFT could be at risk of initiating a similar conflict with local fishery in Skagerrak and Kattegat if they continue to migrate to these waters and increase in numbers. Hence, understanding structure and function of the impact of a top predator such as the ABFT on trophic relationships is important in developing functional management. Such understanding is needed to develop proper management tools and conservation measures, and to mitigate conflict with commercial fisheries at an early stage. An important first step is to better understand ABFT prey composition, i.e. what do ABFT eat when visiting Skagerrak, Kattegat, and Öresund.

In this study, I aim to gain an insight into ABFT feeding habits on the feeding grounds of Skagerrak, Kattegat and Öresund, by stomach content analysis of ABFT caught within an ongoing research program in the area, and from unintended commercial bycatch. Estimations on future tuna impact on prey species will then be made based on the stomach-content analysis. Based on the diurnal feeding habits shown in the Mediterranean (Battaglia et al. 2013), analysis of possible diurnal feeding in the waters of this study is of interest and will be analysed to further understand ABFT feeding habits and preferences. With this insight into feeding habits and prey species, I hope to provide results that open new doors in developing management actions and further research on ABFT and its management.

2. Method

2.1. Atlantic bluefin tuna biology

Bluefin tuna is a long-lived species, with a lifespan of about 32 years as indicated by radiocarbon deposition (ICCAT 2017b). It can reach 330 cm (SFL) and weigh up to 725 kg (ICCAT 2017a). The growth is rapid, the weight at age 1 is around 4kg and at age 20 around 400kg (Fromentin & Fonteneau 2001). Bluefin tuna is a highly migrating species that migrate from spawning grounds in the south to foraging grounds in the north including Skagerrak and Kattegatt (Figure 3).

2.1.1. Spawning

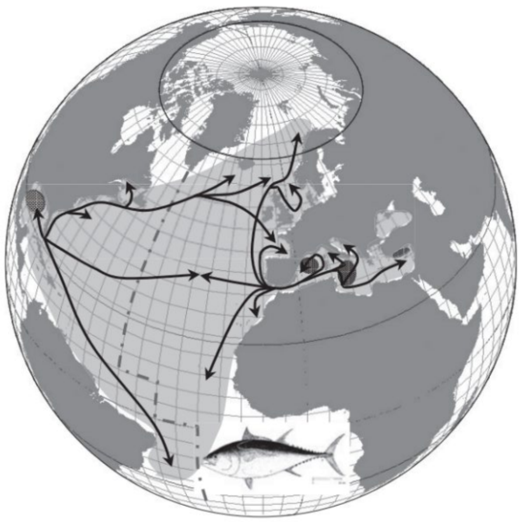

Figure 3 ABFT spatial distribution with spawning grounds marked in dark grey. Dashed dotted line marks the two ICCAT management units (Fromentin and Powers, 2005).

Spawning grounds for the ABFT that is present in Skagerrak and Kattegatt are currently not fully known. ABFT have at least two main known spawning areas: the western population in the Gulf of Mexico and the eastern population in and around the Mediterranean Sea (Safina & Klinger 2008; ICCAT 2017b). ABFT fisheries are managed as two separate management units based on their respective spawning grounds: i.e. the eastern stock, and the western stock. These are separated by the 45°W meridian (see Figure 3) (Safina & Klinger 2008; ICCAT 2017a). The two populations have different ages for spawning, with the western population reaching maturity at age 8 and peak spawning at the age of 15, while the eastern population reach maturity at age 4 (115 cm / 30 kg) and peak spawning at age 5 (Fromentin & Fonteneau 2001; Fromentin & Powers 2005; ICCAT 2017b;

a). At spawning age, they produce one cohort per year (Fromentin & Fonteneau 2001). The eastern population start spawning later in the year compared to the western. There is also a difference within the eastern population where fish in the eastern Mediterranean spawn mid-May to mid-June and fish in the western Mediterranean have spawning times mid-June to mid-July (ICCAT 2017b).

Both the western and the eastern populations migrate annually and mix at the foraging grounds in the north Atlantic (Lutcavage et al. 1999; Nemerson et al. 2000; Block et al. 2005; Carlsson et al. 2007; Safina & Klinger 2008; Figure 3). The western spawning stock is considerably smaller than the eastern stock with less than 50 000 metric tonnes biomass in 1975 and a drastic decrease in the decades following. The eastern spawning stock was in 1975 over 300 000 metric tonnes, but have also decreased dramatically since and were in the early 2000s passing 100 000 metric tonnes at a negative slope (Korman 2010). In 2017, ICCAT ABFT stock assesment for 2015 estimated the spawning stock biomass at 600 000 metric tonnes for the eastern population (ICCAT 2017b).

2.1.2. Energy requirements and feeding

Bluefin tuna has a digestion system of high visceral temperature (Chase 2002; ICCAT 2017a) that is considerably faster compared to that of ectotherm fishes (Carey & Teal 1969; Carey & Gibson 1983; Carey et al. 1984; Stevens & McLeese 1984) and this characteristic is thought important for meeting the energy requirements of the species (Carey et al. 1984). ABFT can sustain a constant body temperature within a wide range of sea temperatures (Chase 2002; ICCAT 2017a). A constant visceral temperature requires high metabolic heat production and functions to minimize circulatory system convective heat loss, both highly developed systems in ABFT (Carey & Gibson 1983; Carey et al. 1984). The stomach can be up to 15°C warmer than surrounding water temperatures depending on water temperatures and ingested prey temperature, leading to constant visceral temperature and considerably faster digestion and prey constituent uptake (Carey & Teal 1969; Carey & Gibson 1983; Carey et al. 1984; Stevens & McLeese 1984). Full digestion of a medium sized fish is completed in 24 hours (Battaglia et al. 2013).

It is thought that this high visceral temperature is important in ABFT summer feeding in cold, rich northern waters where they stock up on fat reserves on sporadically abundant high calorie prey (Carey et al. 1984). For the eastern population, these northern waters includes the North Sea, including Skagerrak and Kattegat (Safina & Klinger 2008), it is not yet known if this includes the western population as well.

ABFT are opportunistic feeders, and feed on a large range of fish species, crustaceans, cephalopods and zooplankton (Chase 2002; Battaglia et al. 2013). Juvenile ABFT use ram-feeding, where they swim through dense schools of small prey with open mouth. Mature individuals also use ram-feeding but also more selective feeding methods focused on larger prey (Chase 2002).

In the Mediterranean, ABFT tend to have a daily feeding activity pattern (Battaglia et al. 2013). During daylight, feeding is concentrated on larger prey, while the darker hours of the day are focused on diel vertical migrating species (*Myctophidae, Stomiidae, Paralepididae*, crustaceans and cephalopods) (Battaglia et al. 2013). Other important prey species for the Mediterranean population is pelagic species including sand lance (*Ammodytes tobianus*), herring (*Clupea harengus*), mackerel (*Scomber scombrus*), krill (*Meganyctiphanes norvegica*) and anchovy (*Engraulis encrasicolus*) (Tiews 1978; Eggleston & Bochenek 1990; Chase 2002; Logan et al. 2011).

Studies on Southern bluefin tuna (*Thunnus maccoyii*) have shown energy requirements of about 0,15 megajoules (36 kcal) of gross energy per kilogram of body weight per day (water temperature <15°C) and estimated 56 megajoules (13375 kcal) of gross energy for 1 kilogram of body mass gain (water temperature 16°C) (Glencross et al. 2002). Mackerel contains about 16 KJ/g and herring contains about 13 KJ/g in the northeast Atlantic in September (Stansby & Lemon 1941; Bachiller et al. 2018).

2.2. Research area

Skagerrak and Kattegatt seas are two areas connected to (Kattegatt) and included in (Skagerrak) the North Sea, dividing Sweden, Denmark and Norway. Both seas are valuable and intensively utilized fishing grounds (Hornborg et al. 2020). Öresund is a shallow sound between Sweden and Denmark, connecting the salty Kattegat with brackish Baltic Sea. The sound is one of the most heavily trafficked marine areas in the world. Trawling fisheries have been largely prohibited in the sound since 1932 (Skåne county administrative board 2021), but is extensively being conducted in Skagerrak and Kattegatt. Tunas in this study were caught in two areas: at the northern inlet of Öresund, and between Orust in Sweden and Skagen in Denmark.

2.3. Stomach collection

19 stomachs from ABFT caught in Skagerrak and Kattegatt were analysed for content. All of the stomachs were collected from ABFT within the Scandinavian Atlantic Bluefin Tuna Tagging Program (SABFTP) between 2017 and 2021. The SABFTP catch fish via recreational fishing and tag them with electronic tags that allow tracking of tunas across the Atlantic. 450 ABFT are included in the project and about 300 have been electronically tagged by the SABFTP since 2017.

Catching of large tunas is not free of risks to the fish. Evidence of high survival is ample, but tagging mortality is documented between 3-10% (Stokesbury et al. 2011; ICCAT 2016). Processes evolve and less than 2% of all fish that were caught and tagged in this study died in data collection, these were included in a special ICCAT mortality quota. Of the tuna samples, 5 fish died during tagging due to different circumstances and mishaps in handling. One tuna was caught in a herring trawl, and this sample was processed in advance of this study, thus, no stomach and stomach content weight data were gathered. One stomach sample consisted of intact prey fish regurgitated on deck when handling the ABFT during tagging. The tuna was then released into the ocean, but the otoliths of the vomited prey was saved.

Time of capture is defined as time of hooking and not time of landing the fish. After the bite, this study assumes the ABFT did not ingest any additional prey. Time of hooking for each ABFT sample were divided into two categories: AM (before 12:00), and PM (after 12:00). These two categories represented morning feeding and afternoon feeding of the ABFT. All tuna were caught during daytime.

After collecting the fish, all were taken back into port for extensive sampling and analysis, including the removal of stomach. Generally, the entire contents of the abdomen were cut out and frozen at a minimum -18 degrees Celsius for later processing. If not secured previously, after thawing samples were taken from liver, muscle and fat tissue, the stomach and intestine were separated from the other organs. In some instances the stomach had to be refrozen.

2.4. Stomach processing and content extraction

Stomachs were removed from the freezer 24-48 hours before content extraction and examination. As the stomachs differed in size and weight, thawing times were individually determined to minimize time spent fully thawed as this could result in further post-mortem digestion and spoilage of stomach content.

2.4.1. Data collection for future studies

Samples were collected for further environmental DNA (E-DNA) analysis. E-DNA will be used by a planned future study as a complement to the stomach content analysis performed in this study, and for additional comparison of results in stomach content analysis method development. The samples for E-DNA analysis were collected by washing the corner of the bag containing the stomach with DNA remover or chlorine to remove DNA. This was then washed off with water before making a small incision and collecting 40 ml, or as much as possible, of the liquid surrounding the stomach and other intestines. The bag was then fully opened, and the stomach were removed. A sterile scalpel or scissor were used to open the stomach and 40 ml stomach slurry were collected using a pipette. This study did not use E-DNA in the analysis due to time limitations. Liver sample and muscle sample from the cardia were also collected for future research.

2.4.2. Content extraction

After E-DNA sample collection, the stomach was fully opened. If baitfish were found, it was discarded and not included in the analysis. Whole fish were removed and placed separately for measuring. The stomach was then thoroughly rinsed and examined for all stomach content. Whole fish was identified to lowest taxonomic level and measured in full centimetres (rounded down). Their otoliths were removed if present. Whole prey fish were categorized in four digestive stages. Category 0 represents almost intact prey, category 1 represents partially digested prey, category 2 represents quite digested prey but with flesh still showing, and category 3 represents only skeletal material present. Only whole prey fish that where measured was divided into digestive state categories. Much of the category 3 material (intact spine) was considered too broken up or possibly broken up, this material was not used as measurements would risk misreading and thus not being representative of actual prey size. All undamaged spines were measured.

Only prey identified as digestion stage 1 were weighted as weight on other digestive stages on prey would not be relevant. Weight may be misleading as different species and different size of prey may be digested at different speeds. Otoliths may also break down at different rates but will give a better estimate on feeding habits as they are not digested as rapidly as soft tissue and bones (Tollit et al. 1997a). After otolith removal from intact prey, careful rinse was done for otoliths stuck to prey with caution to minimize risk of prey digestive system damage and possible bias with secondary consumption from this. On measured individuals with intact skulls, otoliths were removed and noted as taken from measured prey to prevent double counting (otolith and measured prey) and thus risking overestimation in prey abundance.

Remaining content was washed in water multiple times to remove all soft tissue, leaving only bones and otoliths. Otoliths are the most dense structures found in teleost (Treacy & Crawford 1981) and were expected to remain at the bottom of the rinsing vessel used. Methods developed for cormorant stomach content analysis was used as it ensures otolith retrieval, while being quick and easily conducted with limited tool and facility requirements (Boström et al. 2012).

All stomachs of tuna caught by the Swedish tagging team were weighted before opening and after they were emptied and rinsed. Stomachs from Danish fish were already opened for E-DNA extraction when weighted. These were instead weighted in their bag with all contents, and weighted emptied and rinsed with that same bag for rough content weight, although without stomach slurry of gastric juices.

Other objects were also collected for identification out of curiosity or for further research, these included foreign objects such as plastics, wood pieces etc., parasites in stomach and intestine, and abnormalities such as cysts on tuna tissue. Objects risking spoilage were put in freezer storage and other object were dried or put in preservatory liquid.

2.5. Stomach content processing

Otolith microstructure analysis is a common method used to determine species, size and age of fish. Otoliths are calcium carbonate bio-crystal structures found in vertebrate inner ears (Sahney & Wilson 2001; Lundberg et al. 2015). On Osteichthyes, or bony fish, otoliths are relatively large compared to other vertebrates and analysis of these allow researchers to determine fish species, size and age with annual and daily growth layers, or growth rings (Stevenson & Campana 1992; Lundberg et al. 2015).

Osteichthyes have three pairs of otoliths in their inner ears used in detecting acceleration, gravity and head movement in all axes. Two of the three otolith pairs, the utricle and lagena, are too small to be efficiently studied in a stomach content analysis and digest more quickly than the larger saccule (Lundberg et al. 2015). Saccule will hereby be referred to as otolith. Otoliths have distinct morphologies which is used in species determination. Different characteristics are used in species determination, such as the general shape and size, sulcus development and shape, rostrum shape, and denticle shape and size (Schwarzhans & Carnevale 2021). (Figure 4) shows important characteristics present on otoliths, although the figure presents two species that are not present in this study, these characteristics are present on all otoliths found in this study.

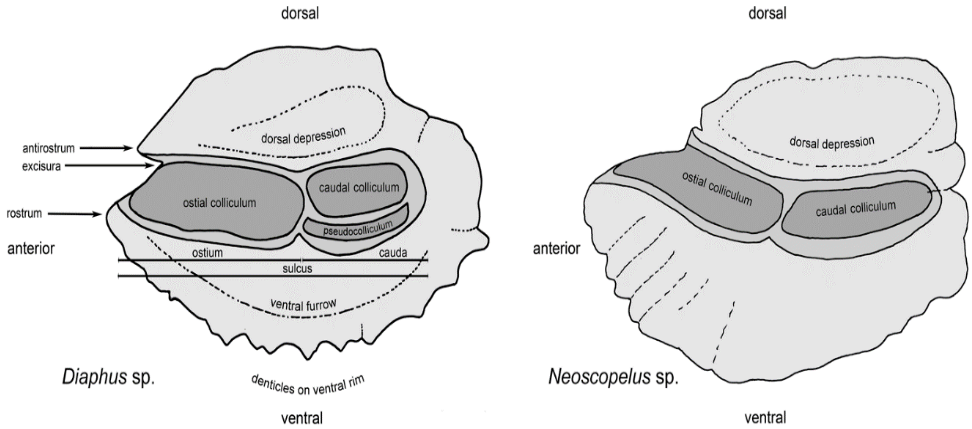

Figure 4 Otolith characteristics (laying flay) used in species determination. Primary characteristics used for species determination was sulcus (lateral depression), rostrum (left side point), denticles (downside) and general shape (Schwarzhans and Carnevale, 2021.

The otoliths and bones were dried after separation from stomach content. Bone materials were examined under microscope for otoliths. Once all otoliths were recovered, they were measured in width and length (Boström et al. 2012; Figure 5).

The otoliths were sorted, by ABFT stomach, into species or lowest possible taxon. All otoliths were then classified based on erosion, or wear-class (figure 6). Erosion is classified into three categories as of Boström et al. (2012) with:

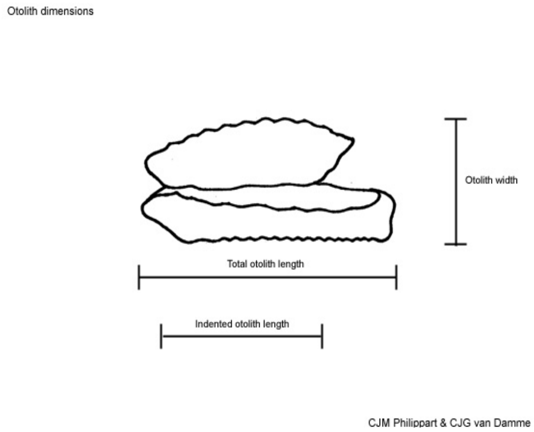

Figure 5 Otolith measurements used in this analysis was total otolith length and otolith width (Leopold et al. 2001)

> "…class 1 being minimally eroded with clear lobations and a well-defined sulcus, class 2 having signs of erosion with less pronounced lobations, a less distinct sulcus, more rounded rostra, and less pointed ends, and class 3 being highly eroded with no lobations or sulcus, and with visible, smoothed edges."

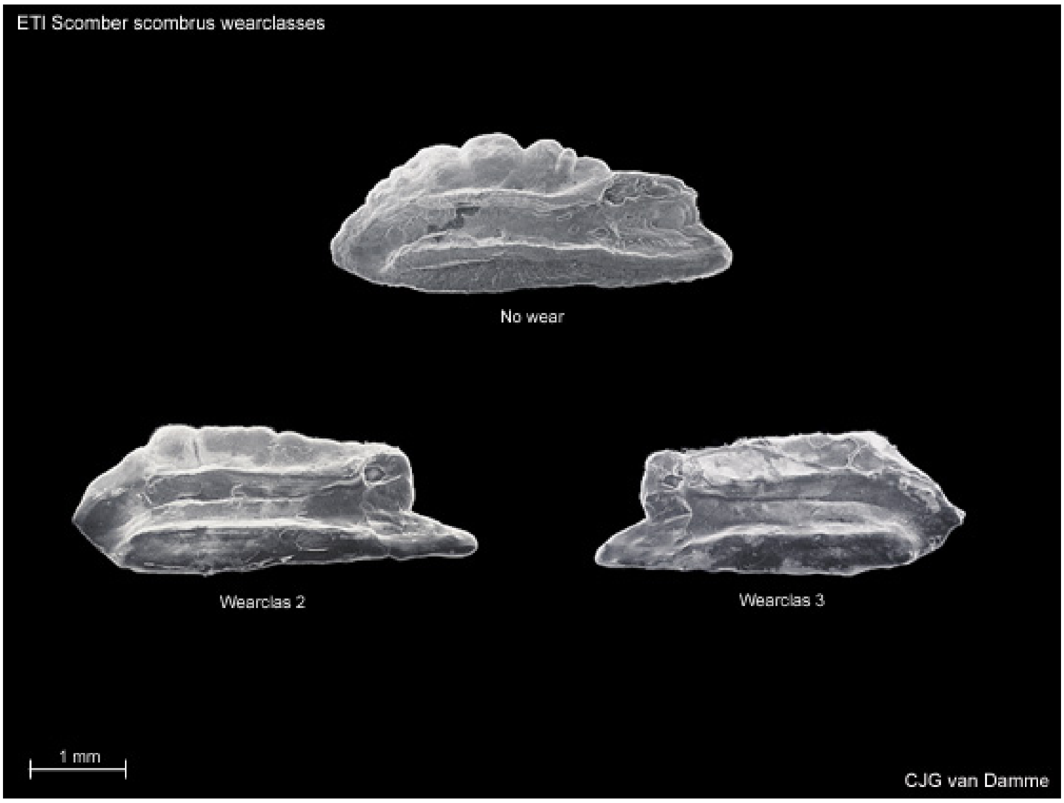

Figure 6 Example of the three wear classes on otoliths used with wear class 1 (no wear), wear class 2 (with signs of erosion) and wear class 3 (most eroded class). Mackerel (Scomber scombrus) otoliths are representing the wear classes in this figure (Leopold et al. 2001)

For cephalopod identification, guides by M. J. Smale et al. (1993) and Xavier & Cherel (2009) and the key by Clarke (1986) were used. Cephalopod beaks are, as otoliths, more resistant to digestion than other cephalopod parts and are therefore commonly used for cephalopod identification in stomach content analysis (Santos et al. 2001; Battaglia et al. 2013). When determination of cephalopods species was conducted, species commonly present in the research area was noted down as the most likely prey. Cephalopod beak identification is complex and requires a trained eye. With predetermined possible species defined by the area, narrowing down beaks found to lowest possible taxon was done with less difficulty. Size and weight estimations with regressions for cephalopods are available for some species (M. J. Smale et al. 1993; Xavier & Cherel 2009), but not for species expected to be found in these northern European waters.

2.6. Analysis

2.6.1. Prey fish size calculation

Size correction factors (SCFs) were used to calculate original otolith size as they were before effects of digestion/erosion. SCF was calculated as the ratio between average otolith size in wear-class 1 and class 2 and 3 respectively (Tollit et al. 1997b; Lundström et al. 2005; Boström et al. 2012). It was assumed that the digestion effects on otolith erosion was proportional to wear-class and that erosion was the same in all ABFT in this study (Boström et al. 2012). All otoliths were calculated with species specific SCFs to wear-class 1, before regressions for fish size and weight calculations were carried out. Of the otoliths measured, sufficient numbers of otoliths were present to be able to calculate species specific SCFs for garfish (*Belone belone*), herring, haddock (*Melanogrammus aeglefinus*), blue whitling (*Micromesistius poutassou*) and mackerel (Table 1).

Table 1 Size correction factors (SCF) for calculable species (meaning enough otoliths in each wear class for calculation) otolith length and width per erosion class. SCF is calculated as the ratio between wear classes to calculate original size (wear class 1). On species without sufficient otoliths to calculate SCF, average SCF was used to calculate original otolith size.

	SCF, otolith length per erosion class			SCF, otolith width per erosion class		
Species	**1**	**2**	**3**	**1**	**2**	**3**
Garfish	1	1,2525754	1,4719199	1	1,2549233	1,4035758
Herring	1	1,165948	1,4815184	1	1,1526614	1,4161597
Haddock	1	1,0280374	NA	1	1,0789474	NA
Blue whiting	1	1,1928855	NA	1	1,3081378	NA
Mackerel	1	1,3205374	1,7431844	1	1,0508577	1,3058697
Average	1	1,1919967	1,6209	1	1,1691055	1,4334198

Regressions were then used to calculate prey size and weight based on otolith sizes and measured prey lengths (Härkönen 1986; Leopold et al. 2001). Size calculation regressions were applied to either otolith length or width to calculate fish length and weight. For most otoliths in this study, width was used in size calculations as the rostrum (i.e. length) is easily damaged. A damaged or partly damaged rostrum may lead to faulty measurements or no measurements. In cases where measurements on width was not possible, mostly as a result of highly eroded sulcus on herring or mackerel otoliths, causing lateral breakage, length was used in the calculations. Otoliths that reached sizes outside of regression limits after applied SCFs were brought up or down in size to regression limit size.

Post-mortem digestion may affect stomach content quality. Stomachs were not frozen immediately after catch, and it often took several hours to get them into a freezer. For the analysis, the stomachs were thawed for up to 48 hours. All of this may have allowed possible post-mortem digestion, risking bias results if weight and other soft tissue measurements were to be used. As a result of this, otoliths were used as the main material source for the analysis. For otolith erosion class categorization, less otoliths might have been classified as erosion class 1 as a result of post-mortem digestion where otoliths were less digested at the time of death than at stomach content extraction, and this may also in turn affect SCFs.

2.6.2. Descriptive analysis

This study will not be able to conclude feeding quantity but rather give an indication on prey composition. Otoliths differ greatly in size between species and also differ in the pace of digestion after prey consumption. This study assumed that all otoliths found in the sampled stomachs were consumed within a 24-hour period (medium size fish complete digestion time) and thereby represented a ABFT daily feeding habit in the area (Battaglia et al. 2013). Although one should be wary of ABFTs opportunistic feeding habits and expand the sample if one wishes to include all possible prey species, to make more exact scientifically based assumptions. With abundance data of prey species, speculations are possible in this study on how prey species preference by ABFT may differ as a function of other variables, such as time of day and area, and could be further studied with a larger dataset in upcoming studies.

The measured otoliths were sorted into species, origin stomach and whether they were the right or left otolith stone. The side with the most otoliths represented had its otoliths marked for use in the analysis. If all otoliths had been used, some prey individuals where both otoliths were found would therefore be counted twice, thus resulting in faulty data. If otoliths had the same abundance in left or right, one of these sides of measured otoliths were chosen at random.

For species other than fishes, i.e. cephalopods and crustaceans, abundance was not high enough to motivate analysis of the weight and size of the prey.

All data was compiled in Microsoft Excel (version 2203). Excel allowed for efficient data entry and ease in sorting data for relevant parts. In this dataset, all otoliths found were included, resulting in a secondary evaluation of the data when sorting out measured otoliths to avoid double counting. The pivot function in Excel was used for quick summary of the data, and for preparing data for visualization. After processing and sorting of data in Excel, analysis was made in RStudio (version 1.4.1106) where additional sorting, processing and visualization of data was made using the library ggplot2.

2.6.3. Additional data imputation

By presenting four possible scenarios of population sizes visiting Skagerrak and Kattegatt in a season of 90 days (August-October), estimations on ABFT predation effects on prey species populations was analysed. Current population size of ABFT visiting Skagerrak and Kattegat annually is unknown. However, the duration of their stay is starting to be better understood via ongoing tracking studies, and the data suggest approximately three months (August-October) (Aarestrup et al. 2022). In turn, predation in relation to commercial fisheries on the species in question was made. Estimations based on four possible scenarios: 500, 1500, 15 000 and 25 000 individuals could give an indication of the range of challenges and possibilities that may exist. The predation data (i.e. daily feeding) was processed in excel where it was multiplied by number of scenario individuals and number of days in the season.

Using these results, estimations on possible future challenges in relation to the commercial fisheries and prey species populations was made. These estimates were made for the most pronounced, commercially valuable species present in the ABFT stomachs by weight. Harvest data from Swedish commercial fisheries in Skagerrak and Kattegat was collected from the Swedish agency for marine and water management (Havs och Vattenmyndigheten Updated dailyb, Updated dailya). The data provided by the agency for marine and water management are reported by the commercial fishing fleet continuously and presented annually by species. As 19 tuna stomachs constitutes a relatively small sample, all but two stomachs were collected in 2021, and current ABFT population present in Skagerrak and Kattegatt is unknown, these estimations were made to provide possible scenarios and not precise figures. Only harvest data from 2021 was used for comparison.

Calculations on daily needs of prey individuals for important prey was also calculated based on daily required energy intake for tuna. This should further increase our understanding on the effects ABFT may have on prey populations in the studied area.

3. Results

3.1. Prey species

3.1.1. Fish diet

Of 19 examined stomachs and stomach contents (i.e. sample named "Extra") examined, all but one stomach contained prey remnants. In total, eleven fish species were found in the stomachs and two fish families with unidentifiable species were found: Ammodytidae and Gadiformes. Garfish was the most abundant species when summarized over all sample stomachs with almost half (44%) of all individuals recorded being garfish, 143 garfish in total. Ten of the 18 examined stomachs contained garfish. After garfish, herring and mackerel followed in abundance with 78 herring found (24%) and 42 mackerel found (13%). These were the three species most abundant and the only species constituting more than 5% of the total prey found (Figure 7).

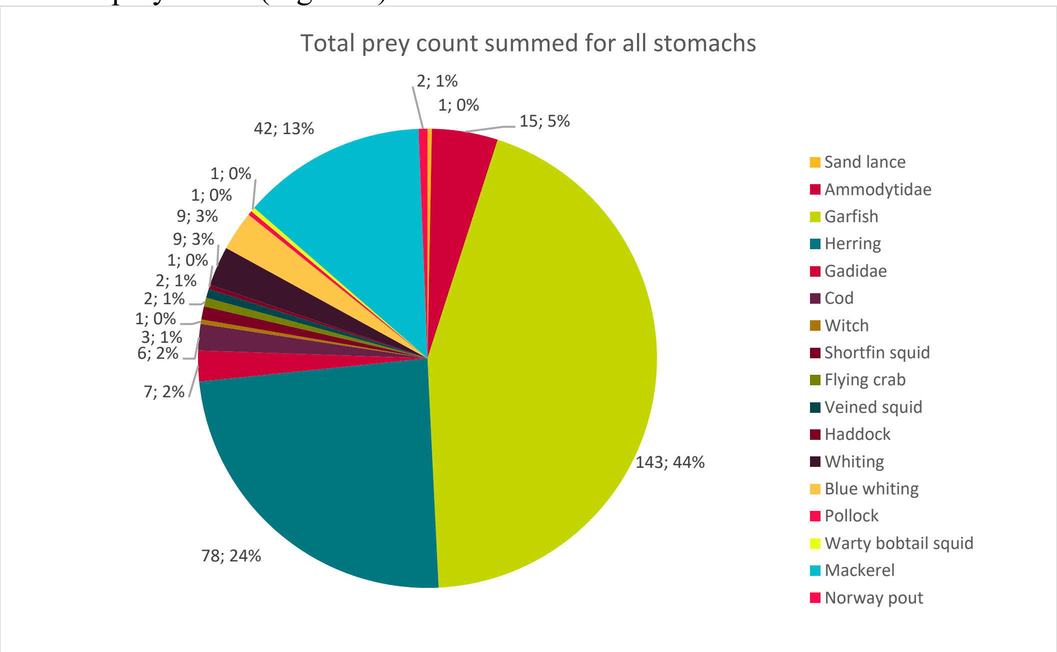

Figure 7 Pie chart of total count of prey species found in stomach contents of 19 bluefin tuna caught in the sea of Skagerrak and Kattegatt.

By weight, garfish was also the most pronounced species overall. Summarized over all 18 sample stomachs, over 40 000 calculated grammes of garfish was found, almost 55 percent of the total calculated biomass (Table 2). In comparison, the second most common species by weight was mackerel with just over 17 000 calculated grammes total biomass. Cod were the third most pronounced species by weight followed by gadiformes and herring (Table 2).

Of the most common species by abundance and weight, garfish, average weight was almost 300 grammes and average length was just above 50 cm. Two prey species had average weights over 1000 grammes: pollock was the prey fish with the highest average weight, averaging almost 1700 grammes, cod were the species with the second largest average weight at almost 1100 grammes. After these two species followed gadiformes with 510 grammes average and mackerel with almost 410 grammes average. The smallest fish by average weight and length was Norway pout with an average weight of 16 grammes and average length of 13 cm (Table 2).

Table 2 Sum of weight, average weight and average length of prey fish species found in stomach contents of 19 bluefin tuna caught in the sea of Skagerrak and Kattegatt.

Species	Sum of Prey weight (g)	Average of Prey weight (g)	Average of Prey length (cm)
Garfish	40854	292	52
Mackerel	17085	407	32
Cod	6518	1086	44
Gadidae	3571	510	20
Herring	3548	46,5	20
Saithe	1680	1680	51
Blue whiting	1485	165	65
Whiting	1228	136	21
Ammodytidae	309	21	19
Witch	207	207	33
Haddock	123	123	24
Norway pout	32	16	13
Sand lance	26.5	26.5	21
Grand Total	**76668**		

By abundance, pelagic species constituted 58% of all prey individuals, followed by 34% benthopelagic individuals and 8% demersal individuals (Figure 8; 10). By weight, 76% of all fish were pelagic species, 21% were benthopelagic and three percent were demersal species (Figure 9). Pelagic species identified were garfish, shortfin squid *(Illex condetii)* and mackerel. Benthopelagic species identified were herring, unidentifiable Gadiform species, Cod (*Gadus morhura),* whiting (*Merlangius merlangus),* blue whiting and norway pout *(Trisopterus esmarkii).* Demersal species found were sand lance, unidentifiable Ammodytidae species, witch (*Glyptocephalus cynoglossus),* flying crab *(Liocarcinus holsatus),* veined squid *(Loligo forbesi),* haddock, saithe (*Pollachius virens)* and warty bobtail squid *(Rossia palpebrosa)* (*Fishbase* 2022).

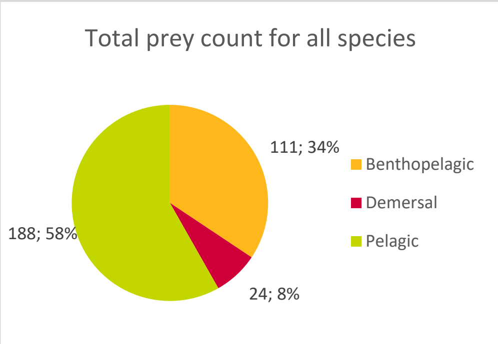

Figure 9 Total prey count per habitat found in stomach contents of 19 bluefin tuna caught in the sea of Skagerrak and Kattegatt with categories being benthopelagic, demersal and pelagic.

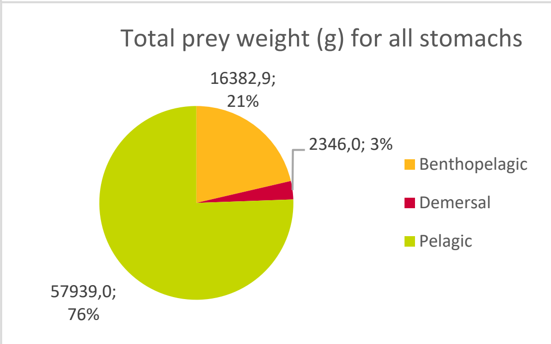

Figure 10 Total prey weight (grammes) per habitat found in stomach contents of 19 bluefin tuna caught in the sea of Skagerrak and Kattegatt with categories being benthopelagic, demersal and pelagic.

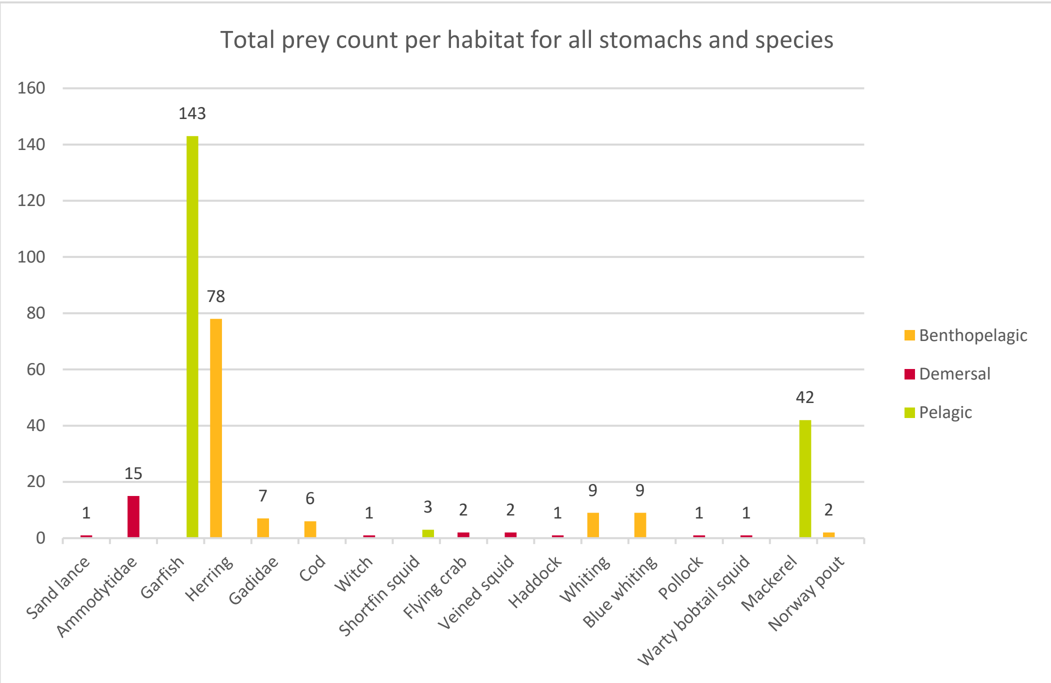

Figure 8 Total count per prey species found in stomach contents of 19 bluefin tuna caught in the sea of Skagerrak and Kattegatt with preferred habitat divided into benthopelagic, demersal and pelagic. Presenting the prey species with category inclusion.

3.1.2. Cephalopods and crabs

Other than the fish species found, two swimming crabs and three species of cephalopods was found. Two samples contained one swimming crab each of the species flying crab each with carapace breadths of 4,3 cm in one sample and 4,2 cm in another sample. One sample contained a total of six cephalopod beak pieces. The beaks were identified to species shortfin squid, veined squid and warty bobtail squid. Beaks found were both upper and lower beaks, totalling a maximum of five possible cephalopods consumed by the tuna: two shortfin squid, two veined squid and one warty bobtail squid.

3.2. Daily feeding habits

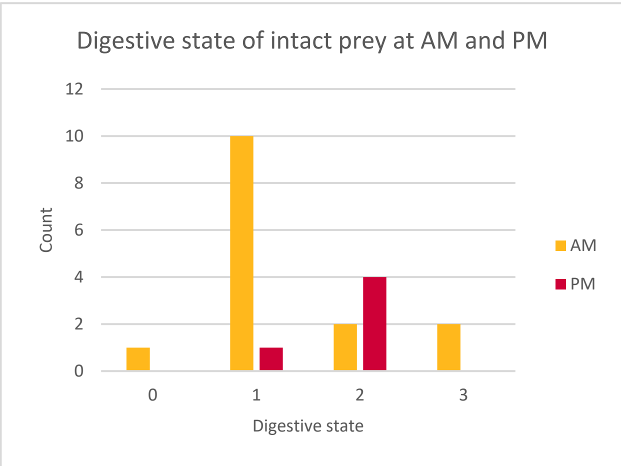

Figure 11 Digestive state of fish found in 19 ABFT stomachs in Skagerrak and Kattegatt, 0 represents almost intact, 1 – partially digested, 2 – almost no flesh and 3 – skeletal material. Divided into morning (AM) and afternoon (PM) hooking time.

Only in the morning, AM, prey species found were of digestion state category 0, almost intact. In category 1, partially digested, 10 prey fish were found in stomachs caught in the morning and 1 were from a stomach caught in the afternoon (PM). Digestion state 2, almost fully digested tissues but still showing flesh had 2 fish from morning hooked stomachs, and 4 fish from afternoon hooked stomachs. In digestion state 3, intact skeletal material (spine), 2 fish were identified in stomachs caught in the morning and none in the evening (Figure 11).

3.3. Feeding in relation to commercial fisheries

My scenario analysis of four different population sizes of ABFT (i.e. population size of 500, 1500, 15 000 or 25 000) suggest that the potential effect of increasing population size may vary between prey species. For example, in none of the scenarios did herring predation surpass Swedish commercial herring harvest in Skagerrak and Kattegatt. Consumption of Mackerel exceeded the entire commercial harvest by the Swedish fishing fleet in Skagerrak and Kattegatt at just over 1500 individuals, and at about 7000 individuals, predation exceed the harvest of cod (Figure 12).

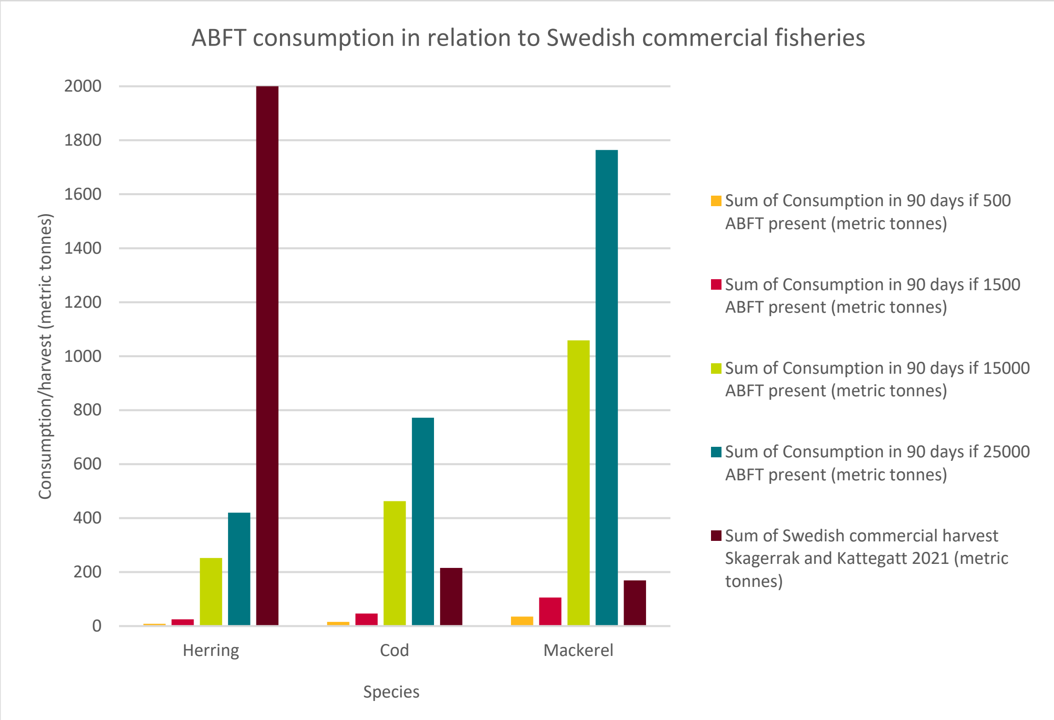

Figure 12 ABFT consumption of herring, cod and mackerel in Skagerrak and Kattegatt in relation to Swedish commercial fisheries in Skagerrak and Kattegatt in 2021. 500, 1500, 15 000 and 25 000 migrating (present) individuals scenario. Y axis cut-off at 2000 metric tonnes.

3.4. Spatially determined variation in stomach prey content

Twelve tunas were caught in the northern area and four in the southern area. One stomach caught in the southern area did not contain any prey materials. Garfish was most abundant in stomachs caught in the northern area. All species except sand lance, blue whitling and mackerel were most abundant in stomachs from the northern area. Sand lance and blue whitling was only found in stomachs caught in the southern area (Figure 13).

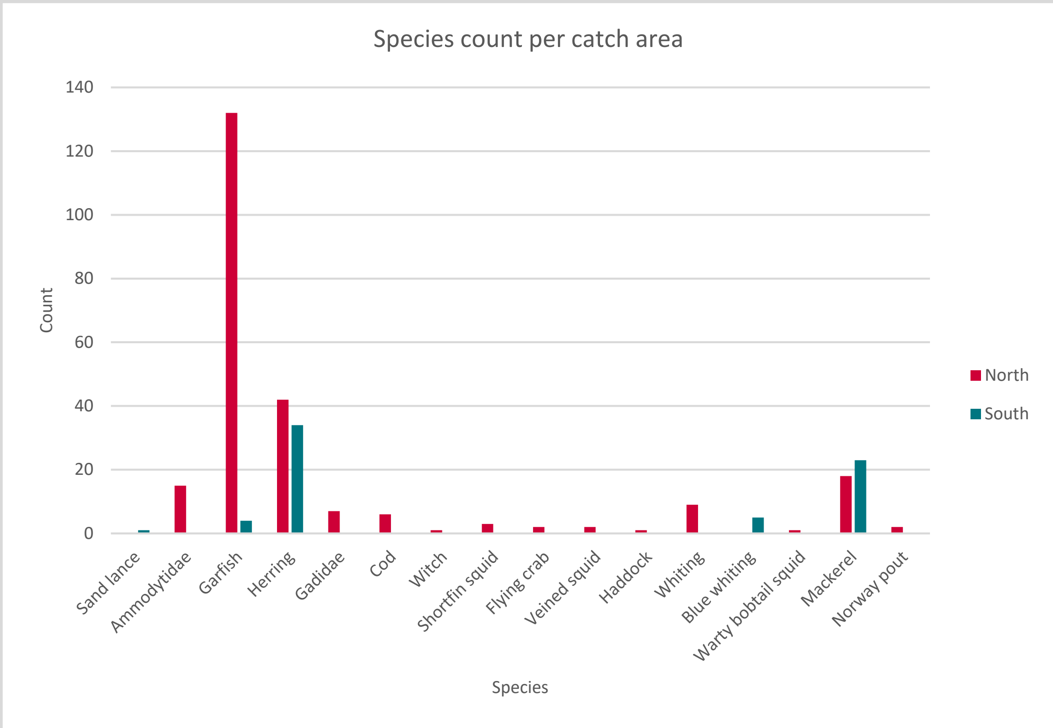

Figure 13 Prey species count per catch area from stomachs of 19 ABFT in Skagerrak and Kattegatt Northern area located between Orust and Skagen, southern area located at the northern inlet of Öresund.

4. Discussion

The stomach content analysis revealed garfish being the most common prey by weight and abundance, followed by mackerel, herring and cod. My results suggest that large part of the diet of ABFT is acquired from the pelagic zone. i.e. 58% of prey items are known to use predominately the pelagic zone. This also mean that predation may be directed at these species, presenting greater predation pressure on a few species.

4.1. The most abundant prey species

The three most abundant species in the examined Tuna stomachs were Garfish, Herring and Mackerel. Garfish is a pelagic species swimming in shoals in surface waters. They are migratory and inhabit Skagerrak/Kattegat from spring until autumn (Fishbase n.d.a; SLU artdatabanken n.d.). Herring is a benthopelagic species living in shoals, inhabiting the entire water column from bottom to surface, down to about 200 meters depth. At night time, they swim close to the surface and venture deeper at day time (Fishbase n.d.b). Mackerel is a pelagic species and swim in shoals close to the surface and down to about 200 meters depth. The species is migratory and inhabit Skagerrak/Kattegat from spring until autumn (Fishbase n.d.c).

All three species are pelagic and shoal swimming. Pelagic shoal swimming fish were reported to be an important part of ABFT prey in a study from Greenland waters. Here, tuna stomach analysis reported almost exclusively Mackerel as ABFT prey (Jansen et al. 2021). In the Mediterranean Sea, benthopelagic and mesopelagic prey species have been reported as the preferred prey for ABFT (Battaglia et al. 2013). The reason why pelagic fish species may be over abundant in the diet of Bluefin tuna may be related to the energy gained by choosing one prey over another. Mesopelagic fish are more lipid rich and thus carry more energy per weight than less lipid rich fish species (Benson & Lee 1972; Saito & Murata 1998; Lea et al. 2002). Herring and Mackerel which made up a large proportion of the diet of Bluefin tuna in this study are energy rich. Mackerel contains about 16 KJ/g and herring contains about 13 KJ/g in the northeast Atlantic in September which is much higher than the energy content of other possible prey items available to bluefin tuna in this region (Stansby & Lemon 1941; Bachiller et al. 2018). The herring found in the stomachs weighted an average of 46,5 grammes and the mackerel an average of 406,8 grammes. That equals to 604,5 KJ (0,6045MJ) per herring and 6508,8 KJ (6,51MJ) per mackerel. To maintain body mass, a 250 kg tuna needs 37,5 MJ of gross energy (0,15 MJ/kg), equalling 62 herring or 5,8 mackerel daily. To gain weight, 92,6 herring or 8,6 mackerel (56 MJ/kg) per kg of body mass gain is needed daily. As a highly calory dependent predator these calory rich prey are vital for ABFT. The ABFT in this study would require large amounts of fish just to maintain body mass. In turns of management this could impose challenges as managers and fisheries of these species may not be adapted to working with this new predator. Herring trawls may need to be adapted with tuna in mind, harvest quota models may need revision amongst other challenges.

4.1.1. Daily feeding habits

As shown in figure 11, ABFT feeding seems to be more focused on morning hours. Digestion state 0 were only represented in stomachs hooked in the morning hours and digestion state 1 was represented far more in the morning than the afternoon. The only digestion state where afternoon was represented more than morning was in digestion state 2. However, in digestion state 3 only the morning category was represented. This could be because of feeding the previous day and prey spines not being fully digested yet and thus remaining in the stomach. ABFT can fully digest a medium sized prey fish in about 24 hours (Battaglia et al. 2013) and digestion category 3 is almost fully digested intact prey, these prey individuals could therefore have been consumed any time within a 24-hour timespan. Both individuals in digestion state category 3 were garfish from a single sample. Garfish are slender fish, and these were 16- and 17-centimetre-long spines, suggesting rather small and thus, quickly digested prey. One should keep in mind that the sample is small and that only two fishes represented the digestion state 3 category.

With this analysis suggesting feeding focused on dawn, along with the findings by Battaglia et al. (2013), ABFT could be considered a crepuscular feeder. Further understanding on daily movement habits could provide additional insight into their feeding preferences in relation to this crepuscular behaviour. This could also be of value if the population grew large enough to be an issue for fisheries as precautions to minimize bycatch tuna could be developed around feeding and movement habits.

4.1.2. Other prey species

As cephalopods were only found in one stomach, and no regressions for size and weight for any of the species found was available, these should, with their scarcity in the samples, be seen as a minor detail in the dataset and an effect of ABFT opportunistic feeding. This is also applicable on the crabs, as these are not abundant enough to be considered in this analysis other than as a product of ABFT opportunistic feeding. The crabs found were intact and separated from other prey in the stomachs. They were thus considered not to be secondary consumption.

In future studies with larger sample sizes, analysis of cephalopod and crustacean abundances, weights and sizes would be interesting to analyse in a ABFT feeding preference analysis.

4.2. Four population scenarios in relation to commercial fisheries

Analysis on possible ABFT population scenarios suggest the possibility of ABFT imposing potentially great effects on commercial fisheries. Their consumption, if the visiting population has the feeding habits suggested in this study, can be substantial depending on the number of visiting ABFT. For example, if the Skagerrak/Kattegat population consists of just over 1500 individuals, their consumption of Mackerel would exceed the entire commercial harvest by the Swedish fishing fleet, and at about 7000 individuals, they would exceed the harvest of cod. Cod is a species with great commercial value and vulnerable status along the Swedish coast (SLU artdatabanken 2020b; a). Currently, commercial harvest of cod surpasses natural recruitment (SLU artdatabanken 2020b). With a top predator further imposing stress and change in the trophic chain and surpassing Swedish commercial harvest at a population of 7000 individuals, it is possible that the impact of large numbers of ABFT on the cod fishery will be increasingly discussed.

ABFT have been a threatened species historically, but as they have improved in population status they may potentially start to have impact on local fish populations, many of great economic and cultural importance. This can potentially be a controversial topic in the future management debate.

The conflict between fisheries and seal management can present a similar case where successful conservation management is faced with concerns from fisheries regarding increasing seal abundance (Waldo et al. 2020). In this conflict, mitigation efforts include participatory management being included in the Swedish fisheries management strategy (Bruckmeier & Höj Larsen 2008), economic compensation for income loss due to seals, i.e. a state subsidized fishing gear insurance (Bruckmeier et al. 2013; Waldo et al. 2020) and technical solutions in fishing gear (Bruckmeier et al. 2013). These may not be applicable for ABFT directly but poses as example for the wide range of tools that exists to mitigate human-wildlife conflict in fisheries management. Thus far, there is no immediate conflict concerning ABFT, but one needs to have these results in mind and the potential conflict that may emerge depending on ABFT population size. Preparation for future challenges in ABFT management may be the preferable next step in the overall management plan.

Waldo et al. (2020) emphasises the importance of taking action in a possible conflict situation rather than acting passively. All involved stakeholders must be prepared to compromise and keep an open discussion in order to mitigate conflict and balance ecological and economical challenges and opportunities that comes with the return of ABFT in Skagerrak and Kattegat. One also needs to see ABFT in the perspective of a highly migratory species and where the management is handled on an international level. Balancing various sized economies from local to global, possible conflict and ecological status of ABFT is vital in developing sustainable management tactics for the species.

If larger studies are to be conducted on ABFT in the waters concerned in this study or adjacent waters, analysis of predation in relation to the body size of the tunas would be of interest. Different sized ABFT may have different feeding habits and prey preferences, this may cause them to have different ecological and trophic effects. Management could consequently be developed differently in reference to ABFT size.

ABFT is a relatively new species in Skagerrak and Kattegat and an economically important species worldwide. If it were to severely impact commercially important fisheries in Sweden and Denmark, pressures for population control via increased harvest could be argued by the fishing industry. This risks further pressure on a recovering species that we know little of in these waters. Hence, the scenario estimates presented here should be seen as strong incentives to lay ground for further studies on the species impact, and the inevitable ecological, trophic and commercial challenges and opportunities it brings. In future studies, spatial distribution of prey in relation to ABFT feeding could reveal prey preferences and further aid in developing ABFT management and mitigating potential conflicts.

4.3. Methodological reflection

As a possible result of post-mortem digestion affecting otoliths, only two otoliths were classified as erosion class 1 in mackerel. These two were used in calculation of SCF for mackerel. Even though this may give a skewed SCF, they were used with the argument of them resulting in a smaller SCF than the average of all species otoliths. Thus risking underestimation rather than overestimation in fish size when applying the SCF.

Sample named “Extra” were not a reliable representation of the complete stomach content of that ABFT. Only fish in digestion categories 0 and 1 were represented and had otoliths removed for analysis. The argument for inclusion of this sample in the analysis is that this provides insight into prey composition.

Further, as of the small sample size, this study should be read as an insight and pilot study into ABFT feeding habits and prey composition in Skagerrak and Kattegat.

4.3.1. Methodological development for ABFT stomach analysis

During stomach content separation and processing, rinsing was conducted using cormorant stomach content analysis methods. It was chosen as the method for these stomachs based on methodological speed and useability. For coming studies, one should be extra cautious for cephalopod beaks in using this method as these are not as dense as otoliths and bones and may easily be lost during rinsing. It is impossible to determine cephalopod beak losses in hindsight and some may have been lost in this study. Although cephalopods are not as commercially valuable as other species found in the study, there may be ecological effects if they are predated upon in great quantities. Further studies should take this into account as to give fair representation on predation on all species, commercially valuable (conflict prone) or not.

4.4. Conclusion

The return of ABFT in the studied north-eastern European waters is a result of successful management actions, but the feeding habits of the tuna may raise concerns for future management if they return in large numbers. In this study, I found garfish, herring, mackerel and cod to be preferred prey for ABFT. Predation on commercially valuable fish species and on already threatened species such as cod can potentially have an impact on both the fishery and on ecosystem ecology, which may result in conflict. We need further research on ABFT population size and feeding habits in the area to develop and implement suitable conflict mitigation measures in this early stage of ABFT recovery.

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Appendix 1

Identity	Date	Time of hooking	Latitude	Longitude	ICES subdivision	CFL (cm)	Lenght (total)(cm)	Weight (kg)	Stomach weight rinsed (g)	Stomach content weight (g)
X1	2021-08-23	11:34	58 04.383	10 54.473	20	255			2272	716
X2	2021-08-30	10:19	58 00.984	10 52.352	20	255			2192	5908
X3	2021-09-02	09:06	58 02.668	11 04.084	20	233			1990	319
#4	2020-09-03	08:10	58.05	11.14833333	20	270			2098	122
Wille 30/8	2020-08-30	07:07	58.07166667	11.05666667	20	267			1881	502
Extra									NA	NA
1	2021-09-11	08:55	57.972383	10.756883	21		256,5	291	1988	433
3	2021-09-14				23		236	219	1712	98
11	2021-09-14	08:00	58.074067	10.46665	21		243,5	219	1616	376
12	2021-09-14	10:00	57.966667	10.75	21		225	193	1521	257
4tuna	2021-09-18	11:10	56.338889	12.316667	21		259	310	1525	903
Bigfish	2021-09-28	17:30	56.150817	12.350783	23	282			2481	170
13	2021-09-14	10:00	57.966667	10.75	21		232	217	1711	382
1Hein	2021-09-28	16:00	56.146382	12.365302	23	269			2128	92
15	2021-09-11	13:07	57.956	10.754933	21		240	227	1907	839
4tuna 2	2021-09-14	12:50	56.200783	12.293483	23		223	192	1161	116
6	2021-09-11	08:45	57.9541	10.729383	21		246,5	246	1787	2301
Seahunter	2021-08-30	14:30	57.993533	10.820017	20	224			1769	2477
#8	2021-09-20	15:30	56.19475	12.2881	21		234	225	NA	