

# The hidden links in trophic food webs: Where do the parasites fit?

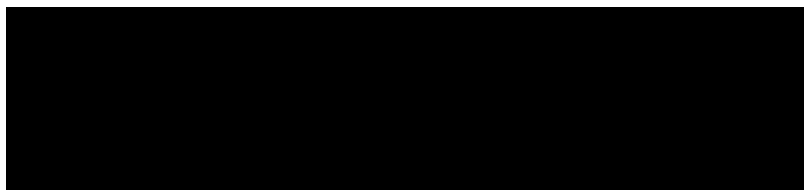
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A thesis submitted in partial fulfilment of the requirements  
of Edinburgh Napier University, for the award of Master by  
Research.

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## **Declaration**

This thesis is a result of my own, independent work. The work has not been submitted for any other degree or professional qualification.

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Matthew John Dicker

17/07/2020

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## Abstract

Parasites have been excluded from most food web constructions, partly because of their assumed negligible contribution to the flow and stock of energy in ecosystems. These assumptions have been disputed. Parasites also present practical and conceptual problems in knowing how best to represent them in trophic networks that use simple graphical descriptions of species as producers, consumers, and prey without ontological changes. Parasites have been erroneously labelled as top predators and have resulted in ecologically unrealistic inflations of trophic levels. A range of methods were assessed here in order to explore how parasites might suitably be included in a food web describing the *Tellina fabula*-community characteristic of Fine Sands (FSd) in the German Bight, North Sea. Parasites were identified through dissection of prominent teleost hosts from the web and an extensive literature search and included as discrete species-specific nodes and as disaggregated, ontogenetic nodes. Parasites in the FSd were relatively less complex than those in other food webs. This is likely a result of the networks small size, relating to network scale variance, and highly connected free-living species. A novel method for calculating flow-based trophic levels in the absence of information on interaction strengths was successful in mitigating unrealistic trophic level inflations and a speculative food web, including parasites in combined nodes with their hosts suggests a useful future method for accurately representing parasites place in and their effects on food webs, without being labelled as top predators or inflating trophic levels. Food webs remain important heuristic tools for teaching and understanding ecology but represent gross simplifications of the dynamic energy flows in ecosystems. Excluding parasites from them exacerbates this distortion. This work shows a range of methods by which parasites can be included and demonstrates the advantages of doing so. It also highlights significant gaps in knowledge that remain.

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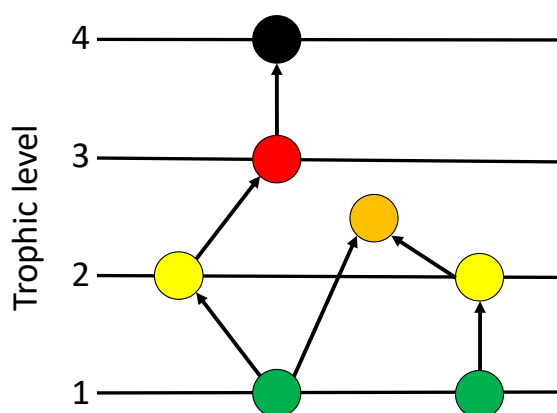
## Abbreviations

|                  |                                                                                                                                               |
|------------------|-----------------------------------------------------------------------------------------------------------------------------------------------|
| BTC              | <i>Bathyporeia-Tellina</i> community food web, developed by Steger <i>et al.</i> , 2019.                                                      |
| FSd              | The <i>Tellina fabula</i> community characteristic of <b>Fine Sands</b> (FSd) in the German Bight. Station of a macrozoobenthic time series.  |
| FSd.D            | The FSd.X excluding concomitant predation.                                                                                                    |
| FSd.F            | Rename of the BTC food web.                                                                                                                   |
| FSd.P            | The FSd.F food web, plus 12 parasites identified in the literature and dissections, only including incoming links from the parasite's hosts.  |
| FSd.X            | The FSd.P food web, plus outgoing links from the parasites to consumers. Including concomitant and direct predatory links.                    |
| FSd.97           | The FSd.F food web plus 12 non-parasite species that comprise 97 % of the cumulative energy flow at the FSd station.                          |
| L                | The number of links in a food web, from a consumer to a resource.                                                                             |
| L/S              | Linkage density, the number of links per species in a food web.                                                                               |
| $L/S^2$          | Directed connectance, the proportion of potential links in a food web that have been realized.                                                |
| $L/S_f(S_f+S_p)$ | Adjusted connectance, used in the FSd.P, LL.P and MM.P webs.                                                                                  |
| LL.F             | The FSd.97 excluding species without a direct link to <i>Limanda limanda</i> .                                                                |
| LL.P             | The LL.F plus parasites isolated from <i>L. limanda</i> in this study. Parasites included only in their role as consumers.                    |
| LL.X             | The LL.P plus outgoing links from parasites to their consumers.                                                                               |
| MM.F             | The FSd.97 excluding species without a direct link to <i>Merlangius merlangus</i> .                                                           |
| MM.P             | The MM.F plus parasites isolated from <i>M. merlangus</i> in this study. Parasites included only in their role as consumers.                  |
| MM.X             | The MM.P plus outgoing links from parasites to their consumers.                                                                               |
| S                | Number of species in the food web.                                                                                                            |
| $S_f$            | Number of free-living and basal species in the food web.                                                                                      |
| $S_p$            | Number of parasite species in the food web.                                                                                                   |
| $TL_{fb}$        | Flow-based trophic level, in which the weighting of each of a species incoming links is based on its trophic efficiency, after the 10 % rule. |
| $TL_{pa}$        | Prey-averaged trophic level, calculated as the mean trophic level of a species' prey +1.                                                      |
| $TL_{sw}$        | Short-weighted trophic level, calculated as the mean of $TL_{pa}$ and the species' shortest chain to a basal species.                         |
| $\Delta TL$      | $TL_{sw} - TL_{fb}$                                                                                                                           |

# 1. Introduction

## 1.1 Trophic food webs

Food webs, the networks of who eats whom in an ecosystem, are central to a number of fundamental concepts in ecosystem ecology, including complexity, diversity, and stability (Lafferty *et al.*, 2008). Food webs are typically visualised as a series of connections, or links, between species nodes, structured according to trophic level (Figure 1.1). The trophic level (TL) of a species is calculated as the mean trophic level of its prey +1, referred to as prey-averaged TL ( $TL_{pa}$ ). As such, basal producers are assigned a TL of 1, primary consumers a TL of 2 and higher order consumers a TL > 2. Prey-averaged TL and shortest chain TL, the minimum number of links (L) between the species and a basal node, are often averaged to produce each species' "short-weighted" TL ( $TL_{sw}$ ) (Williams & Martinez, 2004). The metabolic cost of respiration drains energy from food webs, reducing the pool of energy that is available to subsequent TLs. Typically, 90 % of the energy that enters a trophic level



**Figure 1.1:** Simplified food web, displaying basal (green), omnivorous (orange), primary (yellow), secondary (red) and tertiary (black) consumers and the links between them; arrows point from the resource species/node to the consumer species/node. Height refers to prey-averaged trophic level (TL); the mean trophic level of the node's prey + 1.



will be unavailable to the next, resulting in an average trophic efficiency of only 10 % (Lindeman, 1942). This is one of the few universal laws of ecology.

Basic topological food web matrices describe the presence or absence of feeding links between species in an interconnected network. The focus of topological analyses is increasingly on quantifying network complexity (Hernandez & Sukhdeo, 2008). Complex food webs are typically characterised by high levels of connectance ( $L/S^2$ ), the realized proportion of potential links, and linkage density ( $L/S$ ), the mean number of links per species. Connectance, considered the more robust index, has been used to make inferences concerning a range of food web properties, from network stability (Dunne *et al.*, 2002; 2006) and persistence (Gravel *et al.*, 2011), to the likelihood of successful invasion from non-native species (Baiser *et al.*, 2010). As such, food web-based analyses might become powerful tools for ecosystem management. For example, humans remove significant amounts of biomass from many marine food webs, which can have devastating repercussions for ecosystems; up to and including total collapse (Jackson *et al.*, 2001). Food web-based assessment of ecosystem robustness to species loss could assist in rescuing ecosystems from extinction cascades (Sahasrabudhe & Motter, 2011) and aid fisheries management, as the move towards ecosystem-based fisheries management continues (Smith *et al.*, 2007).

## **1.2 Parasites' exclusion from food webs**

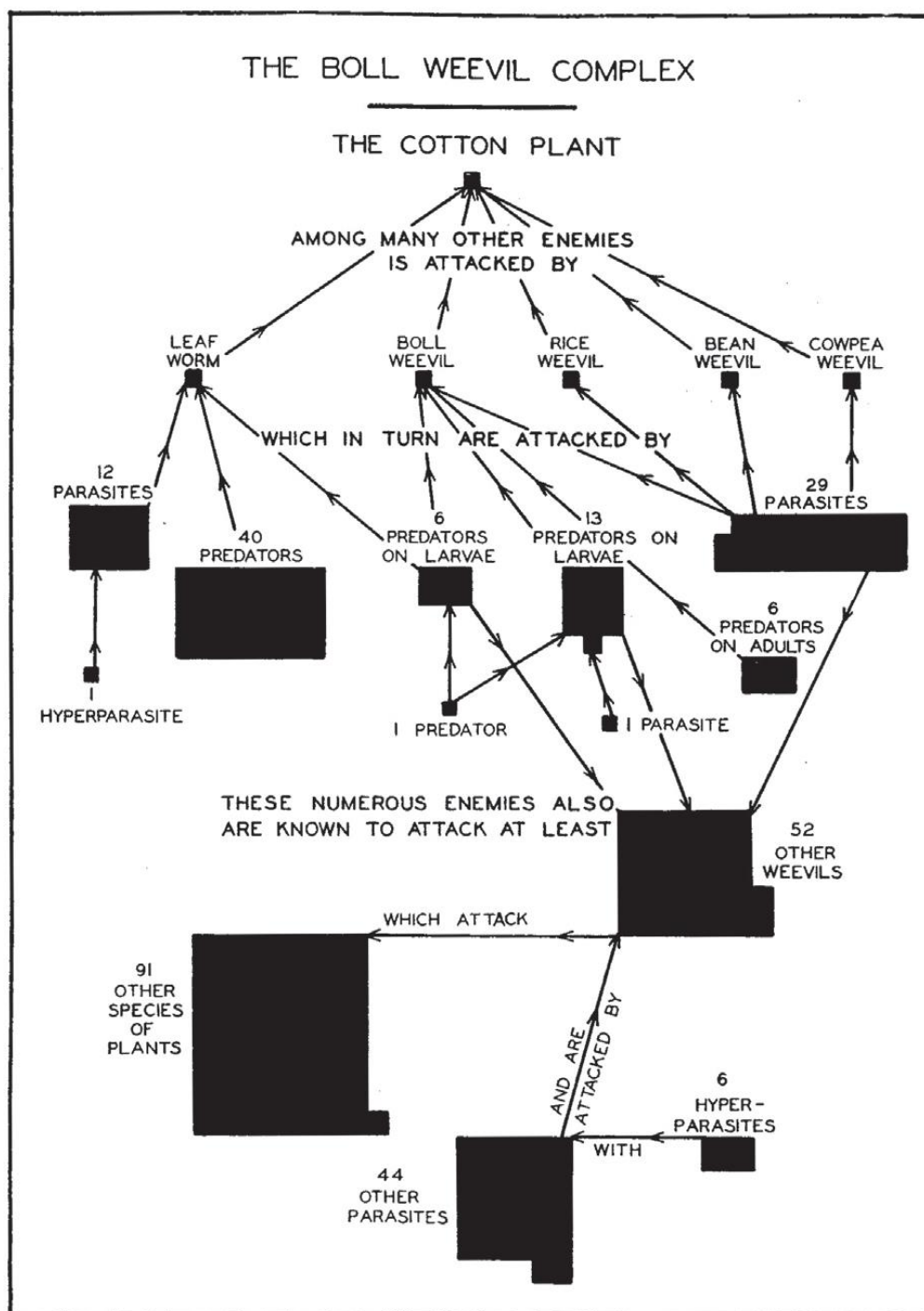
Darwin (1839) included two parasite species, a fly (*Olfersia* spp. Leach 1817) and a tick (*Acari* Leach, 1817), in his summary of the terrestrial fauna of St Paul, which is considered to be the first detailed description of a food web. Perhaps the first 'food web diagram' (Figure

1.2), which outlines the associated assemblage of boll weevil-afflicted cotton plants, contains four parasitic and two hyperparasitic nodes (Pierce *et al.*, 1912). Parasitism is the most common consumer strategy in the animal kingdom (Price, 1980; de Meeûs & Renaud, 2002) and parasites are ubiquitous in nearly every ecosystem (Sabadel *et al.*, 2018). They also participate in 70 % of trophic interactions in some ecosystems (Lafferty *et al.*, 2008). It is perhaps surprising then, that since the formalisation of feeding networks into “food webs” (Elton, 1927), parasites have been excluded from the majority of food web constructions (Lafferty *et al.*, 2006a).

This is partly explained by difficulties in observing them (Huxham *et al.*, 1995), as host dissection is a prerequisite to identifying endoparasites, and many ectoparasites, and physical identification often requires a high level of taxonomic expertise. Parasites’ relatively small size and typically non-lethal interactions resulted in the common, but erroneous assumption that their contribution to the total biomass and energy flow through food webs is negligible (Marcogliese & Cone, 1997; Warren *et al.*, 2010). Since the first substantial inclusion of parasites in food web analyses (Huxham *et al.*, 1995), various pleas for their further inclusion have been made (Marcogliese & Cone, 1997; Lafferty *et al.*, 2006a; Sukhdeo, 2012). To date, these pleas have garnered a limited, but growing response (Lafferty *et al.*, 2006b; Sabadel *et al.*, 2018).

### **1.3 A case for parasite inclusion**

Parasites are released from activities such as homeostasis, food gathering and mobility. As such, they convert energy from their host more efficiently than free-living predators and exhibit accordingly higher rates of productivity (Lafferty *et al.*, 2006b), particularly in



**Figure 1.2:** Perhaps the first specific 'food web' to be published (Pierce *et al.*, 1912), containing four parasitic and two hyperparasitic nodes. Area of a node is proportional to its relative contribution to total biomass in the system.

relation to the production of free-living infective stages. Consequently, parasites can comprise a large proportion of the total biomass in some ecosystems (Kuris *et al.*, 2008). In three Carpinteria salt marshes, currently the most highly resolved food webs to include parasites, the total biomass of trematode helminths is estimated to be between three and nine times greater than that of wading birds, the food web's top predators (Kuris *et al.*, 2008). Parasites often augment the energy flow along links between free-living species through host behaviour modification (Moore, 2013). Trophically-transmitted parasites with complex life cycles and obligate intermediate hosts require stable, long-term interactions between their hosts in order for subsequent generations to reliably mature to adulthood and reproduce. Many of these parasites have evolved to stimulate risky behaviour in their host, in order to strengthen the links between their hosts and maintain dependable pathways of transmission. For example, the most abundant trematode parasite in the Carpinteria saltmarshes, *Euhaplorchis californiensis* Martin, 1950, stimulates erratic swimming behaviour in its killifish host (*Fundulus parvipellis* Girard, 1854), increasing the rate of predation by wading birds 10 to 30 times (Lafferty & Morris, 1996). In this way, the parasite substantially increases the interaction strength of the link between killifish and their avian predators and consequently diverts energy from other predative interactions (Lafferty & Morris, 1996). Conversely, some parasites may increase the feeding rate of their hosts, in order to compensate for the cost of resistance to the parasite (Anaya-Rojas *et al.*, 2016; Bernardo & Singer, 2017). The respirative costs of host resistance furthers a parasite's impact on the flow of energy through a food web, as energy is drained from the system (Lafferty *et al.*, 2006a; Kuris *et al.*, 2008).

Some parasites facilitate the creation or loss of links between free-living species (Mouritsen & Poulin, 2003). For example, the trematode genus *Acanthoparyphium* Dietz, 1909 prevents

infected cockles (*Austrovenus stutchburyi* (W. Wood, 1828)) from burrowing into the sediment, leaving them vulnerable to new predators such as the labrid fish *Notolabrus celidotus* (Bloch & Schneider, 1801) (Thompson *et al.*, 2005). More extreme forms of parasite-induced behaviour modification include host castration. Some castrating trematode larvae consume the reproductive tissue of their gastropod intermediate hosts in order to produce free-swimming, non-feeding, infective cercaria, which removes a portion of the snail's population from the food web, since their reproductive potential has been destroyed, and provides a significant food source for small fish and invertebrates, in the form of free-living cercaria (Lafferty *et al.*, 2006b). Another species of trematode, which castrates the intertidal mud-snail *Peringia ulvae* (Pennant, 1777), can be responsible for drastic changes in ecosystem functioning such as trophic cascade (Buck & Ripple, 2017). *Peringia ulvae* acts as an ecosystem engineer in some soft-bottom intertidal zones through its role as a bioturbator and grazer on benthic diatoms. Trematode infestation decreases the overall activity of the mud-snail, reducing its capacity as an ecosystem engineer, which has significant, indirect consequences for the organisation and function of both the microphytobenthos and zoobenthic community in turn (Mouritsen & Haun, 2008). Including parasites in food webs may also shed light on links between free-living species in the web. Species that serve as an intermediate host to one or more of a predator's known parasites are likely to be a resource for that predator (Marcogliese 2002). Due to their longevity in the gut, some endoparasites may even provide a more rigorous method for determining links than gut content analyses, which offer insights into a very limited temporal window of feeding activity (Lafferty *et al.*, 2006b).

## 1.4 Including parasites in topological food webs

Parasitism differs from predation as a trophic strategy in several ways. For instance, whilst parasites typically infest a single host throughout their lifetime, or a series of single hosts in species with complex life histories, predators will often kill and consume numerous prey items throughout their lives. Parasitic interactions persist temporally, whereas predation usually involves a single event and the proportion of a resource's energy that is transferred to the predator is greater than that to the parasite. As such, it is appropriate for some distinction to be made between parasitic and predatory links in trophic food webs. Typically, this is done by splitting the food web into four subwebs and analysing each in combination (Figure 1.3). The first two subwebs are perhaps the most obvious: subweb A, the predator-prey subweb, contains links between free-living consumers and resources, and the parasite-host subweb (B) contains links between parasitic consumers and their free-living hosts. Subweb C contains predator-parasite links, including (1) direct predation of free-living life stages of parasites such as trematode cercaria and (2) concomitant links, whereby the parasite is digested by its hosts' predator, indicating that the hosts' predator was an unsuitable host for the parasite. Finally, subweb D contains parasite-parasite links, incorporating both hyperparasitic links, wherein parasites infest other parasites, and intra-host competition, which includes competition between for example trematode cercaria inside their gastropod host (Brose *et al.*, 2006).

Parasites are typically included in these subwebs as discrete species nodes; however, this may be neglecting a crucial aspect of parasite biology (Preston *et al.*, 2014). Many parasites employ complex life histories, in which a series of hosts are required for the life cycle to be completed and reproduction attained. Whilst many free-living species display ontogenetic

|             | Free-Living            | Parasites              |
|-------------|------------------------|------------------------|
| Free-Living | A) Predator - Prey     | B) Parasite - Host     |
| Parasites   | C) Predator - Parasite | D) Parasite - Parasite |

**Figure 1.3:** Simplified parasite food web matrix including parasites, with species acting as consumers along the top and resources down the left. Cells represent the four subwebs.

feeding niche shift, few are as discrete or specific as those observed in many parasites. In seven of the most highly resolved food webs, such feeding niche shifts were found for over 70 % of parasites (Dunne *et al.*, 2013). Parasites often display high levels of host specificity, particularly at the intermediate life stages; over 60 % of parasites in some food webs rely on a single host species at some point in their life cycle (Lafferty & Kuris, 2009). If parasite life stages are aggregated into a single node, they appear to have a low host specificity, as opposed to having a series of more specific links which may misrepresent their contribution towards ecosystem stability (Torchin *et al.*, 2005). Conversely, if parasites are disaggregated into life stage nodes, the extra species richness will expand the number of potential links in the network, without proportionally increasing the number of links that parasites contribute. As such, representing ontogenetic parasitic nodes will deflate complexity measures such as connectance and linkage density.

In place of discrete parasitic nodes, parasites could be included in combined nodes with their infected hosts (Byers, 2006). Nodes in a food web that display the same incoming and

outgoing links are typically reduced into a single “trophic species”. As such, only combined host-parasite nodes in which the parasite facilitated new or lost links in the host would be effectively included in the food web. This might allow for life stages to be represented in the food web and may address issues concerning the insignificant contribution of some parasites to the overall ecosystem biomass. However, it is also likely that many adult life stages are excluded since behaviour modification is typically the arena of larval stages. The proposal remains unexplored.

### **1.5 Effects of parasites on food web structure and topology**

The scarcity of parasites in food webs makes it difficult to draw strong conclusions on how parasites affect food web topology. Intuitively, the inclusion of parasites increases species richness, number of links, trophic level, and chain length (Dunne *et al.*, 2013). Initial studies reported that the inclusion of parasites decreased connectance (Huxham *et al.*, 1995; Thompson *et al.*, 2005), however this was based on a miscalculation: Since parasites were included only in their role as consumers, the maximum number of potential links that parasites contributed was restricted to subweb B (Figure 1.3). However, the standard calculation for directed connectance includes subwebs B, C and D (number of links/number of species<sup>2</sup>), erroneously decreasing the output. This was corrected by Lafferty *et al.* (2006a), who revealed that the inclusion of parasites usually increases “adjusted connectance”. Inclusion of parasites generally promotes increases in diversity and complexity; Thompson *et al.* (2005) suggested that one species alone could contribute significant effects to food web topology, providing it has a complex life history and



sufficiently general feeding niche. However, these increases can be attributed to generic gains that would occur when any species is added to the food web (Dunne *et al.*, 2013).

Parasites uniquely alter food web topology only when concomitant links are included (Dunne *et al.*, 2013). Concomitant predation occurs when the parasite is digested by a predator of its host, which is itself an unsuitable host for the parasite and so bars trophic transmission. A parasites' role as a resource for other species is not limited to concomitant predation, however. Clams, polychaetes (Lafferty *et al.*, 2006b) and small fish (Kaplan *et al.*, 2009) predate the free-living cercarial life stages of trematode helminths and juvenile fish feed on the free-living life stages of parasitic copepods (Gaard & Reinert, 2002). Some species are obligate hyperparasites, only using other parasites as their host, and trematode cercaria within a gastropod host will kill one another along a size-determined dominance hierarchy (Stouffer *et al.*, 2007). The calculation for adjusted connectance excludes these types of parasitic links since they fall outside the bounds of subwebs A & B (Figure 1.3). As such, the role of concomitant predation in previous studies (e.g. Dunne *et al.*, 2013) has been conflated with the role of parasites as a resource in general. Whilst this has not been a problem in other studies, it is appropriate to make a distinction between the role of concomitant links and the role of parasites as consumers for the purposes of this study, since the differential effects of parasites as resources with and without concomitant links will be explored.

Food webs that include parasites as resources exhibit a significantly different structure to webs that include no parasites or parasites only as consumers (Dunne *et al.*, 2013). Food web structure refers to the proportional abundance of 13 possible motifs that can occur between any three nodes in a food web. Double links, wherein two species are each a

consumer of the other are typically rare in food web analyses (Stouffer *et al.*, 2007), but become common when parasites and concomitant links are included (Dunne *et al.*, 2013). Since predators typically attack prey items that are smaller than themselves, many food web models, such as the seminal “cascade model” (Cohen & Newman, 1985), assume a positive correlation between predator body size and the breadth of its potential feeding niche. Parasites mandatorily parasitize species larger than themselves and therefore reverse the first assumption and an analysis of seven food webs including parasites (Dunne *et al.*, 2013) suggests that many parasites’ feeding niches are significantly broader and less contiguous than those of free-living predators.

Including parasites in food web models could affect their stability in a number of ways and evidence is available to support both stabilising and destabilising effects. Food web theory states that weak trophic links redirect energy from potentially oscillating consumer-resource interactions, resulting in a stabilising effect on food web structure and persistence (McCann *et al.*, 1998). Since many parasites are characterised by a series of very strong interactions, it might be expected that their inclusion would reduce the overall stability of an ecosystem. However, more recent network analysis suggest that tightly coupled predator-prey interactions may be the sole factor allowing for the maintenance of large, complex ecosystems and that weak interactions, contrary to conventional wisdom, may destabilize predator-prey systems (Allesina & Tang, 2012). Higher degrees of food web nestedness, an index quantifying the degree to which species-poor communities are subsets of a larger, species-rich community, has also been suggested as a destabilising factor in ecological networks (Allesina & Tang, 2012). Parasite communities tend to display a degree of nestedness that differs insignificantly from random networks (Poulin, 1996), which may have a stabilising effect on the food web. Conversely, trophic coherence, a measure of how

neatly species fall into trophic levels has been suggested as a key determinant of food web stability (Johnson *et al.*, 2014). Due to many parasites' complex, multiple host life histories, they often parasitize multiple trophic levels, which reduces trophic coherence and thus stability.

Due to the close relationship that they have with their hosts, parasites are more vulnerable to secondary extinction than free-living species (Torchin *et al.*, 2005). For example, the abundant gastropod *Cerithideopsis californica* (Haldeman, 1840) serves as an obligate host for a number of trematode species in the Carpinteria salt marsh. Local extinction of *C. californica* would result in the secondary extinction of 19 parasite species and 977 corresponding links (Lafferty *et al.*, 2006a). Over 60 % of parasites in the Carpinteria salt marshes depend on a single host at some point in their life cycle (Lafferty & Kuris, 2009). This serves to reduce the robustness of food webs to species loss (Lafferty & Kuris, 2009).

### **1.6 Case study: A benthic food web in the German Bight, North Sea**

In this study, we use a benthic food web in the German Bight (North Sea) that has been investigated in detail (Steger *et al.* 2019) as a case study for parasite importance in food webs. The German Bight is a highly dynamic, shallow water region of the North Sea. Through consistent, intense bottom-trawling, ship-traffic routes and offshore wind farm construction (Reiss *et al.*, 2009), the German Bight has come to be regarded as one of the most heavily exploited areas of shelf-sea worldwide. At any time, around 3000 ships are sailing in the North Sea (Aulinger *et al.*, 2016), many heading to or from the ports of Hamburg and Bremen-Bremerhaven in the German Bight, two of the five busiest ports handling containers in Europe, between 2008 and 2018 (Eurostat, 2020). This anthropogenic

disturbance, alongside natural factors such as the recent introduction of invasive non-native species (Gollasch *et al.*, 2009) and regular events like storm-induced sediment re-working (Eisma *et al.*, 1987) and exceptionally cold winters (Kröncke *et al.*, 2013) has selected for small, opportunistic species (Shojaei *et al.*, 2016). The FSd.F food web contains 10 Teleost, 25 invertebrates and 2 basal nodes, it does not include any parasite species.

### 1.7 Aims and hypotheses

Parasites were incorporated into a benthic food web constructed around the *Tellina fabula* community characteristic of fine sands in the German Bight, North Sea (Steger *et al.*, 2019). In doing so, the following questions were addressed: Which generic and unique effects do parasites produce on food web topology, stability and structure, when included as consumers and as both consumers and resources? How are trophic levels affected by the inclusion of parasites, are the changes ecologically realistically and, if not, can they be mitigated for? How can parasites be included in a food web diagram without the erroneous label of top predators and how do food webs change if parasites are included in combined nodes with their hosts?

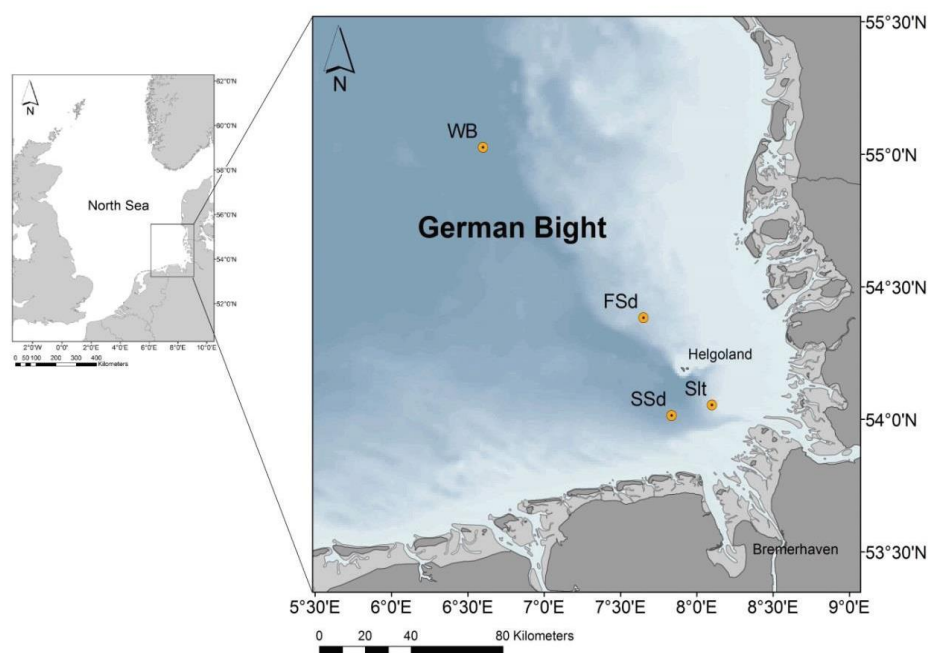
Parasites, included in their role as consumers, are expected to generically increase the food webs' complexity. Complexity is expected to be further increased after parasites are included in their role as consumers and resources. In turn this is expected to have a positive impact on food web stability, which may be counteracted by the low host specificity of some parasite life stages and susceptibility of many parasites to secondary extinction. Parasites' inclusion is expected to raise the proportion of double-link motifs in the FSd.X food web. Prey-averaged TLs are expected to be "stretched after the inclusion of parasites as

consumers and resources. The degree of stretch is expected to be lesser in short-weighted TLs than prey-averaged TLs. A method for calculating flow-based TL, using the 10% rule of trophic efficiency (Lindeman, 1942), is expected to compensate for some of the short-weighted TL stretch that is expected to occur when parasites are included as consumers and resources. All parasites will be labelled as top predators when included only in their role as consumers. Included in their role as consumers and resources, most parasites are expected to have one or more outgoing link to a consumer and are therefore not expected to be top predators. Intermediate parasite life stages are not expected to occupy the highest TLs when disaggregated into ontogenetic nodes. Parasites are not expected to be modelled as top predators in a combined link-modifier web, it is expected that their inclusion will produce only small changes in topology.

## 2. Materials and methods

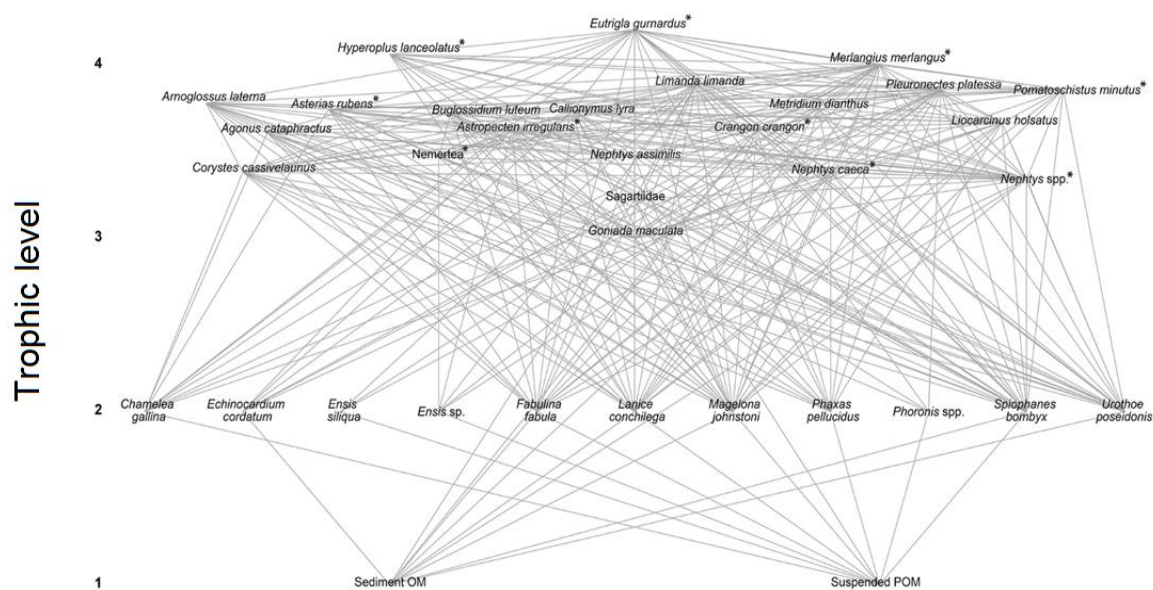
### 2.1 Study area

The *Tellina fabula* community, characteristic of fine sands in the German Bight ( $54^{\circ} 22.50' \text{ N}$ ,  $007^{\circ} 37.00' \text{ E}$ ), also referred to as the *Bathyporeia-Tellina* Community (BTC; Steger *et al.*, 2019), has been sampled annually since 1969 by the Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research (AWI), as part of a macrozoobenthos time series (Schroeder, 2005). The station (FSd; Figure 2.1) is located northwest of Helgoland, at 26 m depth and is composed of homogenous fine sand with a median grain size  $\sim 180 \mu\text{m}$ ). A food web situated at the station, hence referred to as the “FSd.F” food web, was constructed by Steger *et al.* (2019) using an integrative approach, combining an extensive literature search on species-specific interactions and stable isotope analysis, including benthic infauna, epifauna and demersal fish, but excluding parasites. Particulate organic matter forms the



**Figure 2.1:** Map of the German Bight including the FSd target station, taken from Shojaei *et al.* (2016).

base of this food web which is characterised by high prevalence of suspension and interface feeders (Steger *et al.*, 2019), such as the food webs namesake *Fabulina fabula* (Gmelin, 1791). Higher level consumers include asteroids, Decapoda and teleosts such as the grey gurnard (*Eutriglia gurnardus* (Linnaeus, 1758)), whiting (*Merlangius merlangus* (Linnaeus, 1758)) and dab (*Limanda limanda* (Linnaeus, 1758)). The FSd.F food web forms the basis of this study and contains 33 free-living species; of which 10 species are teleosts and 23 species are invertebrates, and two basal nodes (Figure 2.2); suspended and sedimentary particulate organic matter (POM). Here, we present the first study with parasites included into a fully submerged, marine food web.



**Figure 2.2:** The benthic food web of the *community at the FSd station*. Species are arranged vertically according to their prey-averaged trophic levels (numbers on the left). Cannibalistic species are marked with an asterisk. OM: organic matter, POM: particulate organic matter. Taken from Steger *et al.* (2019).

## 2.2 Host dissection and parasite identification

During the HE480 cruise (March 2017) with *RV Heincke*, fish were caught at the FSd station using an otter trawl for an average of 32 minutes at speeds between 2.78 and 3.55 knots. In

total, 25 common dab (*Limanda limanda*) and 30 whiting (*Merlangius merlangus*) were frozen directly on board for later inspection. Before dissection, the skin, fins, nasal capsules, buccal and branchial cavities, eyes, and gills were inspected for metazoan parasites whilst the fish were still in a partly frozen state. The fishes were fully thawed, weighed (0.1 g accuracy) and measured (0.1 cm accuracy) for standard length. The fish were opened from the cloaca and cut to the extremes of the body cavity. The oesophagus was cut, and the stomach, intestine, pyloric caeca, gonads, liver, and spleen were removed from the body cavity and kept separately in a 0.9 % saline solution. The empty fish was weighed, the heart was removed and kept in saline solution and a scraping was taken of the kidneys and pressed between the lid and the bottom of a petri dish. The eyes and gills were removed and kept separately in 0.9 % saline solution. The body, eye and gill cavities were examined for parasites. Each fish was filleted, and the musculature, kidneys, liver, gonads, heart, and spleen were separately pressed between a petri dish lid and bottom and viewed under a dissecting microscope. Individually, the intestine and stomach were cut lengthways, and their contents were examined for parasites under a dissecting microscope. The stomach and intestinal walls were pressed between the lid and bottom of a petri dish and inspected under a dissecting microscope. The eyes were punctured and emptied into saline solution for examination and the gills were individually examined for parasites under a dissecting microscope.

All parasites were fixed with absolute ethanol, 40 % formaldehyde and acetic acid (AFA) for 24 hours and then transferred into 70 % ethanol for storage. Digenea were stained with carmine and mounted in glycerol gelatine on a glass microscope slide for dissection.

Nematoda were transferred into a solution of 2-parts 70 % ethanol and 1-part liquid glycerol and left for the ethanol to evaporate. After much of the ethanol had evaporated, the



solution was topped up with liquid glycerol and left for the remaining ethanol to evaporate. Copepoda were kept in 70 % ethanol for identification. Parasites were identified morphologically using relevant keys (Overstreet & Hochsberg, 1975; Kabata, 1979; Gibson & Bray, 1986; Moravec, 1994; Gibson, 1996; Gibson *et al.*, 2002; Bray & Cribb, 2008) under a compound microscope.

## **2.3 Link collection**

### **2.3.1 Parasite-host links**

Parasitic links were collected from the peer-reviewed articles, Masters and PhD theses listed in Palm *et al.* (1999) and in a literature search. The Web of Science database (<http://apps.webofknowledge.com>) was used to search for species known to parasitize free-living species from the FSd.F food web (Figure 2.2) using the search term “parasit\* AND *Merlangius merlangus*” for example. The reference list of each relevant article or thesis was examined for further parasitic links to FSd.F species. Links from these parasites, identified in the dissections and literature search, to other species in the FSd.F were collected by searching for the parasite’s genus and species name on the Web of Science and Natural History Museum host-parasite (Natural History Museum, 2019) databases, inspecting appropriate literature and examining published food webs that include parasites. Information on the geographical location of the link and prevalence, proportion of infected fish, was recorded. Current species names and authorities were obtained from the World Register of Marine Species (WoRMS) online database (Horton *et al.*, 2020).

### 2.3.2 Parasite-parasite links

Parasite-parasite links consisted of interspecific antagonism between larval trematodes infesting a gastropod, intermediate host. Links were assigned along a body size-based hierarchy (Lafferty *et al.*, 1994; Sousa, 1993, wherein a parasite-parasite link was assigned from one species to every smaller species that infests the same species of gastropod. Estimates for cercarial body volume were obtained in the literature and links were assigned according to the hierarchy. Hyperparasitic links, wherein one parasite serves as host to another were collected searching the Web of Science: “*Clavella adunca*” AND hyperparasit\*”, for example. Links were assigned only at a species-level resolution, no hyperparasitic links were inferred between higher-level taxa.

### 2.3.3 Predator-parasite links

Potential direct predative links were inferred to clams, polychaetes (Lafferty *et al.*, 2006b) and fish smaller than 8 cm (Kaplan *et al.*, 2009) from free-living trematode cercaria, providing the free-living predator is not a suitable host for the particular life stage. Unsuitable, gadoid fish hosts were assigned direct predative links to the free-living life stages of parasitic copepods (Gaard & Reinert, 2002). Suitable fish were assigned predative links if the free-living cercaria require an intermediate host before becoming infective to the fish. Concomitant links, whereby parasites are digested by the predators of their host, were inferred from endoparasites to all of their hosts predators, which were not themselves host to the parasite. Trophic transmission is an unviable pathway for ectoparasites and were assigned concomitant links from all of their hosts’ predators.

### 2.3.4 Parasite-inferred predator-prey links

Due to the reliance on inferred links from parasites to invertebrate species acting as intermediate hosts; inferred parasite links between free-living species were deemed unsuitable for inclusion in the FSd.F web.

### 2.3.5 Expanded FSd.97 food web

Steger et al. (2019) constructed the benthic “FSd.F” food web based on those species that were found at the FSd station up to a cumulative energetic flow of 90 % of the total energy flow, as quantified by Dannheim *et al.* (2014). Here, we expanded this food web version up to 97 % threshold, hence referred to as the FSd.97 web, in order to incorporate obligate intermediate host taxa, such as the gastropod *Euspira nitida* (Donovan, 1804), that were missing in the cumulative 90 % FSd.F web. Species-specific links were collected through a literature search on Web of Science, using search term “*Cancer pagurus* AND (diet OR feed\* OR trophic OR prey OR predat\*)” for example. Supplementary material published by Steger *et al.* (2019) and the MarLIN BIOTIC database (MarLIN, 2016) were consulted. Predative links were inferred to prey in the same class of a known prey item, if the log10 body-mass ratio (BMR) exceeded the thresholds calculated for each predator taxon by Brose *et al.* (2006);  $BMR > 0.37$  for marine invertebrates and  $BMR > 2.57$  for marine ectotherms.  $BMR = \log_{10} \left( \frac{W_c}{W_r} \right)$ , where  $W_c$  = wet weight (g) of the consumer species and  $W_r$  = wet weight (g) of the potential resource. No links were found in the literature or inferred by BMR for the gastropod *E. nitida*, which primarily predares bivalve molluscs. A more speculative link had to be inferred from *E. nitida* to *Phaxas pellucidus* (Pennant, 1777), the only bivalve in the FSd.97 that is smaller than *E. nitida* by wet body mass.

## 2.4 Food web construction

### 2.4.1 Dab and whiting-specific food webs

Parasites were disaggregated into ontogenetic niche shift nodes; nodes were separated when the parasite species in question underwent distinct ontogenetic feeding niche shifts during the course of development (Preston *et al.*, 2014), and included in the expanded FSd.97 food web (section 2.3.5). Feeding niche shifts in this context refer to a change of host for the parasite, or the move to a free-living life stage as in some trematode cercaria. All non-basal nodes without direct links to *Limanda limanda* or *Merlangius merlangus* (respectively) were removed. Links from larvae to adults of the same species, as suggested by Huxham *et al.* (1995), were excluded on account of their being ecologically unrealistic, since a feeding interaction does not take place. Species with the same incoming and outgoing links were aggregated into trophic species.

### 2.4.2 The FSd.P and FSd.X

Parasite diversity has significant effects on food web topology (Dunne *et al.*, 2013). Including all 93 parasite species that were identified in the literature search and dissections was assumed to be ecologically unrealistic. Due to the limited richness and abundance of dissected hosts in the study and similar constraints on time and resources, which precluded the possibility of quantifying the energetic contribution of parasites in the food web, the number of parasite species suitable for inclusion in the FSd.P and FSd.X was inferred from previous studies. The seven food webs including parasites analysed by Dunne *et al.* (2013) include a mean  $30 \pm 8.4$  % of parasitic species. The FSd.F food web (Steger *et al.*, 2019) which forms the basis of this study contains 35 free-living species and basal nodes. Therefore,

rough limits of between 11 and 19 species were set for parasite richness in the FSd.P and FSd.X webs including parasites. The number of potential species was reduced to 26 by excluding any parasite species that have not been identified in the German Bight, infesting a host included in the FSd.F web. This was reduced to a richness more comparable to previous studies with the use of a parasite diversity threshold. Infection intensity is highly dependent on parasite taxa and life stage and can fluctuate significantly, therefore, prevalence of infection, the proportion of infected hosts in each study, formed the basis of the threshold. Information on the diversity of parasites included in previous studies is scarce and only one previous study could be found that included detailed data on the diversity of their included parasites (Hernandez & Sukhdeo; 2008). The authors include parasites with a mean prevalence of 15 %, a threshold which, if extended to the FSd.P and FSd.X webs would include 21 parasites, significantly higher than the rough limits derived from Dunne *et al.* (2013). Hernandez & Sukhdeo (2008) highlight five prominent parasites in the Muskingum Brook food web, the mean prevalence of which is 36 % in all of their teleost hosts (Hechinger & Sukhdeo, 2008). Including a minimum prevalence threshold of 36 % reduced the number of potential parasites included in the FSd.P and FSd.X webs to 12, which falls within one standard deviation of the parameters derived from Dunne *et al.* (2013). No species identified in the literature or dissections had a maximum prevalence between 36 % and 40 %, therefore the threshold is subsequently referred to as the 40 % threshold for simplicity.

### 2.4.3 Combined host-parasite node food web

All parasite nodes were removed from the FSd.P web and new combined nodes were constructed to represent every parasite-host link. Nodes with identical incoming and outgoing links were reduced into trophic species. Information on behaviour modification in parasite species of the FSd.F was collected using the search term “*Anisakis simplex* AND (impact OR effect OR behav\* OR modif\*) for example, in the Web of Science database and inferred from wider literature reading. This was used to infer link changes between uninfected and infected versions of each free-living species. Coinfection of more than one parasite species was not accounted for. Information on synergistic and antagonistic effects of co-infections were not available, therefore co-infection was unaccounted for. Likewise, information on whether links from infected host nodes to other infected host nodes are changed with infection could not be attained.

## 2.5 Food web analyses

### 2.5.1 Network topology

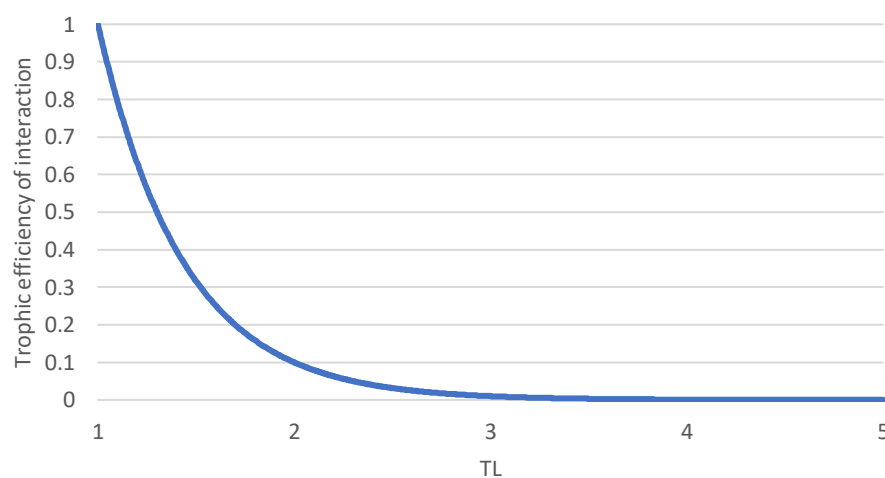
All analyses were conducted on three versions of the FSd web: i) FSd.F – Including no parasite species, ii) FSd.P – Including parasites only as consumers and iii) FSd.X – Including parasites as consumers and resources. The FSd.P and FSd.X food webs were structured according to short-weighted trophic level ( $TL_{sw}$ ), wherein each species' TL is calculated as the mean of its prey-averaged TL ( $TL_{pa}$ ), the mean TL of the species' prey +1, and the length of its shortest chain to a basal node. Topological indices such as number of links (L), from a resource species to its consumer, linkage density (L/S), wherein L = number of links in the

food web, and directed connectance ( $L/S^2$ ) were calculated using the “Cheddar” package (Hudson *et al.*, 2013) in R (R Core Team, 2014). Adjusted connectance (Lafferty *et al.*, 2006a) was calculated manually and used only in the FSd.P web. Adjusted connectance =  $L/S_f(S_f+S_p)$ , where  $S_f$  = free-living species richness,  $S_p$  = parasite species richness was used for the LL.P, MM.P and FSd.P food webs, in which parasites are included only in their role as consumers. Directed connectance ( $L/S^2$ ) was used for the FSd.F and FSd.X web. Histograms of links ( $L$ ) per species were produced, showing how many other species a target node including both incoming links from resource species and outgoing links to consumers. Graphs, charts and tables were produced in Microsoft Excel, histograms in Excel were produced using the ToolPak add-in. Some analyses required species to be aggregated into functional feeding guilds, these were parasites, predators, omnivores, interface feeders, suspension feeders, deposit feeders and basal nodes.

### 2.5.2 Trophic efficiency-weighted trophic levels

Flow-based TLs ( $TL_{fb}$ ) were calculated according to the trophic efficiency (Lindeman, 1942) of each link in order to counteract the inflation of prey-averaged TLs ( $TL_{pa}$ ) when parasites-as-resources links were included.  $TL_{pa}$  was calculated for every species in the FSd.X web using the R Cheddar package (Hudson *et al.*, 2013). Short-weighted trophic levels ( $TL_{sw}$ ) were calculated manually using an average of  $TL_{pa}$  and the shortest chain length to a basal species (Williams & Martinez, 2004). The mean  $TL_{sw}$  of every link in the food web was used to calculate a measure of the link’s trophic efficiency-weighted diet fraction representing the proportion of energy that’s available (Lindeman, 1942) to the corresponding mean TL ( $\bar{x}TL$ ) of each interaction (Figure 2.3). Trophic efficiency-weighted diet fraction was

calculated using the following formula:  $TE = 10^{1-\bar{x}^{TL}}$ . This was calculated for every interaction in Microsoft Excel. The relative trophic efficiency of prey items for each consumer in the food web accounted for that prey item's proportional contribution to the overall flow-based trophic level ( $TL_{fb}$ ) of the consumer.  $TL_{fb}$  was calculated using the R Cheddar package.



**Figure 2.3:** Proportion of the initial energy that is available to each trophic level, according to the 10 % rule, which is the principle on which trophic efficiency weightings are based.

### 2.5.3. Network structure

Four versions of the FSd food web were constructed including only free-living species (the FSd.F food web) and free-living species with parasites in their role as consumers only (FSd.P), as consumers and direct predatory resources (FSd.D) and as consumers and direct and concomitant resources (FSd.X). The number of each of 13 distinct 3-node motifs in each food web was calculated in R using the triad.census function in the igraph package (Csardi & Nepusz, 2006).



### 3. Results

The fishes were weighed on board directly after the catch and again in the lab after freezing, transport and thawing. On board 25 dab (*Limanda limanda*) weighed  $83 \pm 28$  g (mean  $\pm$  SD) and had a mean length of  $21 \pm 2$  cm. The 30 whiting (*Merlangius merlangus*) weighed on average  $28 \pm 25$  g and were on average  $15 \pm 2$  g. Much of the variance in the length of whiting was contributed by a single whiting, 155 cm in length. In the lab the dab weighed  $81 \pm 28$  g and had a standard length, from the anterior extremity to the tip of the peduncle, of  $18 \pm 2$  cm and the whiting weighed  $27 \pm 23$  g and had a standard length of  $14 \pm 2$  cm.

#### 3.1 Parasite diversity

Seven species of metazoan parasite were identified in the dissections of dab and whiting, comprising four digenean trematodes, two nematode roundworms and one species of parasitic copepod (Table 3.1). The majority of individual parasites occurred in the whiting. Only two dab were found to be infested with metazoan parasites; one dab was infested with two *Hemiurus communis* Odhner, 1905 specimens and the other one with a single exemplar of the same species. All were isolated from the stomachs of their hosts. Whiting were infested with considerably more parasites than dab (Table 3.1). Over 90 % of the dissected whiting (28/30) were infested with one or more species; 2.25 species on average with a maximum species richness of 5. In all, 478 individual parasites were recovered from the whiting, the most prevalent was the nematode worm *Hysterothylacium aduncum* (Rudolphi, 1802) (Table 3.1). The most abundant parasites in whiting were metacercarial life stages of the trematode family Heterophyidae (Leiper, 1909) ( $n \approx 325$ ) most likely the species

*Cryptocotyle lingua* (Creplin, 1825), which was found encysted on the skin, fins and eyes.

One parasitic crustacean species, the copepod *Clavella adunca* (Strøm, 1762), was identified; 30 females, all attached to the gills of their hosts, and nine males, attached to the females. Up to three males were found attached to a single female copepod. One whiting specimen (36M18) harboured 62.9 % of all *H. aduncum* and 13.8 % of all *H. communis* isolated from whiting. The specimen was significantly longer and heavier than the other sampled whiting; 25 cm and 155 g compared to means (excluding 36M18) of  $14.91 \pm 1.37$  cm and  $23.86 \pm 6.98$  g.

**Table 3.1:** Diversity and infestation numbers of parasites identified in 25 *Limanda limanda* and 30 *Merlangius merlangus*.

|           |                                 | <i>Limanda limanda</i>           | <i>Merlangius merlangus</i> |
|-----------|---------------------------------|----------------------------------|-----------------------------|
| Digenea   | <i>Derogenes varicus</i>        | Prevalence (%)                   | 37                          |
|           |                                 | Mean intensity (Intensity range) | 1.6 (1-4)                   |
|           |                                 | Abundance                        | 0.6                         |
|           | <i>Hemiurus communis</i>        | Prevalence (%)                   | 8                           |
|           |                                 | Mean intensity (Intensity range) | 1.5                         |
|           |                                 | Abundance                        | 0.12                        |
|           | Heterophyidae indet.            | Prevalence (%)                   | 20                          |
|           |                                 | Mean intensity (Intensity range) | 54.2 (1-240)                |
|           |                                 | Abundance                        | 10.83                       |
|           | <i>Stephanostomum</i> spp.      | Prevalence (%)                   | 13                          |
|           |                                 | Mean intensity (Intensity range) | 1.8 (1-2)                   |
|           |                                 | Abundance                        | 0.2                         |
| Nematoda  | Anisakidae indet.               | Prevalence (%)                   | 3                           |
|           |                                 | Mean intensity (Intensity range) | 1                           |
|           |                                 | Abundance                        | 0.03                        |
|           | <i>Hysterothylacium aduncum</i> | Prevalence (%)                   | 50                          |
|           |                                 | Mean intensity (Intensity range) | 4.1 (1-39)                  |
|           |                                 | Abundance                        | 2.07                        |
| Crustacea | <i>Clavella adunca</i>          | Prevalence (%)                   | 40                          |
|           |                                 | Mean intensity (Intensity range) | 3.3 (1-13)                  |
|           |                                 | Abundance                        | 1.3                         |

### 3.2. Parasite identification

#### 3.2.1 Digenea

Order: Plagiorchiida La Rue, 1957

Superfamily: Hemiuroidea Looss, 1899

Family: Derogenidae Nicoll, 1910

Subfamily: Derogeninae Nicoll, 1910

***Derogenes varicus* (Müller, 1874) Looss, 1901**

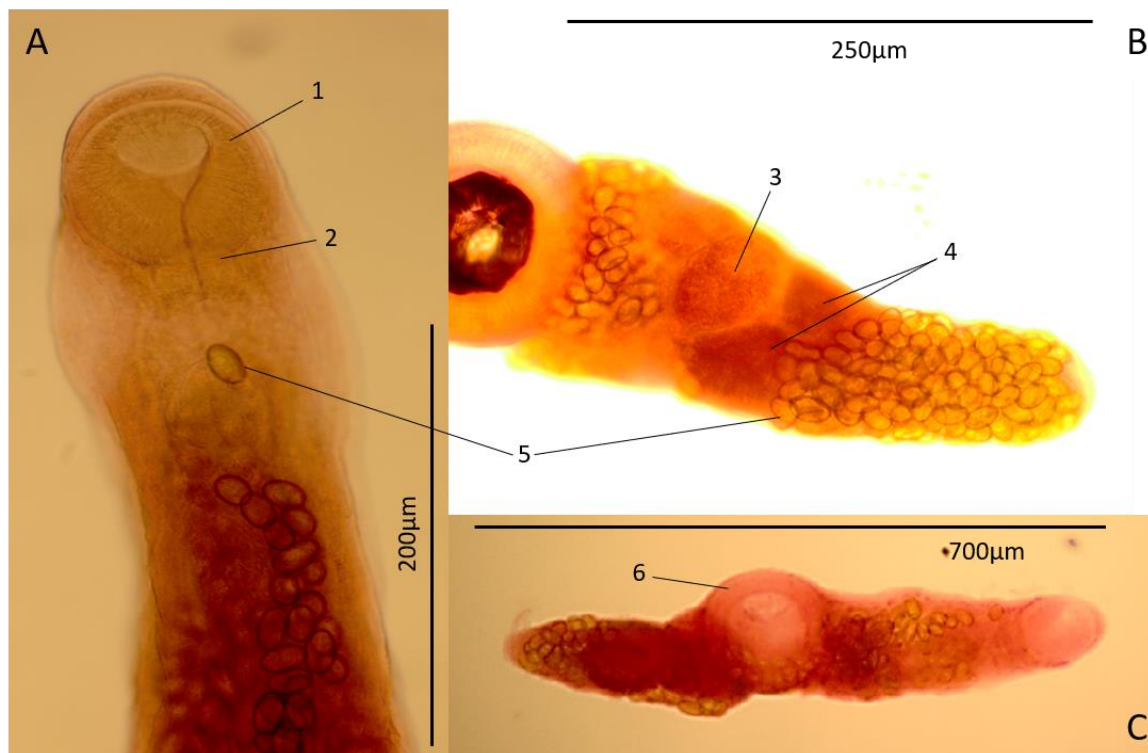
Life stage: Adult and immature specimens

Host: *Merlangius merlangus*

Site of infestation: Stomach

The specimens were identified as members of the superfamily Hemiuroidea due to the infection site in the alimentary canal, the position of their mouth, at the anterior extremity, the absence of a pre-pharynx and the presence of both oral and ventral suckers. Specimens of the superfamily Hemiuroidea are parasitic in marine fishes. The family Derogenidae was determined based on the infection site in the organs of non-Elasmobranch fish, the presence of their two, pre-ovarian testes, absent ecsoma and non-intertesticular ovary. The specimens were not parasitic in the swim bladder of freshwater fish and their ventral sucker was positioned relatively towards the posterior. The subfamily Derogeninae was ascertained by the parasites' pre-ovarian testes. The blindly ending gut caeca, which do not form a cyclocoel, eggs that are not drawn to a point at the anopercular pole and the fact that part of the uterus was posterior to the vitellarium lead to the genus *Derogenes*. The species level

identification of *D. varicus* (Figure 3.1) was made on account of their smooth, fusiform body with a pre-oral lobe. The mean sucker width ratio (oral:ventral) of 1:1.5 conformed with the range of 1:1.4 to 1:1.8 described for this species. The testes and ovary were smooth, the vitellaria composed of two, rounded compact masses and the eggs were operculate.



**Figure 3.1:** *Derogenes varicus* anterior (A) and posterior (B) ends, and whole specimen (C). Annotations show the oral sucker (1), pharynx (2), ovary (3), vitellaria (4), eggs (5) and ventral sucker (6).

Family: Hemiuridae Looss, 1899

Subfamily: Hemiurinae Looss, 1899

***Hemiurus communis* Odhner, 1905**

Life stage: Adult and immature specimens

Host: *Limanda limanda*, *Merlangius merlangus*

Site of infestation: Stomach

The specimens of this species were found in the stomachs of teleosts and displayed two testes and an ecsoma characteristic for the family Hemiuridae. Due to the absence of an ejaculatory vesicle, the presence of a well-developed ecsoma, two oblique vitellaria masses and plicated body surface the specimens were assigned to the subfamily Hemiurinae. The bipartite seminal vesicle indicated the genus *Hemiurus*. The species level identification of *H. communis* (Figure 3.2) was based on the specimens' sucker ratio of around 1:1.5 (oral: ventral), the fact that the specimens were not parasitic in salmon, had a boreal, non-Lusitanian distribution and were present in gadoids (e.g. *Merlangius merlangus*), whereas alternative species in the genus are not.



**Figure 3.2:** Adult specimens of *Hemiurus communis*, showing the whole parasite (A), anterior end (B) and posterior end (C). Annotations show the oral sucker (1), pharynx (2), ventral sucker (3), ecsoma (4) and vitellaria (5).

Superfamily: Opisthorchioidea Braun, 1901

Family: Heterophyidae Leiper, 1909

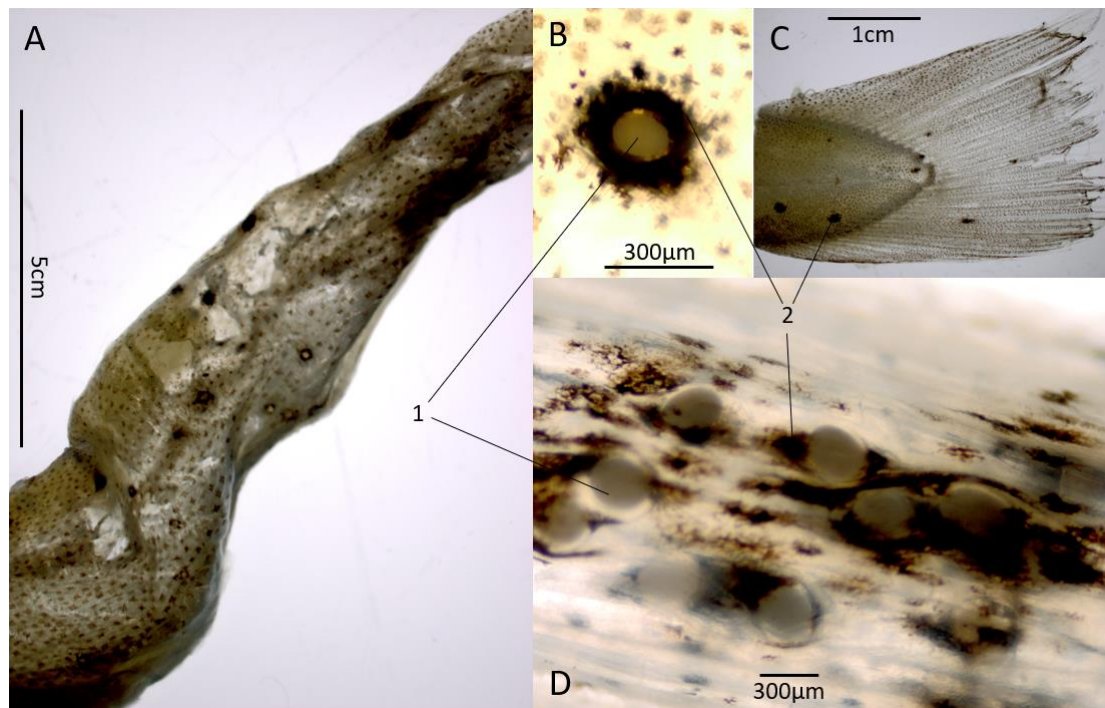
**Heterophyidae gen. et sp. indet.**

Life stage: Metacercaria

Host: *Merlangius merlangus*

Site of infestation: Skin, fins and eyes

Identification of the cysts was based on the surrounding melanophores, or “black spots”, produced by the fish to fight infection of the metacercaria. Black spots are produced around the cysts of Digenea belonging to the families Heterophyidae and Diplostomatidae. The family Heterophyidae (Figure 3.3) was identified on account of the hosts’ habitat, since



**Figure 3.3:** Heterophyidae indet. on the skin of *M. merlangus* (A), as a single cyst (B), on the tail of *M. merlangus* (C) and as multiple cysts on skin (D), metacercaria (1), showing “black-spot” host response of melanophore production (2).

Diplostomatidae are exclusive to freshwater hosts. No attempt to remove the metacercaria from their cyst was made for further identification due to an initial oversight and assumption of the parasite's identity and time restrictions.

Superfamily: Allocreadioidea Looss, 1902

Family: Acanthocolpidae Lühe, 1906

***Stephanostomum* Looss, 1899 sp.**

Life stage: Adult and immature

Host: *Merlangius merlangus*

Site of infestation: Pyloric caeca, intestines

Specimens of the superfamily Allocreadioidea were identified based on their infection site in the alimentary canal, their mouth at the anterior extremity. The vitellaria are situated at the posterior extremity, whereas the ventral sucker is towards the anterior end. All six specimens were accidentally destroyed, as a result of the initial visual misidentification as nematodes, leading to incorrect preparation, which destroyed them. From photographs taken before the specimens were damaged, the genus *Stephanostomum* (Figure 3.4) was identified, on account of their narrow, elongate body, oral sucker which is terminal and wider than long and oval ventral sucker in the anterior fifth of the body. The eggs are large and tanned, and the pharynx is roughly pyriform, with a long pre-pharynx.



**Figure 3.4:** *Stephanostomum* sp. immature anterior (A), immature posterior (B) ends and body fragment (C), displaying the oral sucker (1), pharynx (2), ventral sucker (3) and testes (4).

### 3.2.2 Nematoda

Order: Rhabditida Chitwood, 1933

Superfamily: Ascaridoidea Baird, 1853

Family: Raphidascarididae Hartwich, 1954

Subfamily: Raphidascaridinae Hartwich, 1954

***Hysterothylacium aduncum* (Rudolphi, 1802)**

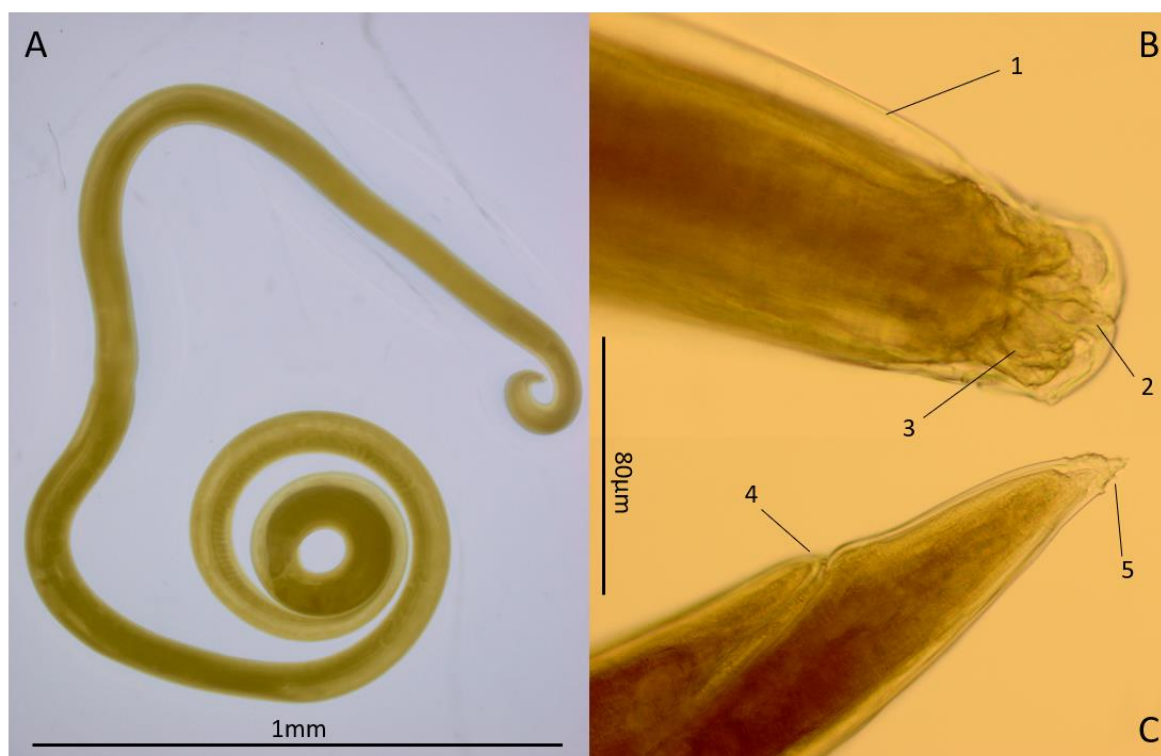
Life stage: L3 & L4 Larvae

Host: *Merlangius merlangus*

Site of infestation: Stomach, intestine, pyloric caeca



Specimens of *Hysterothylacium aduncum* were identified to the family Raphidascarididae by the specimens' triradiate anterior end with three, well-developed lips and the presence of phasmids. The genus was identified because of the lack of cuticular rings and spines and the presence of interlabia between the lips, the anteriorly facing caeca and posterior appendix. The specimen is not a freshwater parasite of Acipenseridae, the lateral alae start narrow, increasing posteriorly and the tail terminates with a "cactus-like" structure. Therefore, the specimens were identified as *Hysterothylacium aduncum* (Figure 3.6).



**Figure 3.6:** *Hysterothylacium aduncum* L4 larvae anterior (B) and posterior (C) from whiting (*Merlangius merlangus*). Annotated is the lateral alae (1), interlabial spines (2), triradiate lips (3), anus (4) and tail end (5).

Superfamily: Ascaridoidea Baird, 1853

Family: Anisakidae Railliet & Henry, 1912

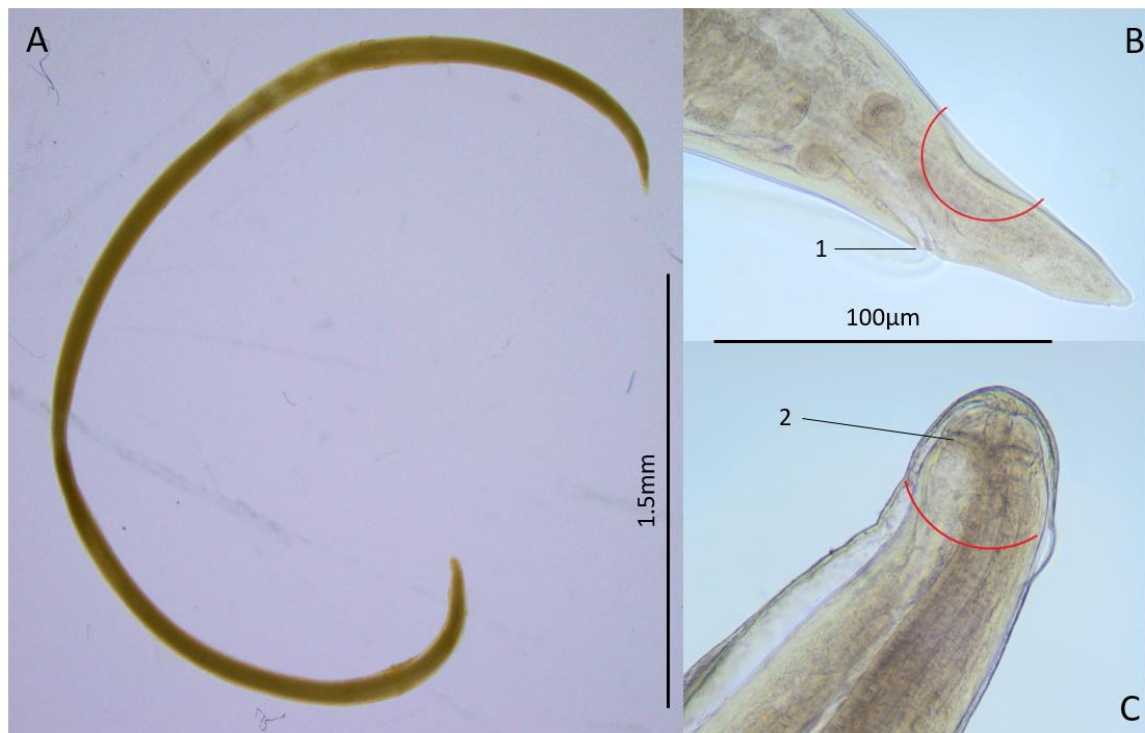
**Anisakidae Railliet & Henry, 1912 gen. et sp. indet.**

Life stage: L3 Larvae

Host: *Merlangius merlangus*

Site of infestation: Body cavity

One specimen was not identified beyond Family level. The specimen was identified as a member of the Anisakidae (Figure 3.5) using Moravec (1994), on account of its triradiate anterior mouth, with three, well-developed lips.



**Figure 3.5:** Anisakidae indet. larvae identified in whiting (*Merlangius merlangus*), showing the full specimen (A), posterior (B) and anterior ends (C). The anus (1) and lips (2). Effort were made to remove the red circles; new pictures could not be taken due to restrictions on movement at the time.

### 3.2.3 Crustacea

Class: Copepoda Milne Edwards, 1840

Order: Siphonostomatoida Burmeister, 1835

Family: Lernaepodidae Milne Edwards, 1840

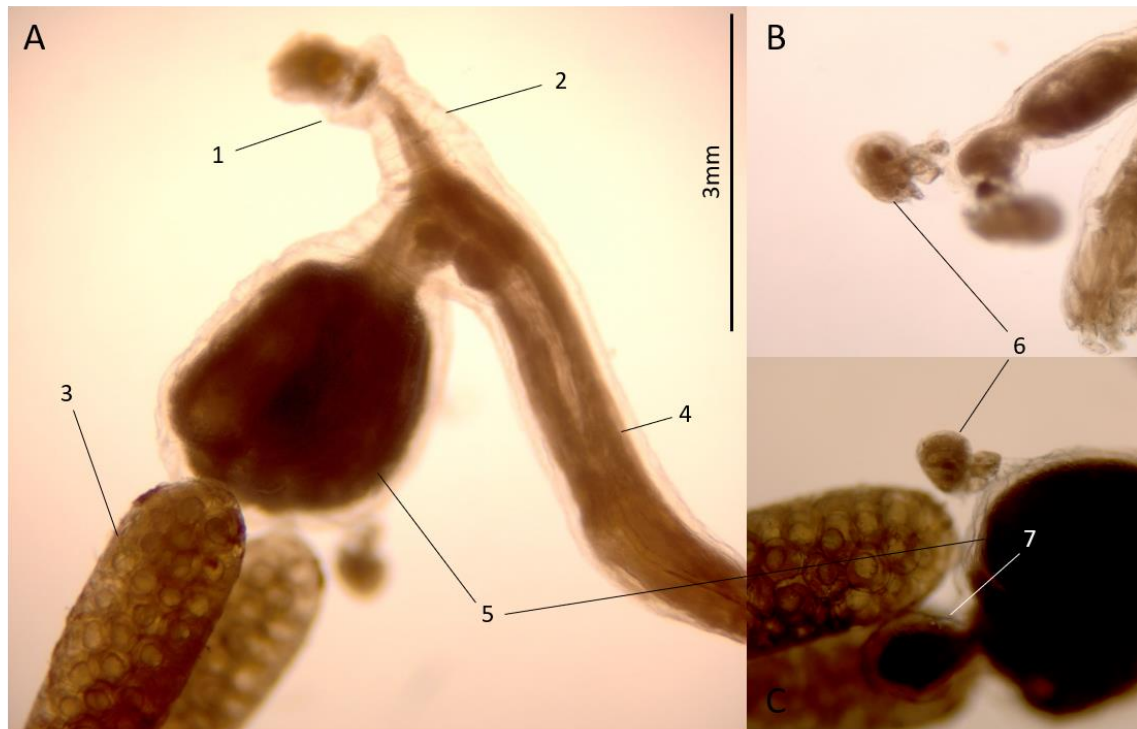
#### ***Clavella adunca* (Strøm, 1762)**

Life stage: Adult

Host: *Merlangius merlangus*

Site of infestation: Gills

The copepod *Clavella adunca* (Figure 3.7) was identified using Kabata (1979). Females of the species were identified to the family Lernaepodidae on account of their body without sharp intersectional divisions, anterior region not buried deep in the host tissue, body consisting of >2 distinguishable parts and identifiable cephalothorax, trunk and second maxillae. The specimen's marine fish host, cylindrical cephalothorax, greater than ¼ of the trunk length and coming from the anterior of the trunk, absent posterior processes and absent lateral swellings at the base of the second maxillae lead to the genus *Clavella*. The specimens were identified to species level based on the absence of spherical swellings at the tip of the second maxillae and absence of papillae at the base of the second maxillae. Males of this species were attached to the females and therefore readily identified.



**Figure 3.7:** *Clavella adunca* female, with male attached to trunk (A), males attached to a female second maxillae (B) and second maxillae fragment (C). Annotations show the bulla (1), second maxillae (2), egg sacks (3), cephalothorax (4), trunk (5), males (6) and genital process (7).

### 3.3. The FSd.97 food web

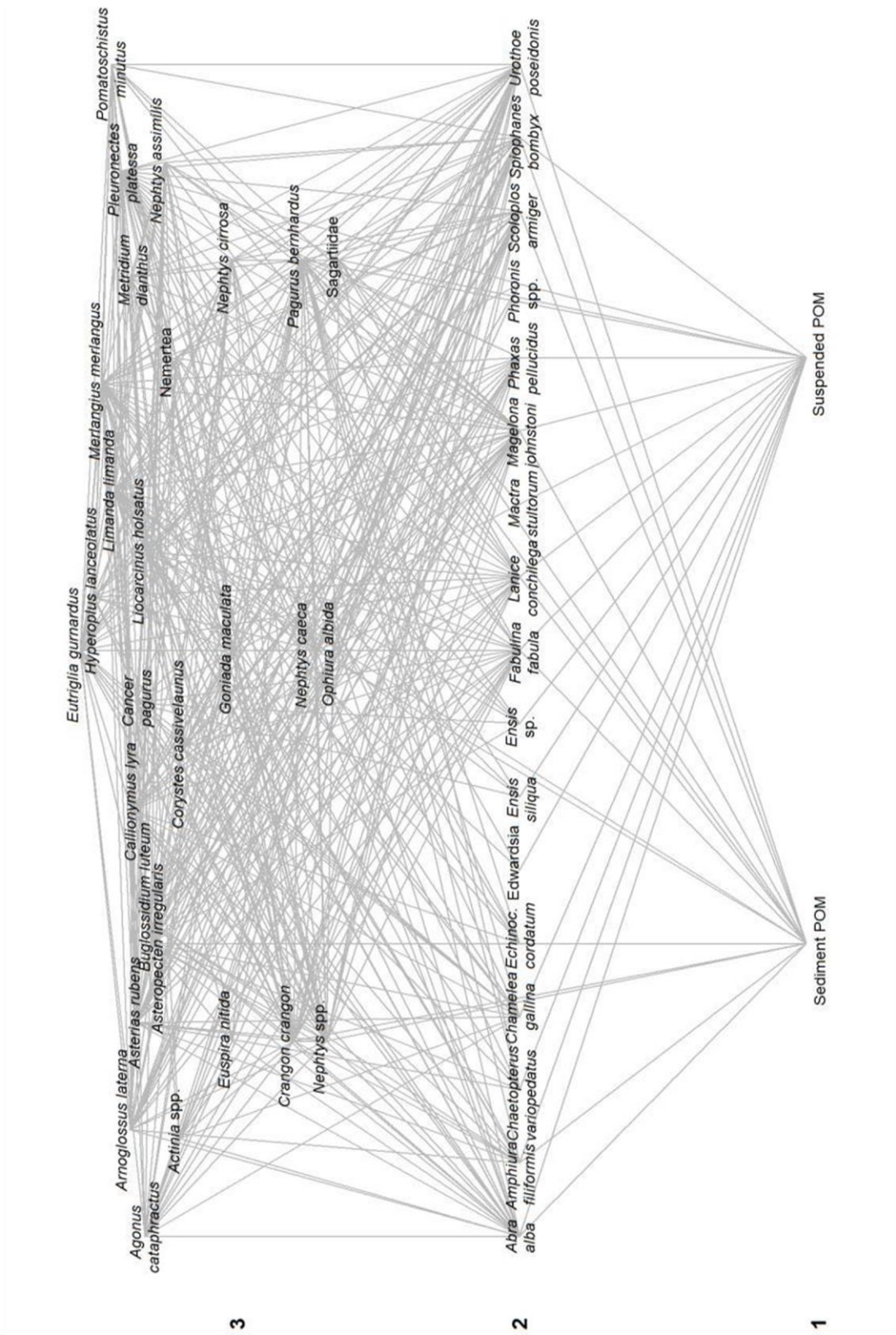
#### 3.3.1 Construction of the FSd.97 food web

The 35 node BTC web (Steger *et al.*, 2019), here referred to as the FSd.F food web, was expanded to include species comprising 97 % of the cumulative energy flow (Dannheim *et al.*, 2014), at the FSd station. Twelve further free-living species were included in the expanded FSd.F food web, called the FSd.97 web (Figure 3.8), this included one gastropod, two bivalve, two ophiuroid, two anemone, two decapod and three polychaete species. Functionally, these additions included two interface feeders, three suspension feeders, one deposit feeder, three omnivores and three predators. The FSd.97 contained 159 more links

than the FSd.F, of which 67 were identified in a literature search (see section 2.3.5) and 92 of which were inferred by body mass ratios after Brose *et al.* (2006). No suitable resources were identified in the FSd.97 for the predatory gastropod *Euspira nitida*. The species feeds exclusively on bivalves, however the mass all bivalve species in the FSd.97 food web was too great for a link to be inferred. A speculative link to *Abra alba* (W. Wood, 1802), the closest species in body mass to *E. nitida* was included in the food web. Other naticid gastropods have shown significant prey selection preference for thin-shelled bivalves (Grey *et al.*, 2005), as the energy required to penetrate the shell is minimised. Therefore, the relatively brittle shell of *Abra alba* (Hayward & Ryland, 2016) suggests that this is a plausible link.

### 3.3.2 Topology of the FSd.97 food web

Linkage density ( $L/S$ ) in the expanded 47-node FSd.97 web, was greater (9.98; Table 3.5) than in the original, 35-node, FSd.F web (8.86, Table 3.4), as was the proportion of omnivorous species; 60 % in the FSd.97 and 53 % in the FSd.F. Conversely, connectance ( $L/S^2$ ) in the expanded FSd.97 was lower than in the FSd.F; 0.21 compared to 0.25, and both the mean and maximum short-weighted trophic levels ( $TL_{sw}$ ) were lower in the FSd.97 than in the FSd.F. Mean  $TL_{sw}$  decreased from 3.05 to 2.93 whilst the maximum  $TL_{sw}$  was reduced from 3.6 to 3.53, the highest  $TL_{sw}$  in each web was occupied by grey gurnard.



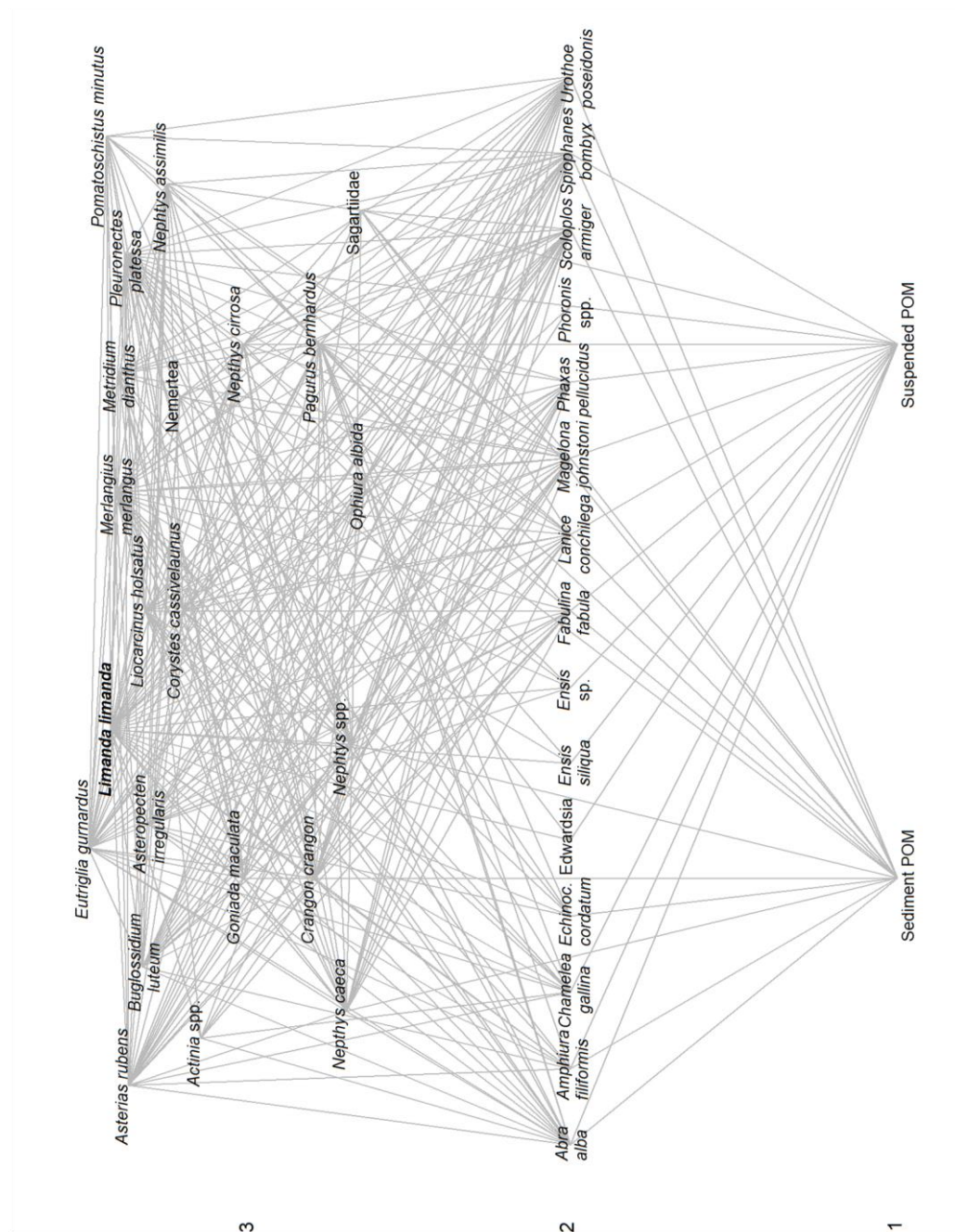
**Figure 3.8:** Fsd.97 food web, including species comprising 97 % of the cumulative energy flow at the Fsd station. Vertical height corresponds to short-weighted trophic level, indicated by the numbers on the vertical axis. The name of the heart urchin *Echinocardium cordatum* has been shortened to “*Echinoc. cordatum*” for space.

### 3.4 The dab and whiting-specific food webs

#### 3.4.1 The dab-specific food webs

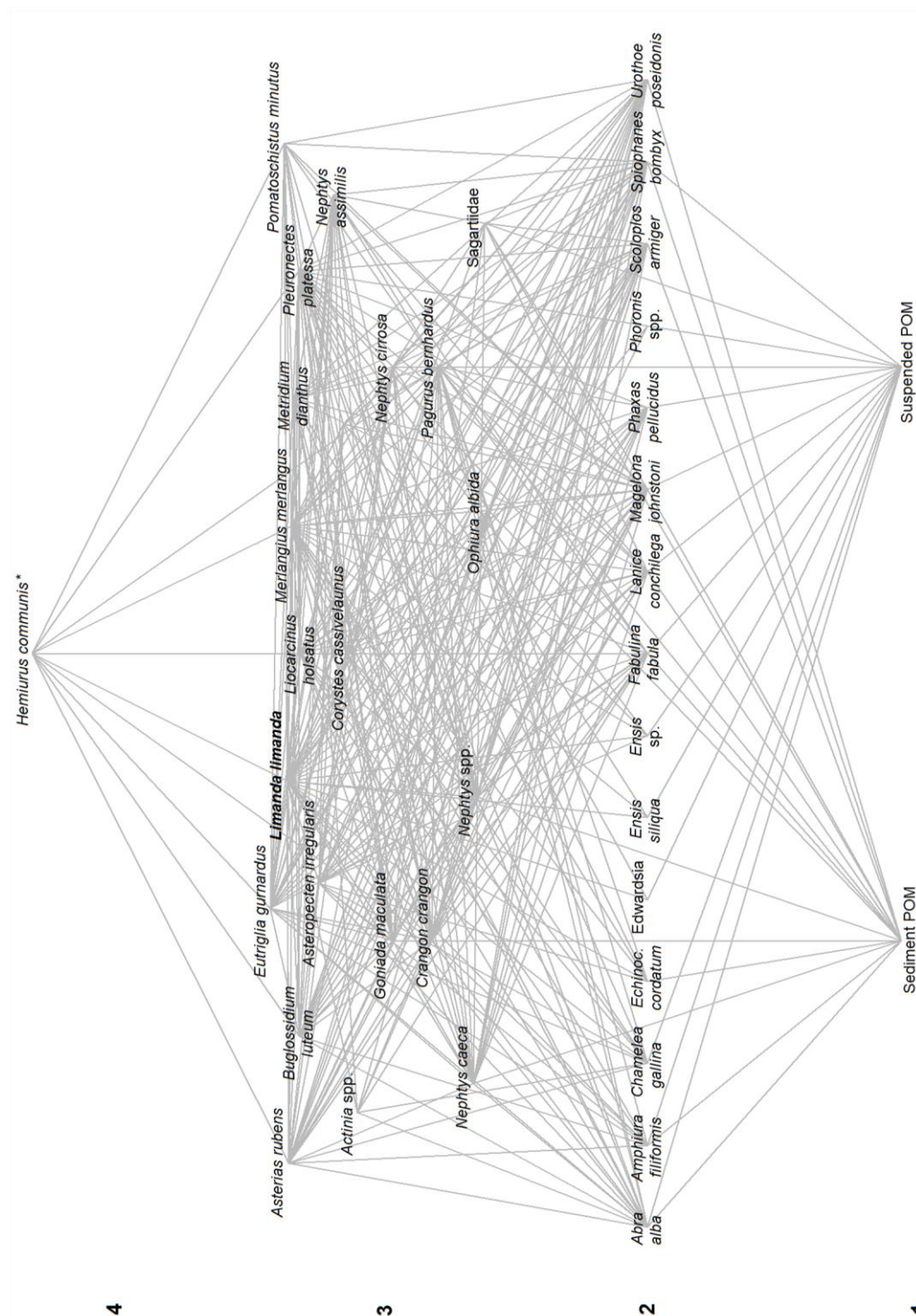
The dab specific food web was constructed to include every species with a direct link to or from dab in the FSd.97, plus the parasite species identified in the dissections of 25 dab from the FSd station. Of the 47 free-living species in the FSd.97 web, eight species had no direct outgoing or incoming link to or from dab. This included three teleosts, one anemone, one decapod, two bivalve and *E. nitida*, the only gastropod in the FSd.97. In all, the parasite-free dab specific food web (LL.F) is comprised of 39 species (Figure 3.9), including 2 basal species and 17 omnivorous species (51.3 %). One parasite (*H. communis*) was identified in the dab dissections and incorporated into the dab specific food webs. The trematode was disaggregated into five distinct ontogenetic niche shift nodes. One ontogenetic node, the adult and immature stage infesting the definitive teleost host, was suitable for inclusion in the LL.P (Figure 3.10), which incorporates parasite life stages only in their role as consumers. One further ontogenetic node, representing the free-living, non-feeding cercarial life stages of *H. communis*, was suitable for inclusion in the LL.X web (Figure 3.11), in which parasites were included in their role both as consumers and resources. Ontogenetic nodes pertaining to the metacercaria were unsuitable for inclusion as they occur exclusively outside of the benthic FSd food web, in planktonic copepod hosts, so too were the parasitic cercaria, which occur in species without direct links to dab in the FSd. Eggs were also excluded since no evidence could be obtained for the role of *H. communis* eggs as an energetically significant resource.





**Figure 3.9:** LL.F, food web including species comprising 97 % of the cumulative energy flow at the FSD station with direct links to or from dab (*Limanda limanda*), which is highlighted in bold, and basal nodes with no direct link to dab. Parasites are excluded from the LL.F. Short-weighted TL is indicated by the numbers on the vertical axis. The name of the heart urchin *Echinocardium cordatum* has been shortened to “*Echinoc. cordatum*” for space.





**Figure 3.10:** LLP food web, including species comprising 97 % of the cumulative energy flow at the Fsd station with direct links to or from dab (*Limanda limanda*), which is highlighted in bold, and basal nodes with no direct link to dab. Metazoan parasites, highlighted with an asterisk after the species name, that were identified in the dissection of 25 dab and a literature search are included in their roles as consumers only. Parasites are disaggregated into ontogenetic niche shift nodes after Preston *et al.* (2014). Short-weighted TL is indicated by the numbers on the vertical axis. The name of the heart urchin *Echinocardium cordatum* has been shortened to “*Echinoc. cordatum*” for space.



### 3.4.2 Topology of the dab-specific food webs

Inclusion of the parasite *H. communis* in its role as a consumer into the dab specific food web (LL.P; Figure 3.10) affected several food web metrics. The parasite's adult/immature and parasitic cercarial life stage nodes were modelled as top predators in the LL.P, with no enemies (Figure 3.10). Complexity, as quantified by connectance, decreased from 0.24 to 0.23 (Table 3.2) and linkage density (L/S) decreased from 9.2 to 9.1 after parasite inclusion. The proportion of omnivorous species increased from 51 % to 53 % after the omnivorous adult/immature life stage node of *H. communis* was included in the food web. Both the mean and maximum  $TL_{sw}$  were increased, from 2.88 to 2.93 and 3.47 to 4.41 respectively.

Incorporating the incoming and outgoing links from the free-living cercaria alongside the adult and immature node of *H. communis* in the LL.X resulted in an L/S of 9.2, greater than in either the LL.F or LL.P webs. Connectance was equivalent to the LL.P, and slightly lower than in the parasite free LL.F web, at around 0.23. Mean  $TL_{sw}$  of species in the LL.X web was lower at 2.74 compared to 2.88 in the LL.F and 2.93 in the LL.P, whereas maximum  $TL_{sw}$  was higher in the LL.X with 4.42 compared to 4.41 in the LL.P and 3.47 in the LL.F. Adult and immature life stages of *H. communis* occupied the highest  $TL_{sw}$  in the LL.X and LL.P, replacing *Eutriglia gurnardus* in the parasite-free LL.F.

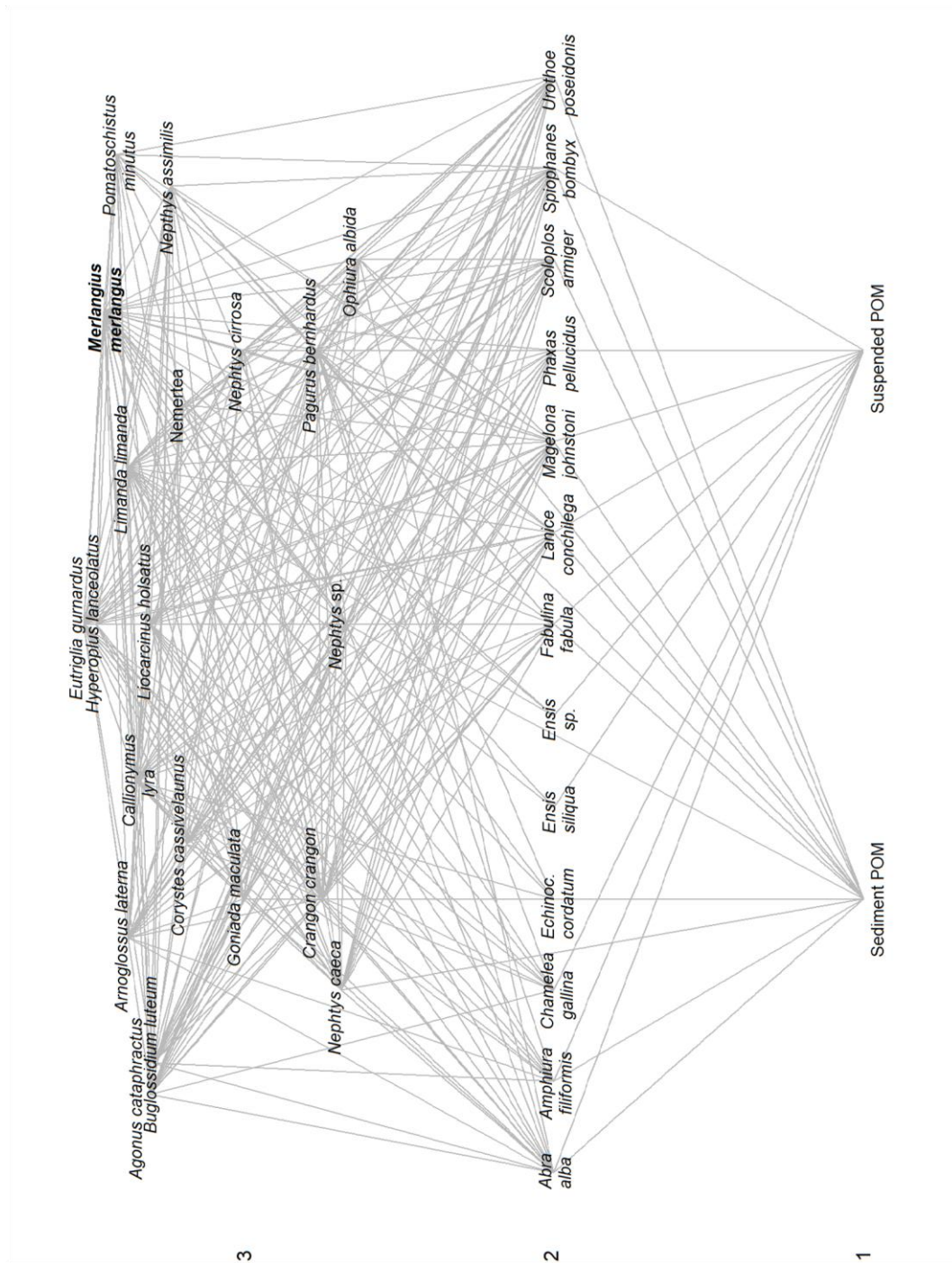
**Table 3.2:** Overall numbers and absolute change in the topology of the dab (*Limanda limanda*) specific food webs, including all parasite species identified in the dissection of their respective hosts, in their role as consumers (LL.P) and including the same parasites in their role as consumers and resources (LL.X) compared to the parasite-free LL.F. Parasites were included as disaggregated ontogenetic niche shift nodes after Preston *et al.* (2014). S=number of nodes/species, L=number of links, Connectance=  $L/S^2$  in the LL.F, LL.X and  $L/S_f(S_f+S_p)$  in the LL.P.  $TL_{sw}$ =short-weighted trophic level.

|                      | Overall numbers |      |      | Absolute change |       |
|----------------------|-----------------|------|------|-----------------|-------|
|                      | LL.F            | LL.P | LL.X | LL.P            | LL.X  |
| S                    | 39              | 40   | 41   | 1               | 2     |
| L                    | 359             | 364  | 379  | 5               | 20    |
| L/S                  | 9.21            | 9.1  | 9.24 | -0.11           | 0.03  |
| Connectance          | 0.24            | 0.23 | 0.23 | -0.01           | -0.01 |
| Omnivorous nodes [%] | 51              | 53   | 51   | 2               | 0     |
| Mean $TL_{sw}$       | 2.88            | 2.93 | 2.74 | 0.05            | -0.14 |
| Maximum $TL_{sw}$    | 3.47            | 4.41 | 4.42 | 0.94            | 0.95  |

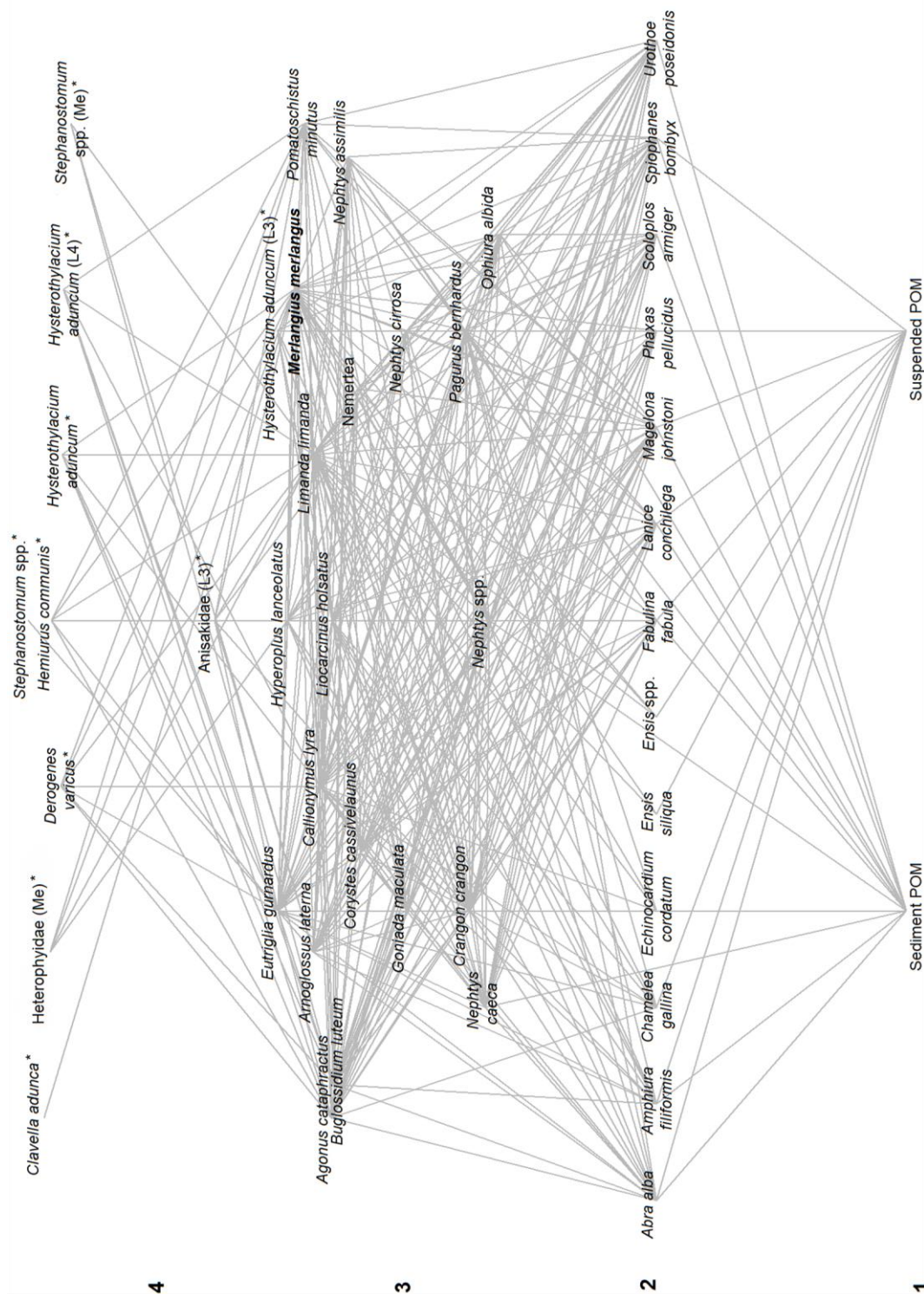
### 3.4.3 The whiting-specific food webs

Whiting had no direct links to 12 non-basal nodes in the FSd.97 web, including the common starfish *Asterias rubens* Linnaeus, 1758, sand sea star *Astropecten irregularis* (Pennant, 1777), three anemones; *Actinia* Linnaeus, 1767 sp., *Metridium dianthus* (Ellis, 1768) and Sagartiidae Gosse, 1858, bivalve *Macra stultorum* (Linnaeus, 1758), edible crab *Cancer pagurus* Linnaeus, 1758, horseshoe worm *Phoronis* Wright, 1856 spp., parchment worm *Chaetopterus variopedatus* (Reiner, 1804), the hooknose *Agonus cataphractus* (Linnaeus, 1758), great sand eel *Hyperoplus lanceolatus* (Le Sauvage, 1824) and European plaice *Pleuronectes platessa* Linnaeus, 1758. Therefore, the parasite-free, whiting specific food web, hereafter referred to as the MM.F web, contains 35 nodes (Figure 3.12). To consider the seven parasite species identified in the whiting dissections (Table 3.1) only in their role as consumers, they were included as ten disaggregated ontogenetic niche shift nodes into the MM.P web (Figure 3.13). Predominantly this comprised adult and immature life stages,



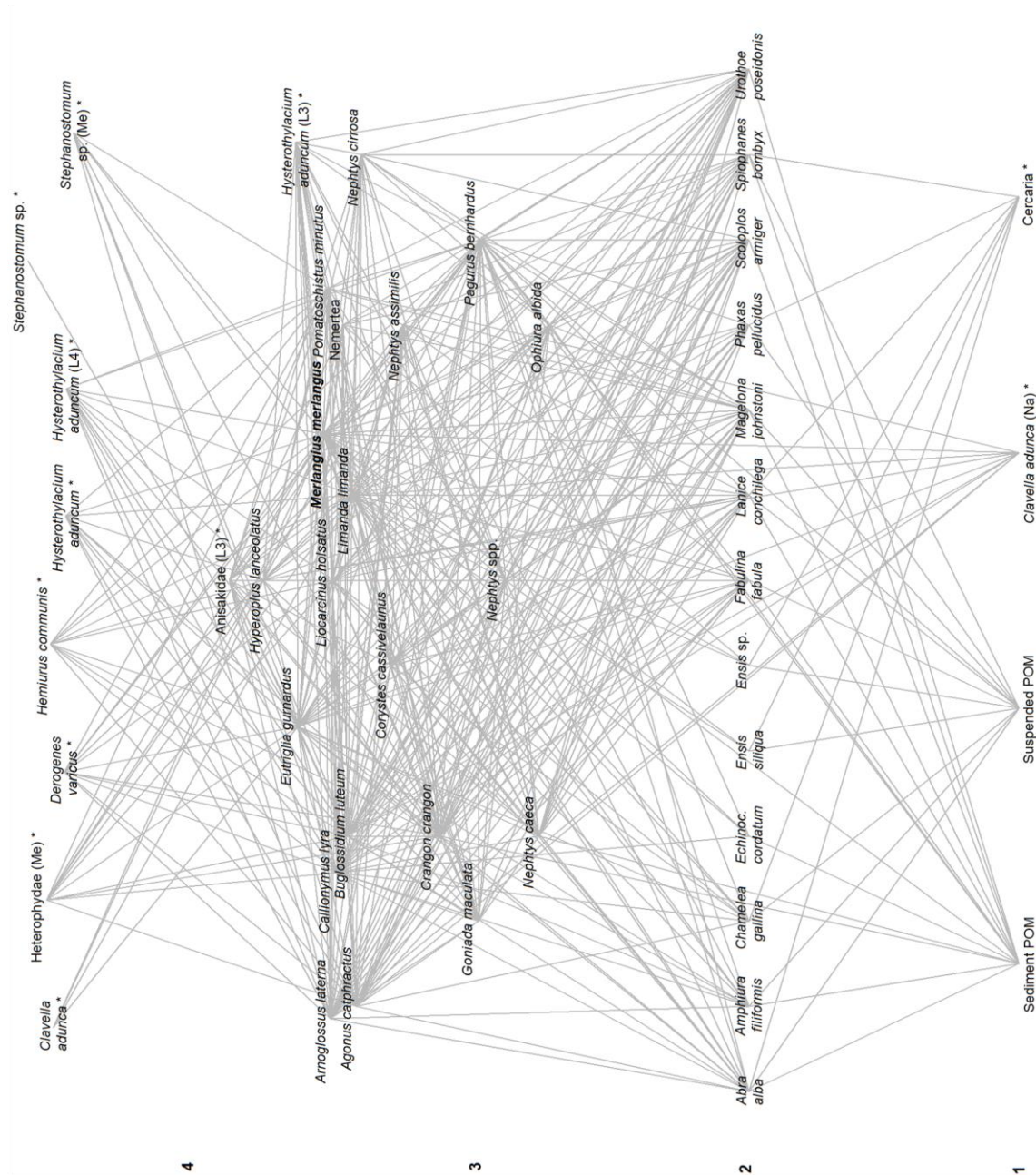


**Figure 3.12:** MM.F food web, including species comprising 97 % of the cumulative energy flow at the Fsd station with direct links to or from whiting (*Merlangius merlangus*), which is highlighted in bold, and basal nodes with no direct link to whiting. Parasites are excluded from the MM.F. Short-weighted TL is indicated by the numbers on the vertical axis. The name of the heart urchin *Echinocardium cordatum* has been shortened to “*Echinoc. cordatum*” for space.



**Figure 3.13:** MM.P food web, including species comprising 97 % of the cumulative energy flow at the F5d station with direct links to or from whiting (*Merlangius merlangus*), which is highlighted in bold, and basal nodes with no direct link to whiting. Metazoan parasites, highlighted with an asterisk after the species name, that were identified in the dissection of 30 whiting and a literature search are included in their roles as consumers only. Parasites are disaggregated into ontogenetic niche shift nodes after Preston *et al.* (2014). Short-weighted TL is indicated by the numbers on the vertical axis. The name of the heart urchin *Echinocardium cordatum* has been shortened to “*Echinoc. cordatum*” for space.





**Figure 3.14:** MM.X food web including species comprising 97 % of the cumulative energy flow at the FSD station with direct links to or from whiting (*Merlangius merlangus*), which is highlighted in bold, and basal nodes with no direct link to whiting. Metazoan parasites, highlighted with an asterisk after the species name, that were identified in the dissection of 30 whiting and a literature search are included in their roles as consumers and resources. Parasites are disaggregated into ontogenetic niche shift nodes after Preston *et al.* (2014). Short-weighted TL is indicated by the numbers on the vertical axis. The name of the heart urchin *Echinocardium cordatum* has been shortened to “*Echinoc. cordatum*” for space, “*Cercaria*” = the free-living cercaria of trematodes *Derogenes varicus*, *Hemimurus communis*, Heterophyidae and *Stephanostomum* sp.

metacercariae of the digenean *Stephanostomum* sp. and Heterophyidae gen. et sp. indet., L3 larvae of the nematodes Anisakidae gen. et sp. indet. and *Hysterothylacium aduncum*, L4 larvae of *H. aduncum* were also included. Free-living life stages of copepod *Clavella adunca* and all digenean trematodes were included alongside these nodes in the MM.X (Figure 3.14). Parasite infections were restricted largely to teleosts, though all decapods and brittlestars in the MM.P and MM.X had links to L3 larvae of *H. aduncum* and the brown shrimp *Crangon crangon* (Linnaeus, 1758) and amphipod *Urothoe poseidonis* Reibish, 1905 had links to Anisakidae gen. et sp. indet. L3 larvae. Since only incoming links to parasites were accounted for, all parasites were modelled as top-level species with no predators in the MM.P web (Figure 3.13). Parasites occupied the highest  $TL_{sw}$  in the MM.X (Figure 3.14).

#### 3.4.4 Topology of the whiting-specific food webs

Adding parasites into the whiting specific food web (MM.P) decreased both connectance and L/S compared to the MM.F (Table 3.3). While there was a slight decrease in connectance from 0.27 to 0.23, L/S showed a drastic decrease from 9.3 to 8. The proportion of omnivorous species (58 %) in the MM.P was 7 % larger than in the MM.F. Both mean and maximum  $TL_{sw}$  increased after parasites were included. Mean  $TL_{sw}$  increased from 2.88 to 3.26 and maximum  $TL_{sw}$  from 3.52 to 4.52. Including parasites as both consumers and resources in the whiting specific MM.X web prompted the inclusion of five more ontogenetic nodes representing the non-feeding, free-living nauplii stages of the copepod *C. adunca*, free-living cercariae of digenean trematodes *Stephanostomum* sp., Heterophyidae gen. et sp. indet., *Derogenes varicus* and *Hemiurus communis*. As the links to each of the trematode free-living cercarial nodes were identical, they were aggregated into a single



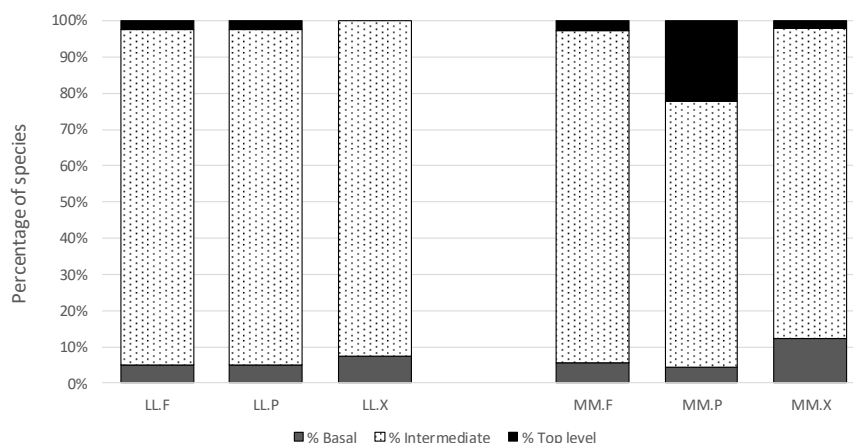
trophic species, represented by “Cercaria” in the LL.X web (Figure 3.11). No incoming links to either the free-living trematode trophic species node or the free-living nauplii node of *C. adunca* were included in the food web, therefore they were effectively modelled as basal species.

**Table 3.3:** Overall numbers and absolute change in the topology of the whiting (*Merlangius merlangus*) specific food webs, including all parasite species identified in the dissection of their respective hosts, in their role as consumers (MM.P) and including the same parasites in their role as consumers and resources (MM.X) compared to the parasite-free MM.F. Parasites were included as disaggregated ontogenetic niche shift nodes after Preston *et al.* (2014). S=number of nodes/species, L=number of links, Connectance=  $L/S^2$  in the MM.F, MM.X and  $L/S_i(S_i+S_p)$  in the MM.P.  $TL_{sw}$ =short-weighted trophic level.

|                      | Overall numbers |      |      | Absolute change |       |
|----------------------|-----------------|------|------|-----------------|-------|
|                      | MM.F            | MM.P | MM.X | MM.P            | MM.X  |
| S                    | 35              | 45   | 47   | 10              | 12    |
| L                    | 326             | 374  | 465  | 48              | 139   |
| L/S                  | 9.31            | 7.96 | 9.89 | -1.35           | 0.58  |
| Connectance          | 0.27            | 0.23 | 0.21 | -0.04           | -0.06 |
| Omnivorous nodes [%] | 51              | 58   | 55   | 7               | 4     |
| Mean $TL_{sw}$       | 2.88            | 3.26 | 3.26 | 0.38            | 0.38  |
| Maximum $TL_{sw}$    | 3.52            | 4.52 | 4.6  | 1               | 1.08  |

### 3.4.5 Compartments of the dab/whiting specific food webs

The whiting specific MM.F web (excluding parasites) contained a slightly higher proportion of basal nodes, i.e. nodes with no incoming links that only act as a resource in the food web, than the dab specific LL.F web; 6 % compared to 5% (Figure 3.15), although this represented the same S (2). The proportion of top-level nodes, i.e. those with no outgoing links that act only as consumers in the food web, was equivalent in the MM.F and LL.F at 3 % of species, meaning that the proportion of intermediate species was also roughly



**Figure 3.15:** Percentage of basal nodes, with no incoming links from resources, top-level nodes, with no outgoing links to consumers and intermediate nodes, with both incoming and outgoing links, in the dab and whiting-specific food webs. The LL.F and MM.F food webs include species comprising 97 % of the cumulative energy at the FSD station with direct links to dab (*Limanda limanda*) and whiting (*Merlangius merlangus*), respectively, and basal nodes with no link to or from dab or whiting. Parasites identified in a literature search and the dissection of 25 dab or 30 whiting, are disaggregated into ontogenetic, niche-shift nodes, after Preston *et al.* (2014), and included in their role as consumers in the LL.P and MM.P, respectively. The LL.P and MM.P are expanded to include links in which the parasites act as resources in the LL.X and MM.X food webs.

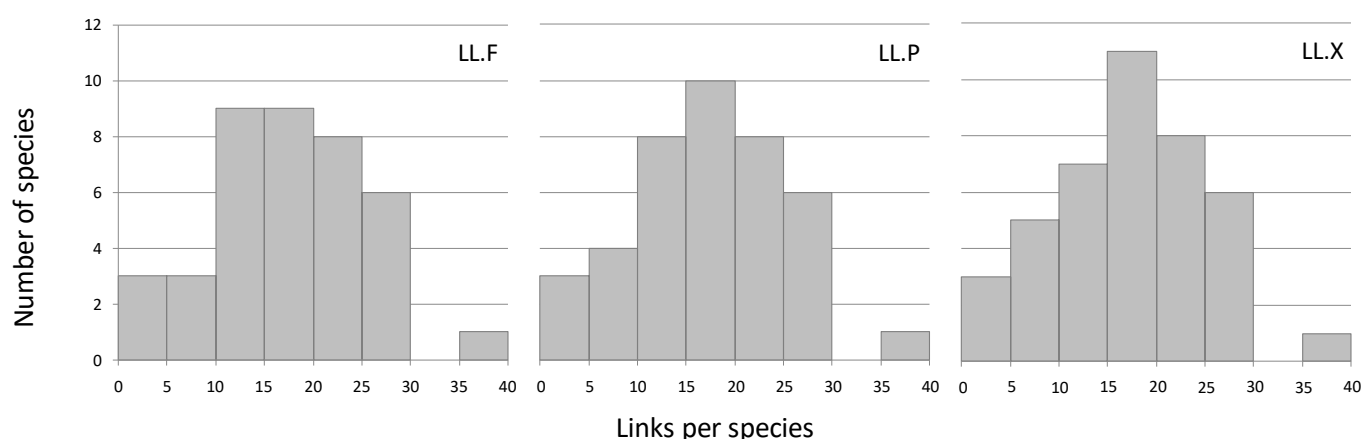
equivalent, comprising 91 % and 93 % of species respectively. Including adult and immature life stages of the trematode *Hemiurus communis* as consumers in the LL.P slightly reduced the proportion of top-level species compared to the LL.F. Both food webs contained a single top-level node but represented by different species. Adding a further ontogenetic node (free-living, non-feeding cercariae) of *H. communis* and outgoing links from the adult/immature node reduced the percentage of top-level nodes to zero in the LL.X.

*Hemiurus communis* free-living cercariae were modelled as a basal species; therefore the proportion of basal nodes was higher in the LL.X than either the LL.P or LL.F. All ten parasite life stage nodes that were included in the MM.P were modelled as top predators; increasing the proportion of top-level nodes in the food web from 3 % to 22 %, compared to the MM.F. Unlike the LL.X, one top predator was present in the MM.X, the adult and immature life stages of the digenea *Allocreadioidea*. All other parasites were concomitantly consumed, and many were also directly predated on. The MM.X contained two more basal nodes

compared to MM.F or MM.P webs, representing the free-living cercariae of four trematode species, reduced to a single trophic species node and the free-living nauplii of the parasitic copepod *C. adunca*.

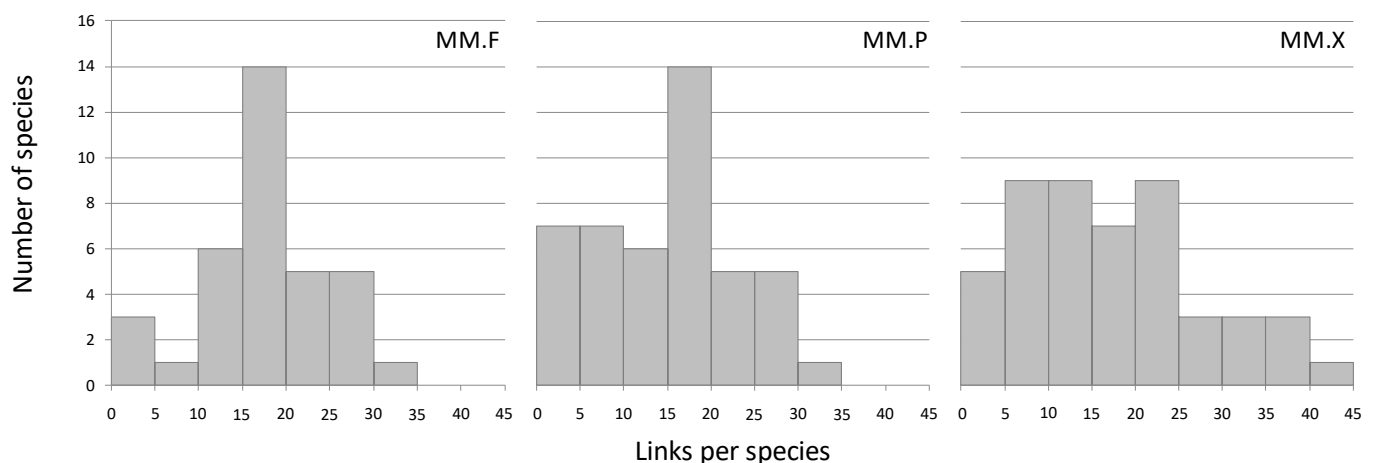
### 3.4.6 Connectivity in the dab/whiting-specific food webs

Most species in all three versions of the dab specific food web were most commonly linked with 15 - 20 other species (Figure 3.16). This included nine species in the LL.F, ten in the LL.P and 11 species in the LL.X. Equally, nine species in the LL.F were linked with between 10 - 15 other nodes. In the LL.F, LL.P and LL.X, three species interacted with less than five other species. Eight species in each version of the dab specific food web interacted with 20 - 25 other species and 6 species interacted with 25 - 30. Dab was the most connected species in all three versions of the food web with interactions to 36 species in the LL.F and 37 species in the LL.P and LL.X.



**Figure 3.16:** Number of trophic links (L) per species in three dab-specific food webs, including species comprising 97 % of the cumulative energy at the FSd station with direct links to or from dab (*Limanda limanda*) and basal nodes with no direct link to or from dab. Parasites are excluded from the LL.F food web, included in their role as consumers only in the LL.P, and as consumers and resources in the LL.X. Parasites are included as disaggregated, ontogenetic niche-shift nodes following Preston *et al.* (2014).

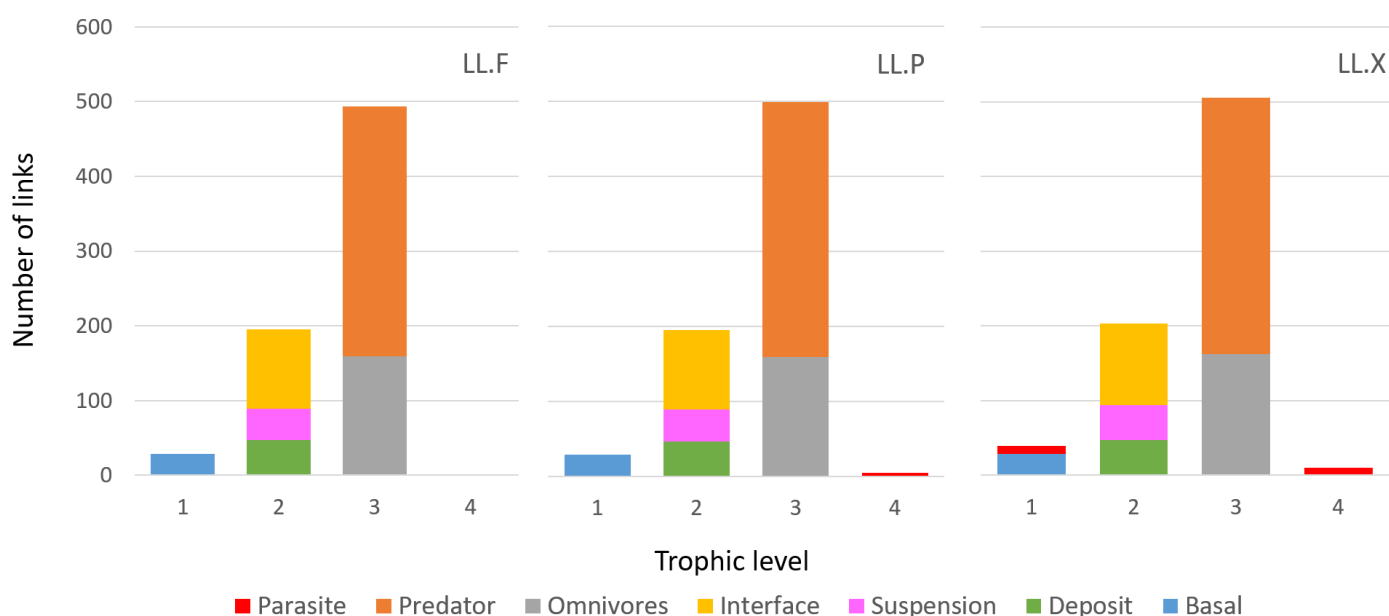
More than twice as many species in the MM.F and in the MM.P were connected to 15 - 20 other species compared to any other category (Figure 3.17). Species in the MM.X were most commonly connected to 5 - 10, 10 - 15 or 20 - 25 nodes, with nine species occupying each category. Half as many species in the MM.X were connected to 15 - 20 nodes ( $n = 7$ ) than in the MM.F and MM.P webs ( $n = 14$ ). The whiting, occupied the highest category in each variation of the whiting specific food web and was linked to 33 other species in the MM.F and MM.P and 42 species in the MM.X. More species occupied the lowest category, interacting with 0 - 5 species in the MM.P ( $n = 7$ ) than in the MM.X ( $n = 5$ ), while the MM.F contained the fewest number of relatively isolated nodes ( $n = 3$ ). All three of the least connected species in the MM.F were primary consumers. The same three species were included in the lowest category of the MM.P and MM.X, joined by 4 and 2 parasite species, respectively.



**Figure 3.17:** Number of trophic links (L) per species in three whiting-specific food webs, including species comprising 97 % of the cumulative energy at the FSd station with direct links to or from whiting (*Merlangius merlangus*) and basal nodes with no direct link to or from whiting. Parasites are excluded from the MM.F food web, included in their role as consumers only in the MM.P, and as consumers and resources in the MM.X. Parasites are included as disaggregated, ontogenetic niche-shift nodes following Preston *et al.* (2014).

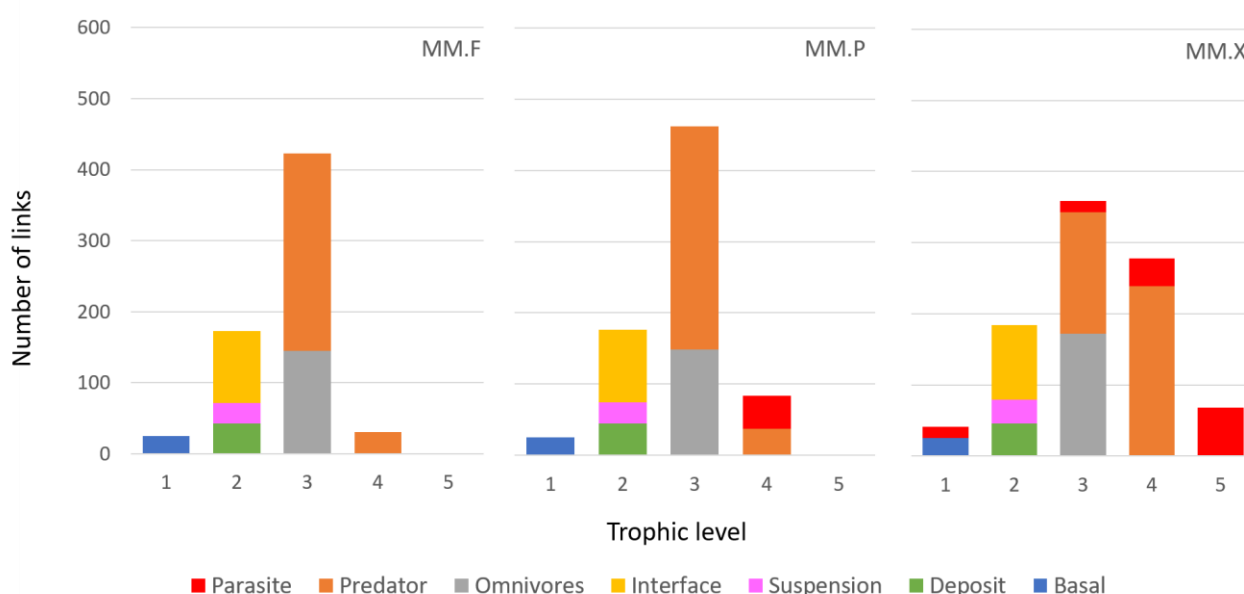
### 3.4.7. Feeding groups in the dab/whiting-specific food webs

Trophic groups were segregated between the different trophic levels in the LL.F web. Basal species exclusively occupied TL1, deposit, suspension and interface feeders were found only in TL2 and omnivores and predator/scavengers were restricted to TL3 (Figure 3.18). The same segregation was observed after the addition of parasites, which were confined to TL4 in LL.P and LL.X, with the exception of some parasites in LL.X that occupied TL1. These were the free-living life stage nodes of parasitic trematode cercaria and copepod nauplii, which essentially acted as basal species in the food web. More links were realised in the LL.F, LL.P and LL.X for species occupying TL3 than in any other TL. In the LL.F, 335 out of 494 L to or from TL3 involved a predator and similar numbers were observed in the LL.P (340 of 499 L) and LL.X (344 of 506 L) webs. The parasite-free, whiting specific food web MM.F was largely similar to the LL.P in that functional groups were segregated, though some predators also



**Figure 3.18:** Number of trophic links (L) between trophic groups in three dab-specific food webs, including species comprising 97 % of the cumulative energy at the FSd station with direct links to or from dab (*Limanda limanda*) and basal nodes with no direct link to or from dab. Parasites are excluded from the LL.F food web, included in their role as consumers only in the LL.P, and as consumers and resources in the LL.X. Parasites are included as disaggregated, ontogenetic niche-shift nodes following Preston *et al.* (2014). Species are arranged horizontally by their short-weighted TL, rounded to the nearest integer.

occupied TL4 in the MM.F, and more links involved a predator in TL3 (344 L) than in any other food web (Figure 3.19). Parasites in the MM.P were restricted to TL4 and were included in 6 % of links in the food web. Predators were involved in more links than any other functional group; 350 of 748 L. Parasites in the MM.X were involved in a greater proportion of links than in the MM.P or MM.F (139 of 703 L).



**Figure 3.19:** Number of trophic links (L) between trophic groups in three whiting-specific food webs, including species comprising 97 % of the cumulative energy at the FSd station with direct links to or from whiting (*Merlangius merlangus*) and basal nodes with no direct link to or from dab. Parasites are excluded from the MM.F food web, included in their role as consumers only in the MM.P, and as consumers and resources in the MM.X. Parasites are included as disaggregated, ontogenetic niche-shift nodes following Preston *et al.* (2014). Species are arranged horizontally by their short-weighted TL, rounded to the nearest integer.

### 3.5 The FSd.P and FSd.X food webs

The FSd.F food web (Figure 3.20) was expanded to include parasites species isolated from dab and whiting, as well as species that are likely to occur in the food web as inferred from a literature search. The 35 node, parasite-free food web (FSd.F) was expanded to include 12 parasite species (Table 3.4), 11 of which were selected from the literature search and four

that were also identified in the dissection of 25 dab and 30 whiting. The parasites represented those species that have infested over 40 % of a host species present in the FSd food web, in this or previous surveys of parasite fauna in the German Bight. Parasites were included only as consumers, i.e. excluding outgoing links from their consumers, in the FSd.P food web (Figure 3.21) and as both consumers and resources, including incoming and outgoing links, in the FSd.X food web (Figure 3.22). The most vulnerable species to parasitism in the FSd.P was dab which had 10 parasitic consumers, the polychaete *Magelona johnstoni* Fiege, Licher & Mackie, 2000 was the most vulnerable species to consumption overall, with 22 predators and two parasites (Figure 3.21). Five free-living species in the FSd.P were free from parasites; two anemones, two asteroids and one nemertean. Each free-living species was parasitized by a mean of  $4.0 \pm 2.83$  parasite species. The most prolific parasite in the FSd.P is the digenean trematode *Zoogonoides viviparus* Olsson, 1868 (Odhner, 1902), which had 15 free-living hosts in the FSd.F, the most prolific consumer in the food web was *E. gurnardus* with 25 prey species. *Clavella adunca* was the most selective parasite in the food web as it only parasitized whiting. On average, parasites had  $8.3 \pm 3.6$  hosts and  $12.3 \pm 2.6$  concomitant and direct predators.

Unlike in the dab and whiting-specific food webs, parasite life stages were aggregated into discrete parasite species nodes in the FSd.P and FSd.X, which accounted for 26 % of all nodes. Parasites were involved in 12.1 % and 23 % of interactions in the FSd.P and FSd.X, respectively. *Eutriglia gurnardus* did not serve as prey to any species in the FSd.F (Figure 3.20) and was therefore considered to be the top predator. This was not the case in the FSd.P (Figure 3.21) or FSd.X (Figure 3.22), in which *E. gurnardus* was parasitized by three nematodes, three digenean trematodes and one larval species of cestode. All parasites were modelled as top predators, with no enemies in the FSd.P, but they had one or more

outgoing links, in which the parasite acts as a resource, in the FSd.X, and were therefore not considered to be top predators. Nonetheless, they did occupy the highest  $TL_{sw}$  in the food web (Figure 3.22). The mean  $TL_{sw}$  of parasites ( $4.04 \pm 0.42$ ) is higher than that of free-living species ( $3.05 \pm 0.52$ ) in the FSd.P ( $t(26) = 6.09, p < 0.05$ ). In the FSd.X, the mean  $TL_{sw}$  of parasites ( $5.67 \pm 0.46$ ) was also significantly higher than that of free-living ( $4.57 \pm 0.95$ ) species ( $t(36) = 4.71, p < 0.05$ ).

**Table 3.4:** Parasites infesting  $\geq 40\%$  of any fish host, caught in the FSd in the German Bight, North Sea. References are taken from Palm *et al.* (1999) and further literature search.

| Taxa      | Parasite Species                                              | Host species                 | References                   |
|-----------|---------------------------------------------------------------|------------------------------|------------------------------|
| Digenea   | <i>Derogenes varicus</i>                                      | <i>Agonus cataphractus</i>   | Klimpel <i>et al.</i> , 2003 |
|           | <i>Hemiurus communis</i>                                      | <i>Merlangius merlangus</i>  | Present study                |
|           | <i>Stephanostomum baccatum</i>                                | <i>Limanda limanda</i>       | Køie, 1983                   |
|           | <i>Zoogonoides viviparus</i>                                  | <i>Limanda limanda</i>       | Ibbeken & Zander, 1999       |
|           |                                                               |                              | Køie, 1983                   |
|           |                                                               | <i>Callionymus lyra</i>      | Klimpel <i>et al.</i> , 2003 |
|           |                                                               | <i>Pleuronectes platessa</i> | Wickins & MacFarlane, 1973   |
| Cestoda   | Tetraphyllidea                                                | <i>Agonus cataphractus</i>   | Klimpel <i>et al.</i> , 2003 |
| Nematoda  | <i>Anisakis simplex</i>                                       | <i>Eutriglia gurnardus</i>   | Levsen & Karl, 2014          |
|           | <i>Ascarophis arctica</i>                                     | <i>Agonus cataphractus</i>   | Klimpel <i>et al.</i> , 2003 |
|           | <i>Capillaria</i><br>( <i>Procapillaria</i> ) <i>gracilis</i> | <i>Agonus cataphractus</i>   | Klimpel <i>et al.</i> , 2003 |
|           | <i>Cucullanus heterochrous</i>                                | <i>Pleuronectes platessa</i> | Wickins & MacFarlane, 1973   |
|           | <i>Hysterothylacium aduncum</i>                               | <i>Agonus cataphractus</i>   | Klimpel <i>et al.</i> , 2003 |
|           |                                                               | <i>Buglossidium luteum</i>   |                              |
|           |                                                               | <i>Callionymus lyra</i>      |                              |
|           |                                                               | <i>Merlangius merlangus</i>  | Present study                |
| Crustacea | <i>Clavella adunca</i>                                        | <i>Merlangius merlangus</i>  | Lang, 1990                   |
|           |                                                               |                              | Pilcher <i>et al.</i> , 1989 |
|           |                                                               |                              | Present study                |
|           | <i>Lernaeocera branchialis</i>                                | <i>Merlangius merlangus</i>  | Lang, 1990                   |



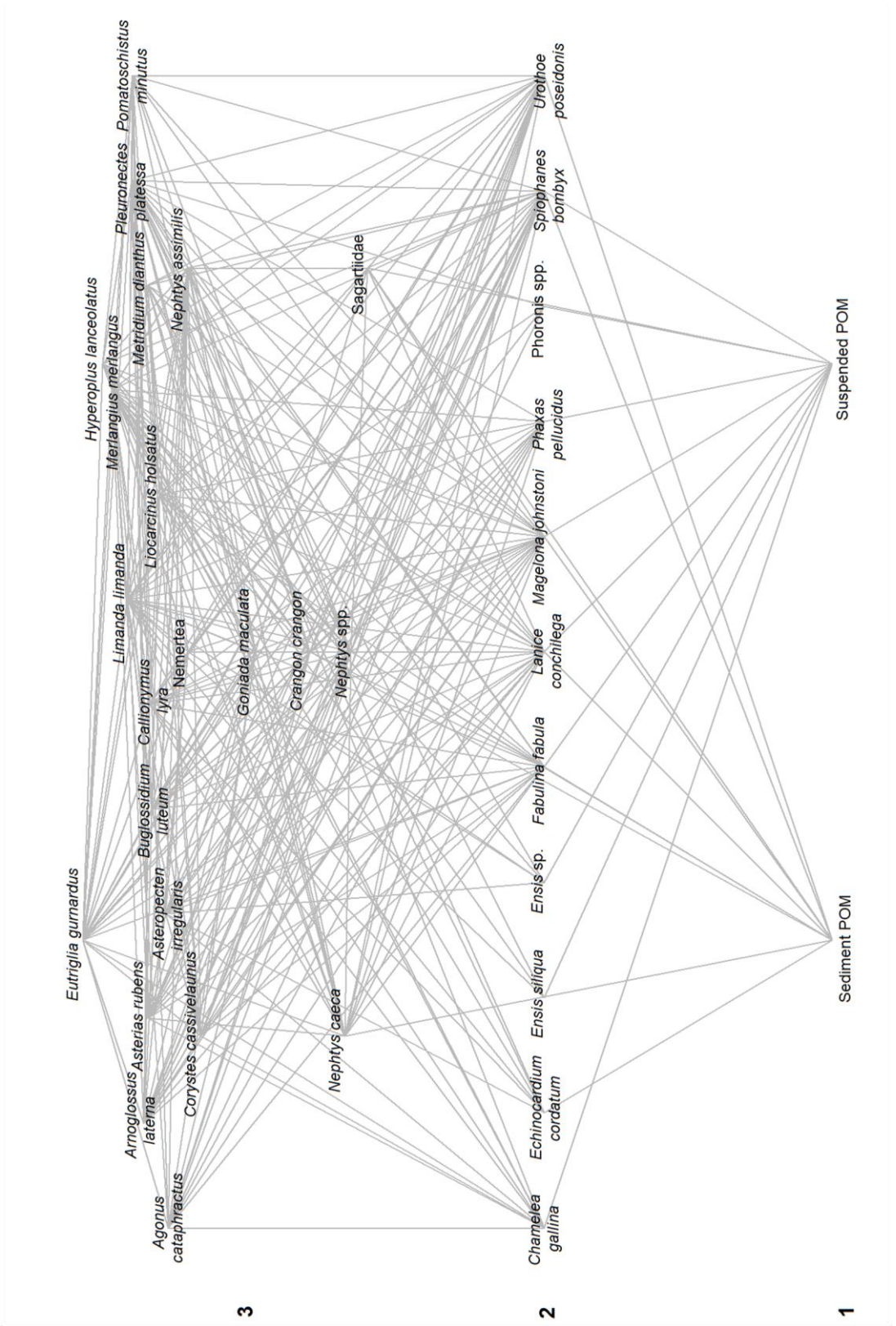
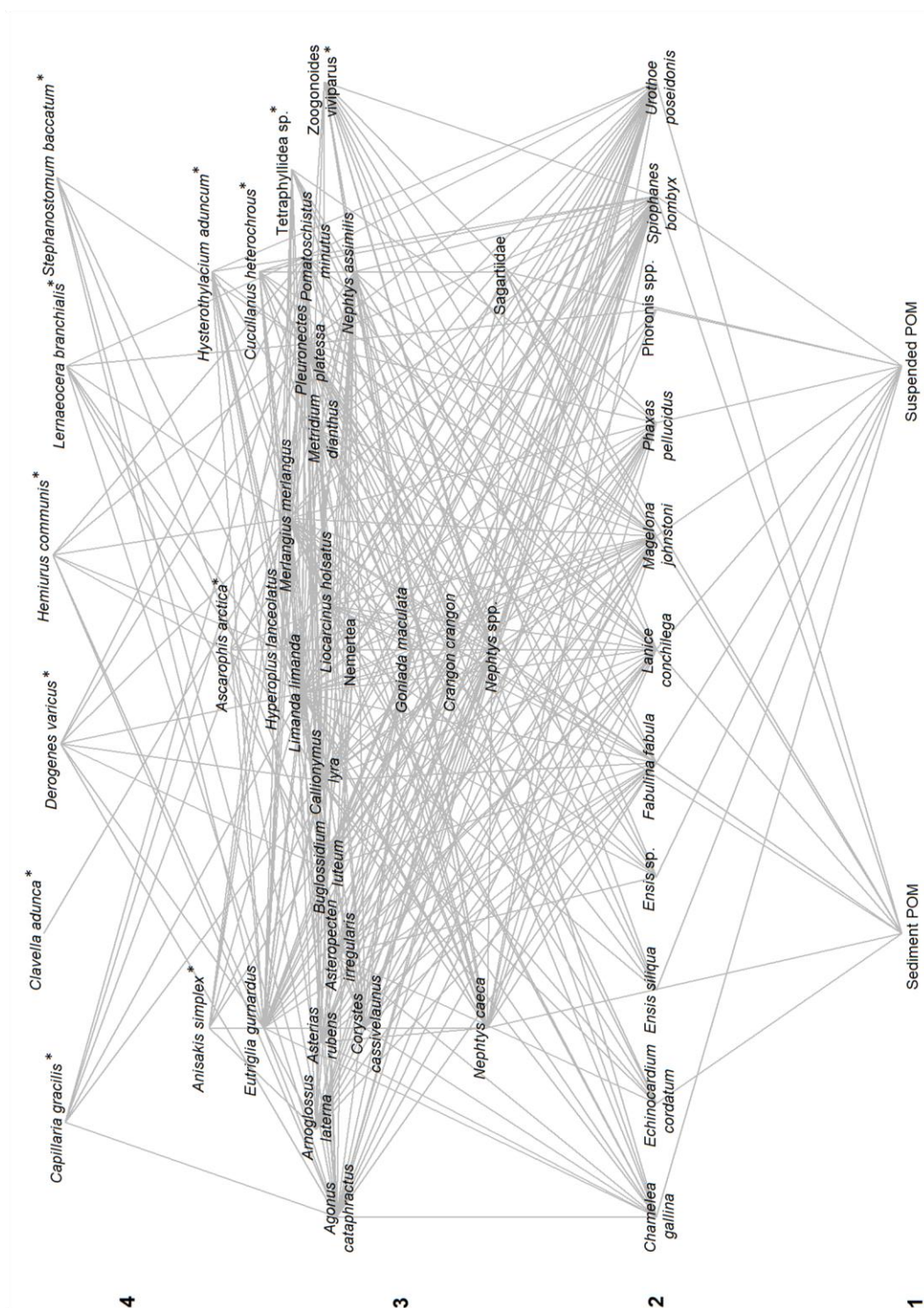
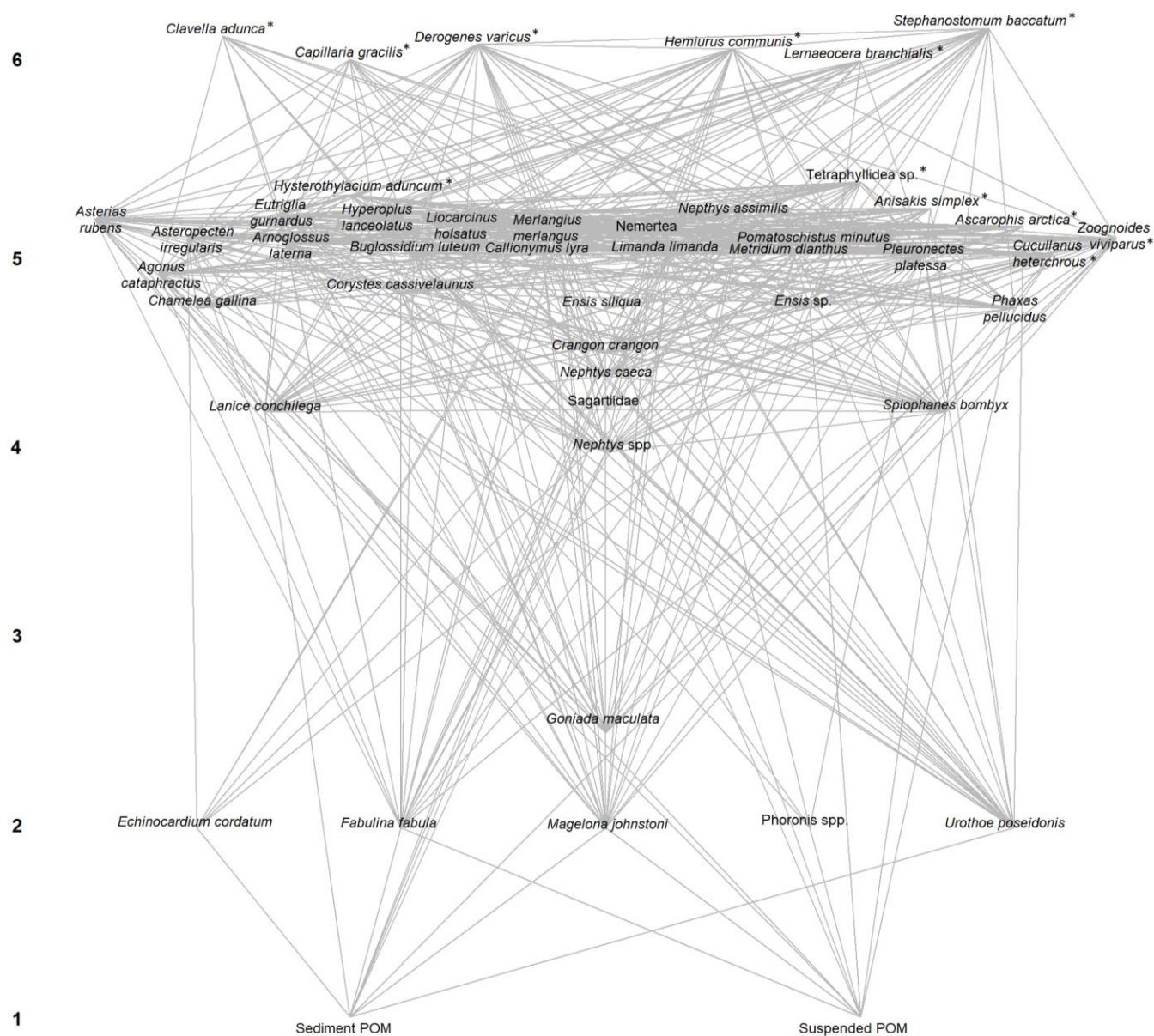


Figure 3.20: Fsd.F food web including free-living species comprising 90 % of the cumulative energy flow at the Fsd station. Vertical height corresponds to short-weighted TL.



**Figure 3.21:** FSD.P food web including species comprising 90 % of the cumulative energy flow at the FSD station and parasites identified in a literature search and the dissections of 25 dab and 30 whiting. Parasites, indicated by and asterisk after the species name, were included as discrete, species-specific nodes in their role as consumers only. Vertical height corresponds to short-weighted trophic level.





**Figure 3.22:** FSD.X food web including species comprising 90 % of the cumulative energy flow at the FSD station and parasites identified in a literature search and the dissections of 25 dab and 30 whiting. Parasites, indicated by an asterisk after the species name, were included as discrete, species-specific nodes in their role as consumers and resources. Vertical height corresponds to short-weighted trophic level.

### 3.5.1 Topology of the FSd.F, FSd.P and FSd.X

Including the 12 parasitic nodes as consumers slightly decreased the number of links per species ( $L/S = 8.7$ ) compared to the parasite-free food web ( $L/S = 8.9$ ). However, the connectance of each food web was equivalent, with a quarter of possible links being realized in either food web (Table 3.5). The percentage of omnivorous nodes was greater in the FSd.P (omnivores = 68 %) than in the parasite-free FSd.F (omnivores = 60 %). The mean and maximum  $TL_{sw}$  were also greater in the FSd.P; mean  $TL_{sw}$  was increased by 0.31 to 3.36 in the FSd.P and the maximum  $TL_{sw}$  in the FSd.P was 4.5, which was 0.9 higher than the maximum  $TL_{sw}$  in the FSd.F. A similar pattern was observed in the mean and maximum  $TL_{sw}$  when outgoing links from parasites, in which parasites act as resources, were included, to produce the FSd.X web. Compared to the FSd.P, mean  $TL_{sw}$  increased by 1.85 and the FSd.X maximum  $TL_{sw}$  (6.22) was over 1.72 higher than the maximum  $TL_{sw}$  in the FSd.P (4.5). The proportion of omnivorous nodes increased when outgoing links from parasites were included and accounted for over 80 % of species in the FSd.X (Table 3.5). The FSd.X was also more complex than either the FSd.P or FSd.F. Species in the FSd.X had on average 11.98

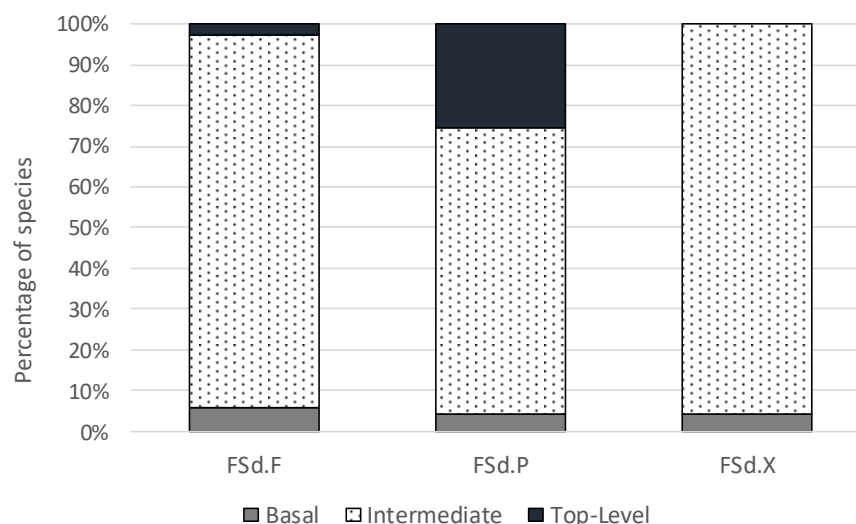
**Table 3.5:** Overall numbers and absolute change in the topology of the FSd food webs, including all parasite species identified in the dissection of dab and whiting and a literature search in their role as consumers (FSd.P) and including the same parasites in their role as consumers and resources (FSd.X) against the parasite-free FSd.F. Parasites were included as discrete, species-specific nodes.  $S$ =number of nodes/species,  $L$ =number of links, Connectance=  $L/S^2$  in the FSd.F, FSd.X and  $L/S_f(S_f+S_p)$  in the FSd.P.  $TL_{sw}$ =short-weighted trophic level.

|                      | Overall numbers |       |       | Absolute change |       |
|----------------------|-----------------|-------|-------|-----------------|-------|
|                      | FSd.F           | FSd.P | FSd.X | FSd.P           | FSd.X |
| $S$                  | 35              | 47    | 47    | 12              | 12    |
| $L$                  | 310             | 409   | 563   | 99              | 253   |
| $L/S$                | 8.86            | 8.7   | 11.98 | -0.16           | 3.12  |
| Connectance          | 0.25            | 0.25  | 0.26  | 0               | 0.01  |
| Omnivorous nodes [%] | 60              | 68    | 81    | 8               | 21    |
| Mean $TL_{sw}$       | 3.05            | 3.36  | 4.9   | 0.31            | 1.85  |
| Maximum $TL_{sw}$    | 3.6             | 4.5   | 6.22  | 0.9             | 2.62  |

trophic links in the food web and over a quarter of the possible links were realized ( $L/S^2 = 0.3$ ) in the food web.

### 3.5.2 Compartments of the FSd.F, FSd.P and FSd.X webs

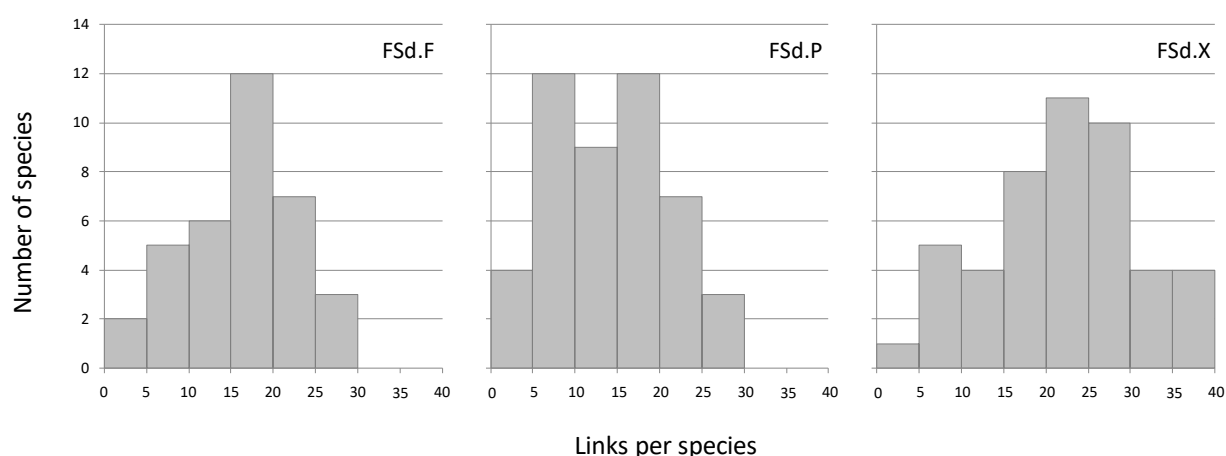
The number of basal species ( $n = 2$ ), that act only as resources in the food web, was equivalent in the FSd.F, FSd.P and FSd.X webs, though the proportion of total nodes that they represented was slightly reduced in the food webs that included parasites, comprising 4 % of nodes in the FSd.P and FSd.X compared to 6 % of nodes in the FSd.F (Figure 3.23). The proportion of top predators, nodes that act only as consumers, increased drastically from 3 % of species in the FSd.F to 26 % when parasites were included as consumers only in the FSd.P. All top predators in the FSd.P were parasites and all parasites were top predators. No species were considered top predators when outgoing links from predators to their consumers were included in the FSd.X.



**Figure 3.23:** Percentage of basal nodes, with no incoming links from resources, top-level nodes, with no outgoing links to consumers and intermediate nodes, with both incoming and outgoing links, in the FSd food webs. The FSd.F includes species comprising 90 % of the cumulative energy at the FSd station, excluding parasites. Parasites are included as discrete, species-specific nodes in their role as consumers only in the FSd.P and in their roles as both consumers and resources in the FSd.X.

### 3.5.3 Connectivity in the FSd.F, FSd.P and FSd.X

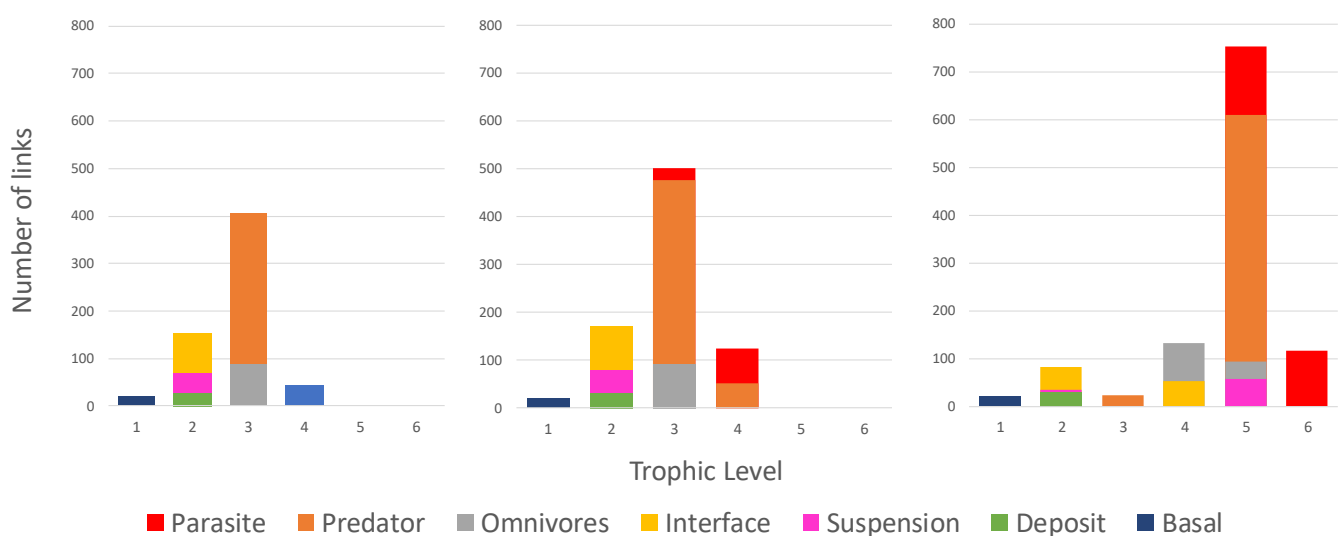
Species in the parasite-free FSd.F were most commonly connected to between 15 - 20 other species (Figure 3.24). Two nodes were connected to less than 6 other species in the FSd.F, these were the basal sediment and suspended POM nodes. No species in the FSd.F was connected to more than 30 of the 34 other species in the food web. This was also the case in the FSd.P, in which parasites were included with only incoming links. Species in the FSd.P were most commonly connected to between 5 - 10 or 15 - 20 other species (Figure 3.24). Four species, including the parasitic copepod *C. adunca* and the digenean trematode *Stephanostomum baccatum* (Nicoll, 1907) Manter, 1934, were connected to 5 or fewer other species. Parasites were on average connected fewer species ( $L = 8 \pm 4$ ) than free-living organisms ( $L = 17 \pm 6$ ) in the FSd.P. The inclusion of outgoing links from parasites in the FSd.X web connected the parasites to an additional 13 free-living species ( $L = 21 \pm 6$ ) and free-living species to seven more parasites ( $L = 24 \pm 9$ ). Parasites and free-living species in the FSd.X were most commonly connected to between 20 - 25 other species. Dab is the most connected species in the FSd.X and has links to 40 of the 46 other species in the network.



**Figure 3.24:** Number of trophic links (L) per species in three food webs, including species comprising 90 % of the cumulative energy at the FSd station. Parasites are excluded from the FSd.F food web, included as discrete, species-specific nodes in their role as consumers in the FSd.P, and in their role as consumers and resources in the FSd.X.

### 3.5.4 Feeding groups in the FSd.F, FSd.P and FSd.X

Most links in the FSd.F (405 out of 620) were either incoming to or outgoing from a species occupying  $TL_{sw}3$  (Figure 3.25). Most links into or out of  $TL_{sw}3$  involved a predator/scavenger (319 of 420), more often than not these were acting as consumers in the interaction (218 of 319). Predators/scavengers were involved in the majority of links across all  $TL_{sw}$  in the FSd.F (361 of 620) and FSd.P (434 of 818). Predators/scavengers were involved in 540 of the 1126 trophic links in the FSd.X food web. Parasites were involved in 99 of the 818 links that occur in the FSd.P and 259 of the 1126 links in the FSd.X. Parasites were exclusively consumers in all links in the FSd.P, but were resources in the majority of their interactions (154 of 259) in the FSd.X. All suspension feeders occupied  $TL_{sw}2$  in the FSd.F and FSd.P webs, however, their  $TL_{sw}$  increased to 5 after the inclusion of direct predative links to parasites in the FSd.X food web. Furthermore, two of the four interface feeders in the FSd occupied  $TL_{sw}4$  in the FSd.X. Both species had direct predative links to trematode cercaria in the FSd.X. Intuitively, all links were outgoing from basal species at  $TL1$  in each version of the food web ( $L = 20$ ).

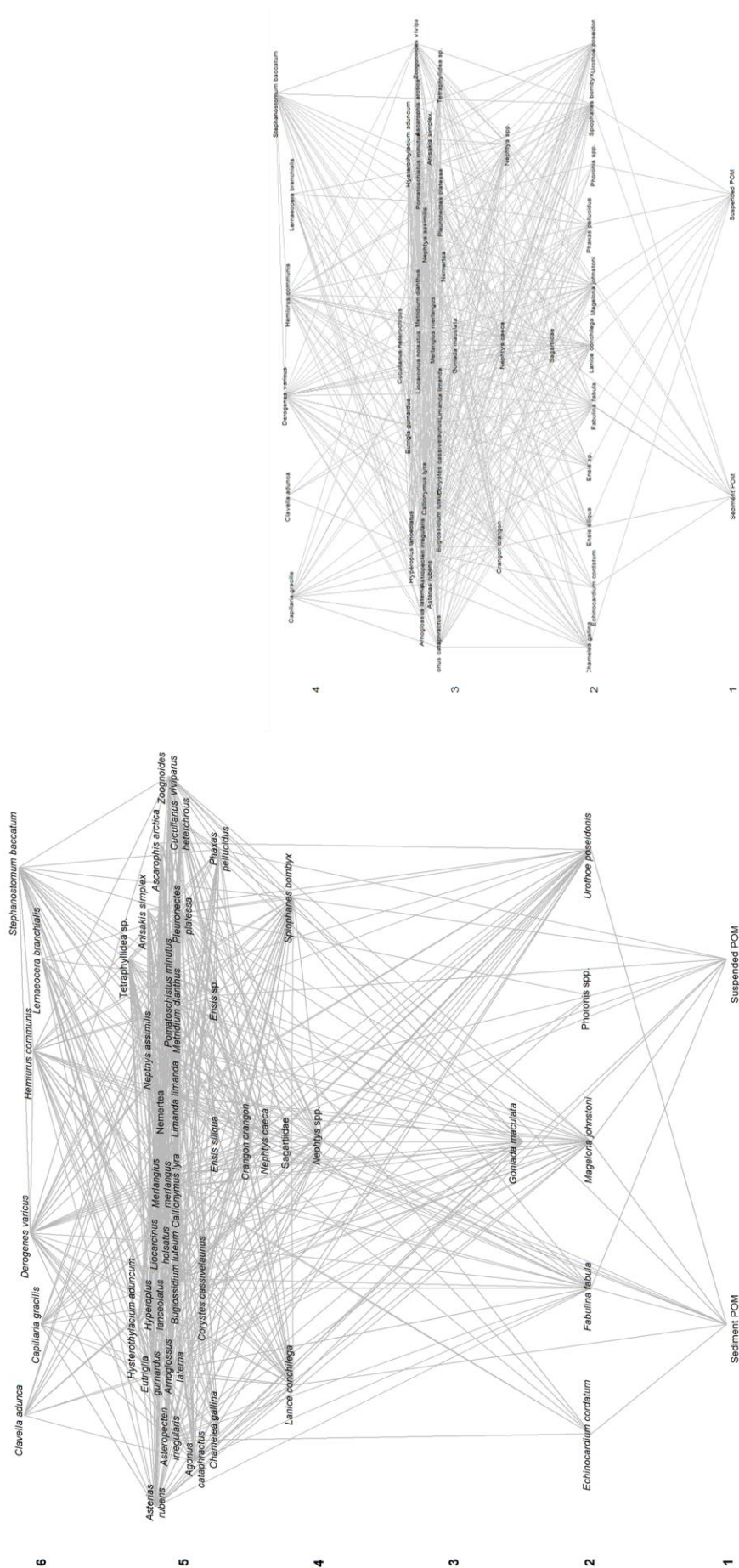


**Figure 3.25:** Number of trophic links (L) between trophic groups in three food webs, including species comprising 90 % of the cumulative energy at the FSd station. Parasites are excluded from the FSd.F food web, included in their role as consumers only in the FSd.P, and as consumers and resources in the FSd.X. Parasites are included as discrete, species-specific nodes. Species are arranged horizontally by their short-weighted TL, rounded to the nearest integer.

### 3.6 Trophic efficiency-weighted trophic levels

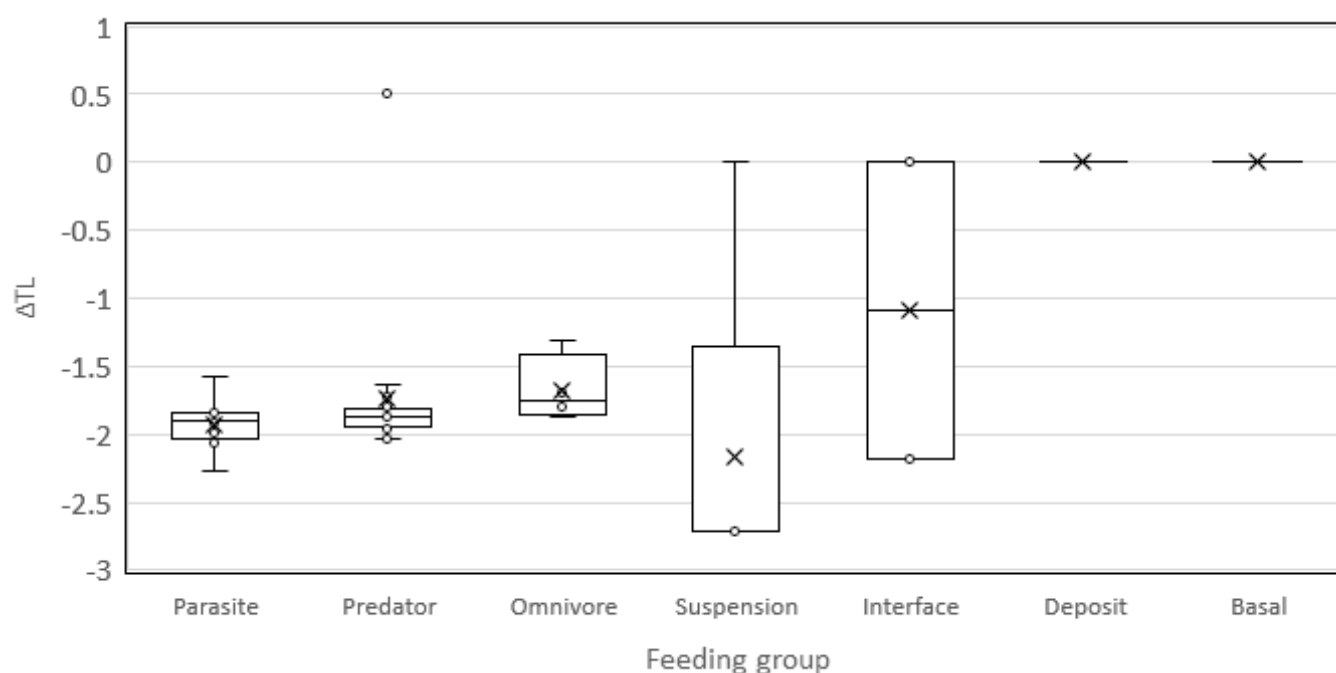
Flow-based trophic levels were calculated for species in the FSd.X web in order to mitigate for the inflation of  $TL_{sw}$  when outgoing links from parasites were included in the food web. Including parasites and concomitant predation inflates prey-averaged TL ( $TL_{pa}$ ) beyond ecological realism and to the point where some intermediate  $TL_{pa}$ s are bereft of species.  $TL_{pa}$  is averaged with the shortest chain from the species to a basal node and so short-weighted TL ( $TL_{sw}$ ) is also affected by the inflation of  $TL_{pa}$  when parasites are included as resources. The mean  $TL_{sw}$  of each of a consumer's feeding interactions was used to estimate the links trophic efficiency, based on the 10 % rule (Lindeman, 1942). The trophic efficiency of each link was then used in place of diet fraction as a factor for calculating the consumers flow-based TL ( $TL_{fb}$ ). The mean  $TL_{fb}$  of species in the FSd.X ( $3.19 \pm 0.61$ ) was lower than the same species'  $TL_{fb}$  ( $4.92 \pm 0.97$ ). Likewise, the maximum  $TL_{fb}$  (4.31) was lower than the maximum  $TL_{sw}$  (4.92), both maximum TLs were occupied by the parasitic digenean trematode *S. baccatum* (Figure 3.26). The  $TL_{fb}$  of basal and deposit feeding species in the FSd.X was equivalent to their  $TL_{sw}$ . The greatest change in TL ( $\Delta TL = TL_{sw} - TL_{fb}$ ), occurred in the suspension feeders (Figure 3.28) with direct predative links to parasites. Specifically, the greatest reductions were observed in three bivalves: the razor clams *Ensis* sp. Schumacher, 1817 and *Ensis siliqua* (Linnaeus, 1758) and the striped Venus clam *Chamelea gallina* (Linnaeus, 1758). One suspension feeding node, *Phoronis* spp. showed no reduction in trophic level.





**Figure 3.26:** FSd.X links, vertically arranged according to short-weighted trophic level (left) and flow-based trophic level (right), based on short-weighted trophic level with each link weighted by trophic efficiency, according to the 10 % rule (Lindeman, 1942).

There was no link from free-living trematode cercariae to that species. Many interface feeders of a taxa known to predate on trematode cercariae also showed great reductions in  $TL_{fb}$ , compared to  $TL_{sw}$ , though the variation in suspension and interface feeding  $\Delta TL$  was considerable. More consistent was the reduction in TL of secondary consumers; parasites, predators and omnivores (Figure 3.27). Of the three groups, parasites included the greatest reduction (2.28), observed in the larvae of Tetraphyllidean cestodes. Of the parasites, a nematode *Cucullanus heterochrous* Rudolphi, 1802 showed the least  $\Delta TL$ , occupying a  $TL_{fb}$  of 3.44, compared to its  $TL_{sw}$  of 5.03. Predators, excluding a polychaete outlier *Goniada maculata* Örsted, 1843, which was the only species with a  $TL_{fb}$  greater than its  $TL_{sw}$ , saw the least variation in reduction of TL. The decapod *Corystes cassivelaunus* (Pennant, 1777) saw the least reduction ( $\Delta TL = -1.63$ ) and Nemertea saw the greatest ( $\Delta TL = -2.04$ ).

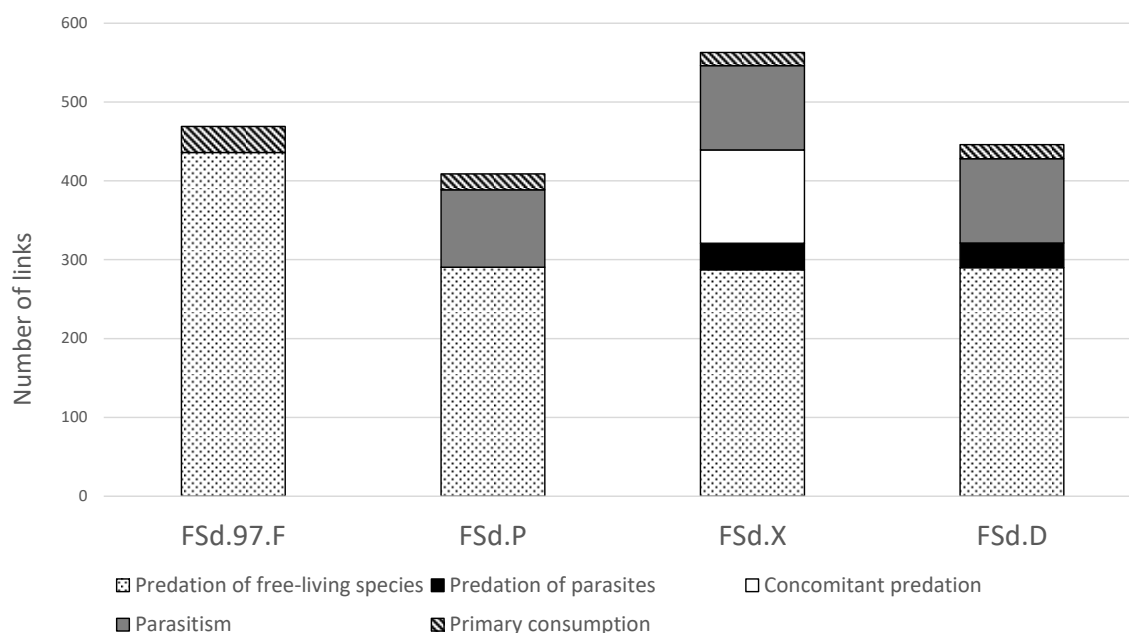


**Figure 3.27:** The mean and range in  $\Delta TL$  ( $TL_{fb} - TL_{sw}$ ) of feeding groups based on corresponding species within the feeding group in the FSd.X; flow-based TL, using the trophic efficiency of each interaction as a measure of diet fraction, compared to the original topological measure of TL.

### 3.7 Concomitant links and the unique role of parasites in food webs

#### 3.7.1 Topology of the 47-node food webs

Four versions of the FSd food web (Figure 3.28), controlled for scale dependence with 47 nodes each, were constructed in order to explore the effects of link type on structure and topology in the FSd.F. The FSd.97 web contained 47 free-living species whereas the FSd.P, FSd.X and the new FSd.D contained 35 free-living species and 12 parasite species. The FSd.97 web contained only free-living links, the FSd.P contained free-living links and incoming links to parasites, the FSd.X contained outgoing and incoming links to parasites, including concomitant predation and the FSd.D was equivalent to the FSd.X, but without concomitant links. Concomitant links from parasites occur when the parasite is digested alongside its host by the predator of its host.



**Figure 3.28:** Proportion of link types in the four 47 node versions of the FSd food webs. Basal nodes aside, the FSd.97 includes only free-living species, the FSd.P contains 12 parasites in their role as consumers, the FSd.X contains 12 parasites in their role as consumers and resources, including concomitant links and the FSd.D contains 12 parasites as consumers and resources excluding concomitant links. All parasites are included as single, aggregated nodes.

Including parasites as consumers only in the FSd.P web produced a lower number of links ( $L = 409$ ) compared to the 47 node FSd.97 web without parasites ( $L = 469$ , Figure 3.28, Table 3.6).  $L$  was also lower than in the FSd.X (563) and FSd.D (446), both of which were expanded versions of the FSd.P (Table 3.6). Since  $S$  was equivalent in each food web,  $L/S^2$  was proportional to  $L$  in each food web. Only in the FSd.P did connectance not correlate with  $L$ , due to the adjusted connectance calculation used for this food web. Conversely, the proportion of omnivores and the mean and maximum  $TL_{sw}$  were associated less with  $L$  and more with link type. The number of omnivores in the food web increased from 25 to 32 when parasites were included as consumers (Table 3.6) and again to 38 when outgoing links from parasites were included, whether concomitant links were included or not. The greatest mean and maximum  $TL_{sw}$  occurred in the FSd.X (mean = 4.9, max = 6.22), followed by the FSd.D (mean = 4.05, max = 5.46), FSd.P (mean = 3.36, max = 4.5) and the FSd.97 (mean = 2.93, max = 3.53) (See Table 3.6).

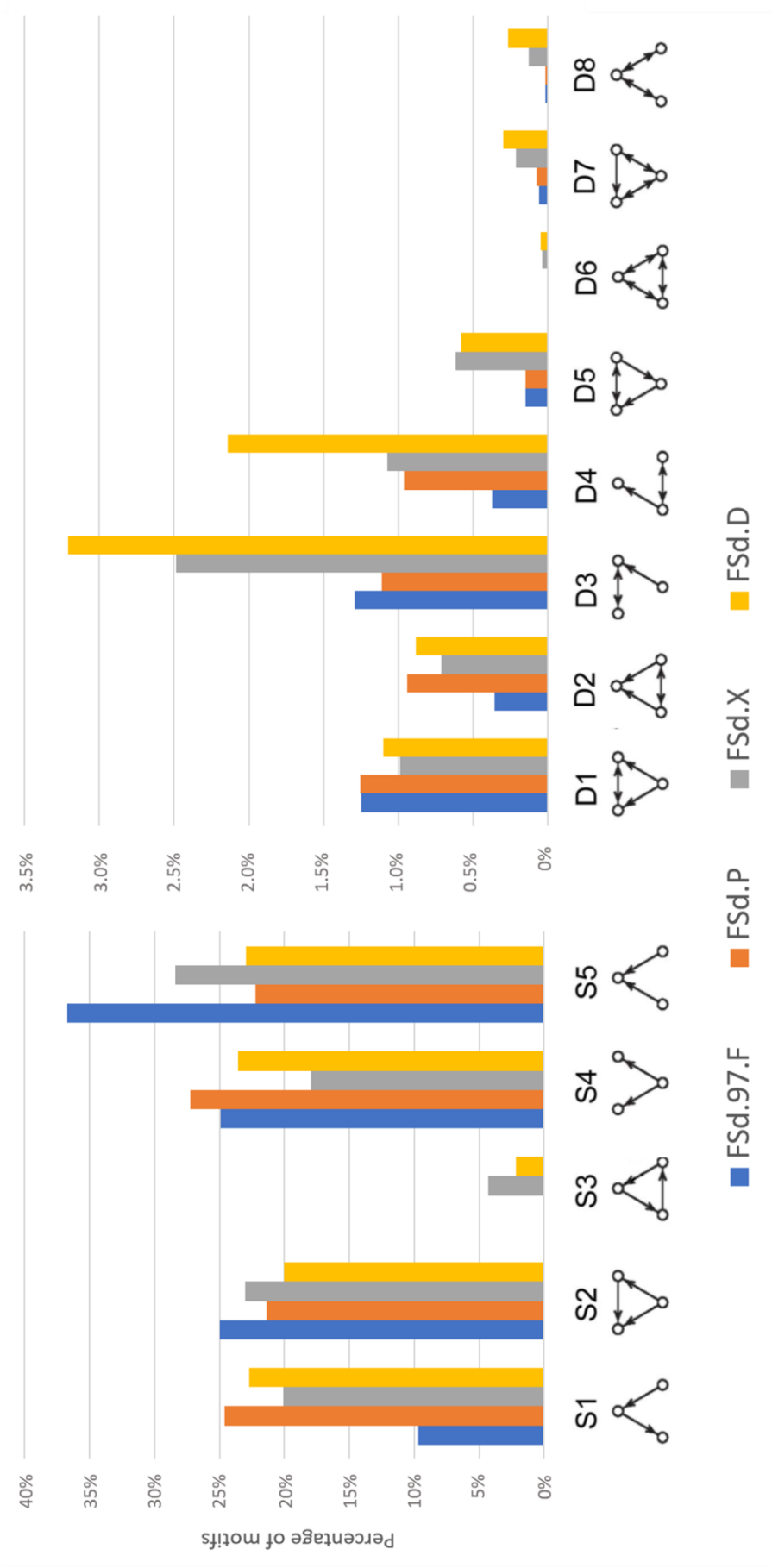
**Table 3.6:** Topology of four variations of the FSd food web with 47 nodes each, including free-living species only (FSd.97), including parasites in discrete species-specific nodes as consumers (FSd.P), as consumers and resources with (FSd.X) and without concomitant links (FSd.D).  $S$ =number of nodes/species,  $L$ =number of links, Connectance=  $L/S^2$  in the LL.X and MM.X and  $L/S_f(S_f+S_p)$  in the LL.P and MM.P.  $TL_{sw}$ =short-weighted trophic level.

|                      | FSd.97 | FSd.P | FSd.X | FSd.D |
|----------------------|--------|-------|-------|-------|
| $S$                  | 47     | 47    | 47    | 47    |
| $L$                  | 469    | 409   | 563   | 446   |
| $L/S$                | 10     | 8.7   | 12    | 9.5   |
| Connectance          | 0.21   | 0.25  | 0.26  | 0.27  |
| Omnivorous nodes / % | 53     | 68    | 81    | 81    |
| Mean $TL_{sw}$       | 2.93   | 3.36  | 4.9   | 4.05  |
| Maximum $TL_{sw}$    | 3.53   | 4.5   | 6.22  | 5.46  |

### 3.7.2 Structure of the 47-node food webs

Network structure in food webs refers to the relative expression of the 13 link combinations, or motifs, that can occur between three nodes. Motifs in which two or more of the three nodes consume one another are referred to as double motifs. The proportion of motifs that exclude double links (Figure 3.29; S1-S5), in which two species consume one another in a 3-node motif, was fairly similar regardless of the number of links or link type. The largest differences occurred in the number of “S1” tri-trophic chains and “S5” apparent competition motifs, which were under- and over-expressed in the FSd.97, respectively. Trophic loops (S3) were absent in the FSd.97, FSd.P and very rare in the food webs that included parasites as resources; comprising 4.3 % and 2.2 % of motifs in the FSd.X and FSd.D, respectively.

All double link motifs were rare in every food web compared to motifs without double links (Figure 3.29). The most prevalent double link motif was “D3”; apparent competition + mutual consumption, which comprised 3.2 % of three node motifs in the FSd.X and 2.5 % of motifs in the FSd.D web. Exploitative competition + mutual consumption (D4) was also relatively common in the FSd.X (1.1 % of motifs), though not in the FSd.D. The largest differences in the proportion of double link motifs between the FSd.97 and FSd.P webs occurred in apparent competition + intraguild consumption (D2) and exploitative competition + mutual consumption (D4).



**Figure 3.29:** Percentage of each of the 13 possible motifs that occur between any three nodes in a network. Including four variations of the Fsd food web containing 47 nodes. The Fsd.97 web contains 47 free-living species whereas the Fsd.P, Fsd.X and Fsd.D contained 25 free-living species and 12 parasite species. The Fsd.97 web contained only free-living links, the Fsd.P contained free-living links to parasites, the Fsd.X contained outgoing and incoming links to parasites, including concomitant predation and the Fsd.D was equivalent to the Fsd.X, but without concomitant links.

### 3.8 Combined host-parasite node food webs

In place of single, species-specific or multiple, disaggregated ontogenetic niche-shift nodes, parasites can be included in combined nodes with their hosts, alongside the original uninfected host node in a food web. Combining every host-parasite interaction into a new node in the FSd.X web produced drastic increases in the size of the network, resulting in a total of 134 nodes (S), 1729 links (L) and a linkage density of 12.9 links per species (L/S). Conversely connectance ( $L/S^2$ ) decreased substantially to  $4.5 \times 10^{-5}$ .

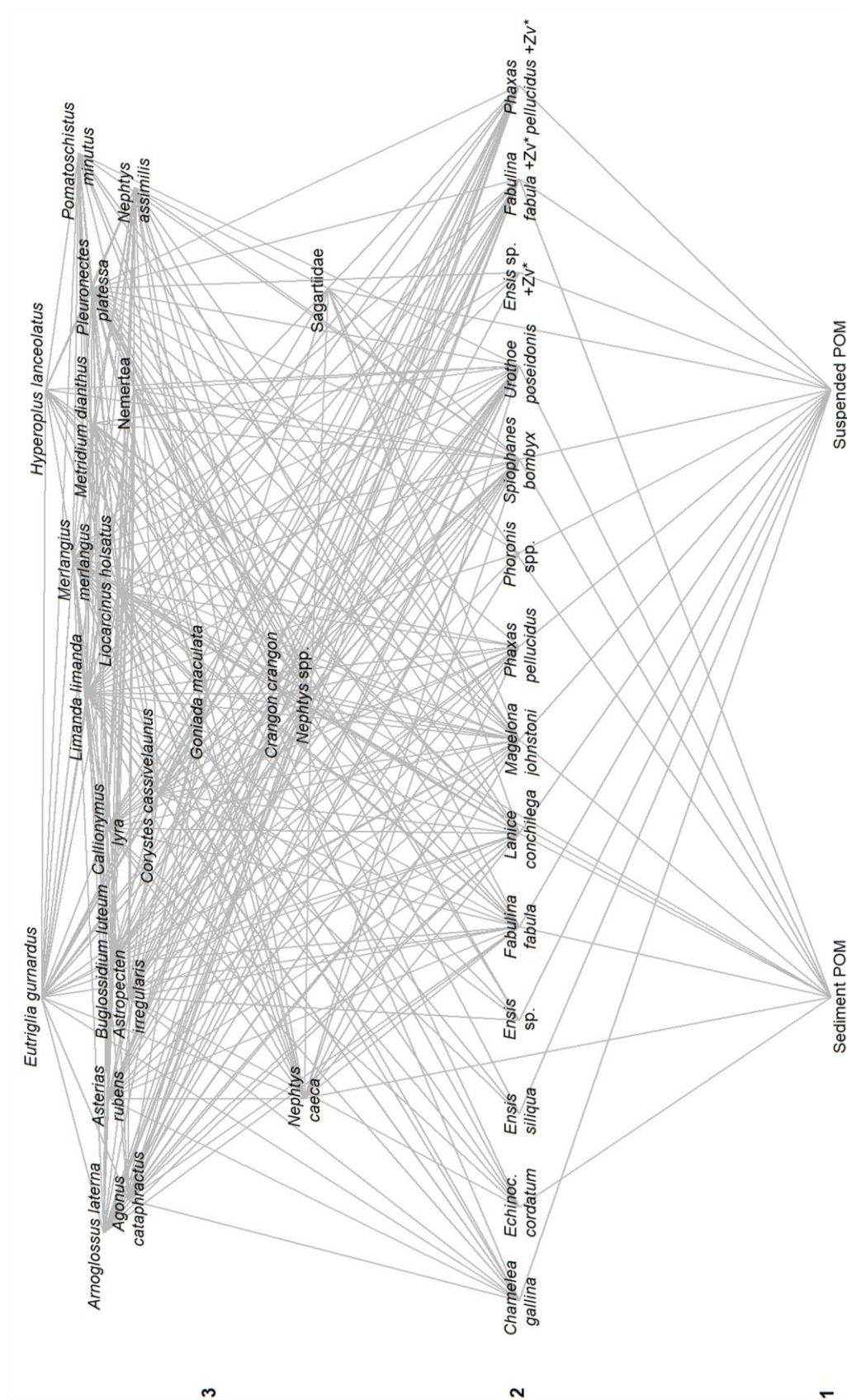
In the proposed, speculative “link-modifier” food web, any host-parasite node with identical incoming and outgoing links as the uninfected species node was reduced into a single trophic species node, alongside the uninfected host species. As such, only parasitic interactions that add or remove a link between their host and another free-living species will be represented in the combined host-parasite node, link-modifier web. After a literature search, no link-modifying interactions in the FSd.P and FSd.X food webs could be identified. Therefore, what follows is a speculative model of the proposed combined node, link modifier food web. Five nodes were included in a speculative model of the combined FSd web including parasites (FSd.Co) comprising five species of Bivalvia, infested with cercaria of the digenean trematode *Zoogonoides viviparus* (Figure 3.30). It was speculated that the infestation, which may prevent burrowing, could remove a link from the bivalve host to its infaunal predators such as Nemertea and “catworm” polychaetes of the genus *Nephtys* Cuvier 1817. A second construction of the combined node FSd web (FSd.Co.X) included potentially energetically significant life stages, such as free-living trematode cercaria, alongside combined host-parasite nodes (Figure 3.31). Including parasites in combined nodes with their hosts resulted in topology very similar to the FSd.F, increasing L/S and

reducing  $L/S^2$  (Table 3.7). Including potentially significant resources; free-living, non-feeding cercaria and nauplii, as discrete nodes alongside the combined host-parasite nodes decreased  $L$ ,  $L/S^2$ , mean  $TL_{sw}$  and the proportion of omnivorous nodes. The proportion of basal species was increased.

**Table 3.7:** Topology of combined host-parasite node food webs. S=number of nodes/species, L=number of links, Connectance=  $L/S^2$  in the LL.X and MM.X and  $L/S_f(S_f+S_p)$  in the LL.P and MM.P.  $TL_{sw}$ =short-weighted trophic level.

|                      | FSd.F | FSd.Co | FSd.Co.X |
|----------------------|-------|--------|----------|
| S                    | 35    | 38     | 42       |
| L                    | 310   | 344    | 369      |
| $L/S$                | 8.9   | 9.1    | 8.8      |
| $L/S^2$              | 0.25  | 0.24   | 0.21     |
| Omnivorous nodes / % | 60    | 55     | 52       |
| Mean $TL_{sw}$       | 3.05  | 2.86   | 2.73     |
| Maximum $TL_{sw}$    | 3.6   | 3.53   | 3.48     |





**Figure 3.30:** FSD.Co food web including species comprising 90 % of the cumulative energy at the FSD station and parasites identified in a literature search and the dissections of 25 *Limanda limanda* and 30 *Merlangius merlangus*. Parasites are disaggregated into life stages and included in combined nodes with their hosts, alongside a node for the uninfected host. The combined host-parasite nodes are highlighted by an asterisk following the species abbreviation. Short-weighted TL is indicated by the numbers on the vertical axis. Zv = *Zoogonoides viviparus*. The name of *Echinocardium cordatum* has been shortened to “*Echinoc. cordatum*” for space.

**Figure 3.31:** Fsd. Co.X food web including species comprising 90 % of the cumulative energy at the Fsd station and parasites identified in a literature search and the dissections of 25 *Limanda limanda* and 30 *Merlangius merlangus*. Parasites are disaggregated into life stages and included in combined nodes with their hosts, alongside a node for the uninfected host. Free-living parasite life stages are included as discrete nodes and aggregated into trophic species. The combined host-parasite nodes are highlighted by an asterisk following the species abbreviation. Short-weighted TL is indicated by the numbers on the vertical axis. Zv = *Zoogonoides viviparus*, Nauplii = free-living copepod nauplii of *Clavella adunca* and *Lernaeocera branchialis*, Cercaria = free-living trematode cercaria of *Derogetes varicus*, *Hemimurus communis*, *Stephanostomum baccatum* and *Zoogonoides viviparus*. The name of *Echinocardium cordatum* has been shortened to “*Echinoc. cordatum*” for space.

## 4. Discussion

Parasites have been excluded from the majority of food web constructions (Sukhdeo, 2012) due to their small size, non-lethal feeding mode and presumed negligible contribution to the total biomass and energy flow in their ecosystems. However, in three Californian saltmarshes, the most resolved food webs into which parasites have so far been incorporated, parasitic digenean trematodes were estimated to comprise a greater total biomass than wading birds (Kuris et al, 2008). Mechanisms by which parasites can alter the energy flow of an ecosystem have also been identified. For example, the trematode *Diplostomum spatheceum* (Rudolphi, 1819) Olsson, 1876 encysts in the eyes of its teleost intermediate hosts, reducing their vision. The typical host response to this infestation is a change of habitat preference to shallower waters, where the light is greater. As a result of this, the fish is more susceptible to predation from avian predators, the definitive hosts of *D. spatheceum* (Seppälä et al., 2004). This increases the energy transferred between the intermediate and definitive hosts of the trematode and most likely diverts energy away from other predators of the intermediate host. As such, parasites warrant consideration in food webs for their impact on energy flow. Parasites have not previously been included into a fully submerged, marine food web and the visual representation of parasites in food webs has been problematic.

This study incorporated parasites into a food web constructed around the *Tellina fabula* community-characteristic of Fine Sands (FSd) in the German Bight, North Sea. The network is composed of 35 nodes comprising two basal nodes, sediment and suspended particulate organic matter which form the base of the food web, and 33 free-living invertebrate and teleost species. Parasites, identified by a literature search and dissections of two prominent

host species from the station, were included into the food web in order to explore three research questions: which generic and unique effects do parasites produce on food web topology, stability and structure, when included as consumers and as both consumers and resources? How are trophic levels affected by the inclusion of parasites, are the changes ecologically realistic and, if not, can they be appropriately modified? How can parasites be included in a food web diagram without the erroneous label of top predators and how do food webs change if parasites are included in combined nodes with their hosts?

#### 4.1 Parasite diversity

Considering the literature review alone, dab (*Limanda limanda*) was more vulnerable to parasitism than any other species in the FSd.F food web. Over 50 species of metazoan parasite were identified for dab worldwide, including Myxosporea, Digenea, Cestoda, Nematoda, Acanthocephala and Crustacea (e.g. Ibekken & Zander, 1997; Lang *et al.*, 2017). Of these species, 28 were reported in the North Sea alone. Yet only two of the 30 dab dissected in the current study contained any parasites at all: three specimens of the same trematode *Hemiurus communis*. Parasite diversity in fishes is negatively correlated with fishing effort (Wood *et al.*, 2014) and the German Bight is one of the most heavily exploited shelf sea ecosystems worldwide (Emeis *et al.* 2015). Pedersen *et al.* (2009) estimated that 118,580 tonnes of fish and shellfish were landed from the German EEZ of the North Sea in 2006 alone. In order to establish themselves in an area, many trophically transmitted parasites with multiple, sequential hosts require tightly coupled feeding interactions between those hosts (Anderson & Sukhdeo, 2011). This may be disrupted by the high levels of anthropogenic and natural disturbance in the German Bight (Shojaei *et al.*, 2016) and the

subsequent preponderance of generalist species in the FSd (Steger *et al.*, 2019). The average strength of interactions between a generalist consumer and its resources is intuitively lower than a trophic specialist, feeding on only one or a few resource species. Therefore, the unexpectedly low abundance and diversity of parasites infesting dab in this study may be a consequence of significant disturbance in the area. However, this is inconsistent with the historical diversity of parasites recorded in German Bight dab (Palm *et al.*, 1999) and in whiting collected in the same samples (Table 3.1). Seasonal trends in parasite diversity may also be considered. Parasite abundance and diversity in marine fishes has been correlated with water temperature and as such the greatest annual prevalence of parasites can be expected to occur in summer (Schade *et al.*, 2016). Fishes dissected in this study were collected in March and so a submaximal abundance of parasites might be expected and may explain some of the disparity between the diversity of parasites in this and historical samples of dab. Collection methods may also go some way towards explaining the lack of parasites in dab, since many parasites, particularly of ectoparasites such as monogenea, can be destroyed by freezing and thawing, resulting in false negatives (Austin & Newaj-Fyzal, 2017). Since parasite intensity patterns are usually very right skewed, with a small number of hosts containing a high number of parasites, it is also possible that this unusually low number of parasites represented random sampling error.

It is sometimes reasonable to assume that every life stage of the parasites included in a food web will occur within the geographical boundaries of the network, such as in the Quick Pond food web in California (Preston *et al.*, 2014). However, this is not true for the FSd food webs. For instance, Heterophyidae metacercaria, included in the FSd.P, FSd.D and FSd.X food webs, only mature to adulthood in an avian or mammalian host (Køie, 1977), neither of which are present at the FSd station. Furthermore, the metacercaria of *Hemiurus communis*



only develops inside planktonic copepods (Køie, 1995), which are also absent from the benthic habitat to which this case study is restricted. Whiting in the North Sea migrate between spawning and feeding areas (Ellis *et al.*, 2012). As such, it may be the case that some parasites found in whiting were obtained outside of the FSd web and the typical range of dab in the food web. Significant further investigation would be required to explore the proposal further. The diets of dab and whiting in the FSd food webs are quite similar - only four species that are predated by whiting are not also consumed by dab – however, these differences, though slight, might explain some of the dearth of parasites in dab. Two species in the web, the teleosts *Agonus cataphractus* and *Buglossidium luteum* (Risso, 1810), which are consumed by whiting, but not dab, host parasite life stages that are infective to dab but were not found in their dissections, namely the L4 larval life stage of the nematode *Hysterothylacium aduncum* and metacercaria of *Stephanostomum* sp., a digenean trematode. It is possible that these host species are the source of infection in whiting in the fine sand communities in the German Bight, which might explain their absence from dab that does not consume *A. cataphractus* or *B. luteum* as a species.

Individual feeding preference does not appear to be influencing the diversity of parasites in dab, however. The stomachs of the two infected fish contained partially digested bivalves *Ensis* spp. and amphipods *Parionus typicus* (Krøyer, 1844). Neither of these prey species are known or likely to be intermediate hosts of *H. communis*, nor was this combination of prey items exclusive to the two parasitized fish. Similarly, Cirtwell *et al.* (2015) found no obvious link between individual fish host diet and helminth infection level. Of the seven species identified in the whiting dissections, only the copepod *Clavella adunca* is not also a known parasite of dab. Therefore, the lack of parasites identified in dab is not due to the absence of known parasites in the food web.

One whiting specimen, referred to as 36M18, harboured 62.9 % of the isolated *Hysterothylacium aduncum* and 13.8 % of the identified *Hemiurus communis*. This specimen was significantly longer and heavier than the other sampled whiting (see section 3.1). Several studies suggest that teleost length at the species level accounts for more of the variance in parasite diversity than any other factor (Sasal *et al.*, 1997; Luque *et al.*, 2004) and at an individual level larger teleost hosts harbour a greater abundance of parasites (Wood *et al.*, 2014). Fish length is typically positively correlated with age (Shotter, 1973), which in turn is often associated with greater prevalence and intensity of parasitic infection (Iyaji *et al.*, 2010). Therefore, it is likely the greater age and/or size of this fish resulted in the significantly greater abundance of parasites that occurred in this fish than in any other whiting.

## **4.2 The role of parasites in the FSd food webs**

### **4.2.1 The effects of parasites on food web complexity**

Network connectance, a common measure of food web complexity, refers to the proportion of potential links that are realised in a topological food web matrix. Connectance was negligibly affected by the inclusion of parasites in their role as consumers, whether they were included as single, species-specific nodes or as disaggregated, ontogenetic niche-shift nodes (after Preston *et al.*, 2014). This opposes the first hypothesis of the study. Parasites increased connectance in five of the seven food webs that were included in a previous analysis of parasites' effect on food web topology (Dunne *et al.*, 2013; Figure 4.1) and a similar increase was expected in the present study. Linkage density, or the number of links per node, was also reduced after parasites' inclusion in their role as consumers, whether

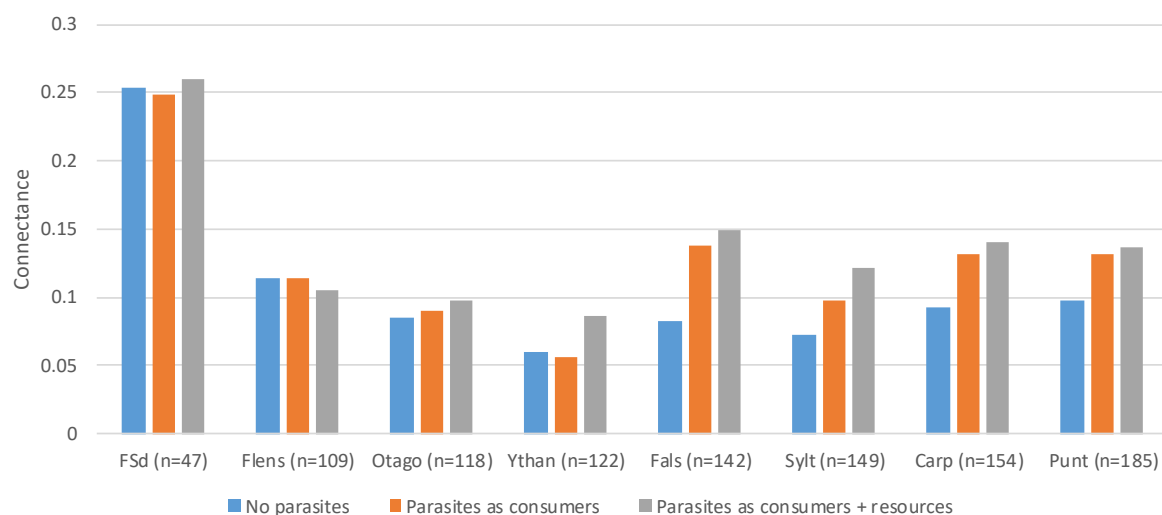
they were included as single species-specific nodes or as disaggregated ontogenetic nodes. As was the case with connectance, linkage density in the seven food webs considered by Dunne *et al.* (2013) typically increased after parasites were included, the same pattern occurred when parasites were disaggregated into ontogenetic niche-shift nodes, as in the Californian Quick Pond food web (Preston *et al.*, 2014), and so similar increases were expected here. This did not occur when parasites were included in their role as consumers, however slight increases in linkage density did occur when outgoing links from parasites, acting as resources, were also included. These links represent both concomitant predation and the direct predation of free-living life stages. However, these are not as substantial as those observed in either the Quick Pond network or the average increase in linkage density of the seven food webs analysed by Dunne *et al.* (2013). The linkage density of the whiting-specific food web was increased by 6 % after the inclusion, whilst linkage density the Quick Pond increased by over 20 %. Likewise, whilst single, species-specific parasite nodes, included in their role as consumers and resources, increased linkage density in the current food web by 35 %, linkage density in the seven food webs analysed by Dunne *et al.* (2013) increased by an average of 125 %. It might be inferred therefore that the species of parasite included in the fine sand community food webs from the German Bight have a higher host specificity or a reduced host niche than parasites included in the food webs analysed by Dunne *et al.* (2013).

However, the FSd station food web is substantially more complex than any of the food webs considered by Dunne *et al.* (2013) (FSd; Figure 4.1). Over twice as many possible links are realized in the parasite-free version of the current case study than in the next most connected food web, situated in the Flensburg Fjord, Baltic Sea (Flens; Figure 4.1). This is partly due to the preponderance of generalists in the German Bight web, brought about by



high levels of anthropogenic and natural disturbance in the ecosystem (Shojaei et al., 2016).

The notably high complexity of the current food web may also be a product of the scale variance, which often shows a negative correlation between connectance and network size (Banašek-Richter et al., 2004). The current food web is comprised of 35 species, fewer than any other food web assessed by Dunne et al. (2013), which ranged between 56 nodes, in the Flensburg Fjord, and 117 nodes, in the Sylt Tidal Basin (Figure 4.1). Therefore, the parasites included here may not be less complex than parasites included in other food webs but only appear less complex in comparison to the highly connected free-living species in the food web.



**Figure 4.1:** Connectance ( $L/S^2$ ) in parasite free food webs, food webs including parasites as consumers ( $L/S_f(S_f+S_p)$ ) and food webs including parasites as consumers and resources. Food webs including the current case study and data published in Dunne *et al.* (2013), the number of species in each food web is included in brackets.

A reduction in network connectance might intuitively be expected when parasites are disaggregated into ontogenetic nodes, as was observed in the whiting-specific food webs, due to the limited overlap in host species between the life stages of each parasite species (Figure 3.13; 3.14). Disaggregated ontogenetic nodes split the same, or a similar, number of links – depending on the degree of overlap in the parasites life stage-specific hosts – between more nodes than if the parasite was included as a single species-specific node. This

increases the number of potential links in a food web matrix, whilst only slightly or not at all increasing the number of realized links, decreasing connectance by definition. However, this is only partly responsible for the reduction observed in the whiting-specific food web, when parasites were included as consumers in ontogenetic nodes. When parasites were included as single, species-specific nodes in the same food web (not included in the results), connectance remained lower in the food web with parasites than in the parasite-free whiting-specific food web (see section 3.4.3). The dab-specific (*Limanda limanda*) food web displayed similar, though dampened, versions of the same patterns observed in the whiting-specific food web after parasites were included. This is due to the limited richness of parasites identified in the dab dissections (see Table 3.1). As such, this discussion refers primarily to the whiting-specific food web as an exemplar of both fish-specific food webs.

Food web complexity typically reflects the proportion of parasitic nodes that are included in the network (Dunne et al., 2013). Food webs in which parasites constitute ~50 % of nodes tend to display the greatest connectance, decreasing in an approximately normal distribution around the mean (Dunne et al., 2013). Only 26 % of nodes in the fine sand communities in the German Bight are parasitic, therefore the maximal increase in connectance would not be expected in this case. A version of the current food web, which was expanded to include 24 parasite species, or 40 % of the total nodes (not included in the results), supports this suggestion. Connectance in this food web increased by 81 % after parasites were included in their role as both consumers and resources. This food web was constructed as part of an attempt to quantify the importance of different parasite inclusion parameters on food web complexity. This aspect of work was not considered to be sufficiently relevant or rigorous to be included as part of the project, though the construction of the various food webs was thorough. Food web connectance is also highly

dependent on sampling effort and ecological knowledge of the species (Blüthgen, et al. 2008). Free-living species are included in the FSd food webs on account of decades of repeated sampling at the site, whilst the parasite species are included based on a literature search and dissection of 55 fish. These factors compounded by an historical emphasis on studying non-parasitic species (Dobson et al., 2008) may have resulted in a relatively lower connectance of parasite species in the current food web. It is possible that habitat is also playing a role in the possible, relatively low connectance of parasites included in the FSd station food webs. Two of the food web analysed by Dunne *et al.* (2013), which are situated in the Flensburg Fjord (Zander *et al.*, 2011) and the Sylt tidal basin (Thieltges *et al.*, 2011), occupy similar habitats to the German Bight. Whilst the *Tellina fabula* community food web is the first marine, submerged food web to include parasites, the Flensburg Fjord, a submerged but brackish ecosystem, and the Sylt tidal basin, a marine but intertidal ecosystem, are situated in relatively comparable habitats. In fact, both food webs include some of the same parasite species as the current case study and occur within 160km of the FSd station. Of the two food webs, parasites in the Flensburg Fjord had a more similar impact on linkage density to parasites in the fine sand communities of the German Bight, showing similar reductions, whilst parasites in the Sylt tidal basin produced a marked increase in linkage density and complexity (Figure 4.1). This provides weak evidence that parasites in fully submerged ecosystems may have a relatively lower contribution to the overall complexity of the food web than those in intertidal, freshwater or terrestrial ecosystems. It may also suggest that the marine component of the web has a lesser role, though the sample size is insufficient to draw any decisive conclusions. Habitat might impact the complexity of parasites in submerged ecosystems due to the relative openness of the habitat to migration of species in and out of the food web. The suggestion is supported by

the fact that some parasites in the FSd food webs have intermediate and/or definitive hosts that occur exclusively outside of the station. For example, the metacercariae of two trematode parasites, *Hemiurus communis* and *Derogenes varicus*, that were identified in the dissections will only develop inside a pelagic copepod host (Køie, 1979; Køie, 1995).

Vertically unrestricted species such as whiting (Rindorf, 2003) might be infested by these trematodes whilst foraging in the pelagic realm, thereby bringing the parasite species into the benthic food web. Other parasites have obligate hosts that occur exclusively in the intertidal realm, such as the edible periwinkle *Littorina littorea* (Linnaeus, 1758), which is the first obligate host of *Cryptocotyle lingua*, a species which also has definitive hosts excluded from the FSd stations benthic parameters. This parasite might be introduced into the food web by species such as dab, which seasonally migrate in and out of the area in relation to temperature and in order to reproduce (Saborowski & Buchholz, 1997). As such, links to some parasite life stages are excluded from the food web, reducing their relative connectance in the food web. Therefore, in order to fully represent parasites in food webs, it is important for the food web to not be restricted to any biological component nor to a particular realm, such as the benthic and pelagic realms in this instance. The impact of parasites on food web complexity might only be fully realised in marine habitats by constructing food webs at the ecosystem scale. Food web complexity and the impact of parasites therein is associated with some of the fundamental principles of ecosystem management, such as the ecosystem's ability to recover from natural and anthropogenic disturbances and persist relatively unchanged through time (see section 4.2.4). As such, parasites support the increasingly advocated, though not always practiced (Carmel *et al.*, 2013), necessity for an ecosystem-wide approach to the investigation and management of marine species and their communities (Smith *et al.* 2007).

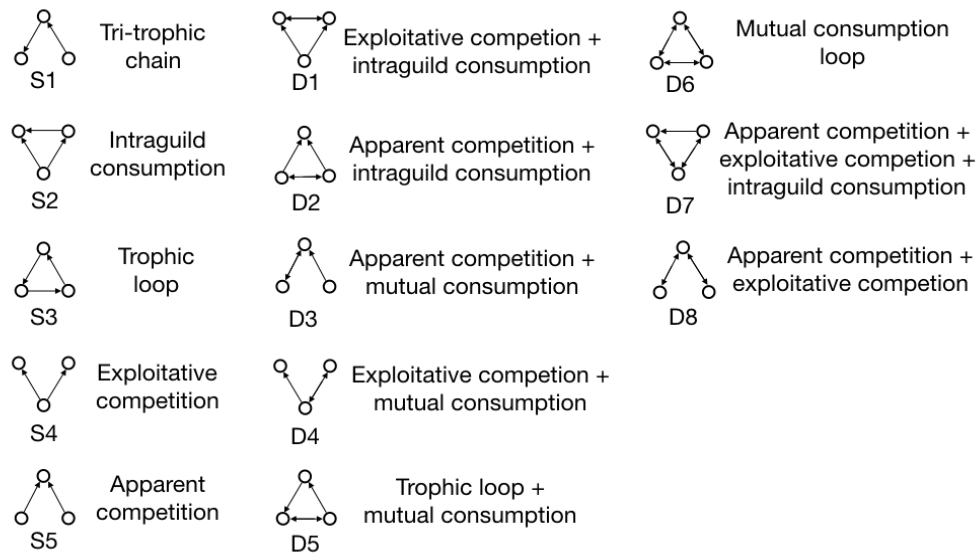
#### 4.2.2 The effects of parasites on food web omnivory

Including parasites into the fine sand community food webs of the German Bight drastically increased the proportion of omnivorous species, when they were included as single, species-specific nodes, in their role as both consumers and resources. Like many free-living species, parasites with complex life histories will consume a range of host species that occupy different trophic levels throughout their lifecycles. However, unlike free-living consumers, there is no temporal overlap between the consumption of each resource species. This is illustrated in the whiting-specific food webs, in which parasites, included as disaggregated, ontogenetic niche-shift nodes, produced only slight increases in the proportion of omnivorous nodes when included in their role as consumers, and no change at all when included as both consumers and resources. The degree of omnivory in a food web has some impact on its stability and ability to persist through time, however the direction and magnitude of this impact is not always consistent between food webs (Kratina *et al.*, 2012). The level of omnivory in food webs may also impact the calculation of trophic levels, which may be disrupted by the increased prevalence of omnivores after the inclusion of single, species-specific parasite nodes (Williams & Martinez, 2004). These issues are discussed further, in relation to the current case study, in sections 4.2.4 and 4.3.1, respectively.

### 4.2.3 The unique role of parasites on food web structure

Structural analyses of trophic networks have suggested that the inclusion of parasites uniquely alters the relative expression of 13 possible motifs, or triangular link patterns, that can occur between three nodes in a network (Figure 4.2). Eight of the 13 unique motifs include double links between two or all three of the nodes (D1-D8; Figure 4.2) whereas 5 of the motifs only include unidirectional links (S1-S5; Figure 4.2). Ecologically, a double link refers to the mutual consumption of two species, which has been attributed to the presence of concomitant predation in food webs that include parasites (Dunne *et al.*, 2013; McLaughlin, 2018). Concomitant predation refers to the process by which a parasite is digested, alongside its host, by the host's predator. McLaughlin (2018) states that a parasite is concomitantly consumed and digested in 71 % of all cases where their host is predated, though how often concomitant predation and digestion occurs when the host's consumer is a viable host of the parasite is unknown. Due to ambiguities in the methods, it is unclear whether concomitant links from parasites to viable hosts were included by Dunne *et al.* (2013) or McLaughlin (2018); however, it appears likely that they were included, due to the attribution of double links to concomitant predation in the text and the large proportion of concomitant links in the webs. Concomitant links to viable hosts of the parasites were excluded here, on the assumption that trophic transmission between viable hosts is typically successful. No evidence was found to suggest that this assumption was incorrect.

As hypothesised, the proportion of double-link motifs was higher in food webs that include parasites in their role as resources (see Figure 3.29). In particular, the "D3" apparent competition and mutual consumption motif and "D4" exploitative competition and mutual consumption motifs (Figure 4.2) were overexpressed in these food webs, compared to the



**Figure 4.2:** The 13 unique motifs that are possible between three nodes in a network. S1-S5 denote single motifs and D1-D8 are double motifs. Diagram taken from McLaughlin (2018).

food webs excluding parasites as resources. A similar overexpression of these motifs occurred in the Palmyra Atoll food web (McLaughlin, 2018) and in most of the food webs considered by Dunne *et al.* (2013). McLaughlin (2018) suggests that the overexpression of D4 motifs in the web highlights a potential for predator loss in the network. It was suggested that if, following a reduction in predation, parasite densities increased faster than the predator, a positive feedback loop could be created, accelerating the predator's decline. However, mutual consumption in the current case study refers largely to the consumption of its host by a parasitic copepod and the direct predation of that copepod's free-swimming nauplii by the same host. It does not refer to the concomitant predation of a parasite by their viable hosts as appears to be the case in the previously mentioned studies. Therefore, it is possible that some of the risks associated with the overexpression of double-link motifs are also attributable to the presence of direct predation on free-living parasite life stages in a food web, as well as concomitant predation of a parasite by a viable host. It should be noted that double link motifs including a parasite as one of its three nodes will only occur in

food webs where parasites are modelled as single, species-specific nodes. This is because copepod nauplii, which are consumed by the free-living predator, are disaggregated from the adult life stage, which parasitizes the same predator, in an ontogenetic niche-shift web (after Preston *et al.*, 2014), precluding mutual consumption and a double link. This highlights the need for parasites to be included appropriately into food webs, according to the topological aspect that is being studied. Also highlighted is the need for more research into the energetic contribution of parasites as resources for their concomitant and direct predators. Particularly regarding the degree to which free-living life stages of copepod parasites represent an energetically significant resources, in the way that some trematode parasites are estimated to in the Carpinteria salt marshes (Kuris *et al.*, 2008).

If concomitant links from parasites are energetically negligible for the consumer, it might be argued they do not warrant inclusion in a topological food web, especially given the significant impact that these links can have on our understanding of trophic networks. Links between free-living species are not assessed for energetic significance in a topological food, however the species are typically only included if they contribute a significant proportion of the ecosystem's total biomass, which is rarely the case for included parasites. Whilst a concomitant link may not be energetically significant for the free-living consumer, it may well have important implications for the parasite's population, McLaughlin suggested that 71 % of parasite individuals are concomitantly consumed. Therefore, if we are to include parasites at all, it may be the case that concomitant links must also be included. Further, extensive data on the success rates of trophic transmission in many parasites is required in order to elucidate the unique effects of parasites as resources on food web structure.



#### 4.2.4 The effects of parasites on food web stability and robustness to species loss

The potential for predator loss, as highlighted by the overexpression of D4 motifs in the food webs (see section 4.2.3) represents one mechanism by which parasites may decrease the overall stability of a food web. However, there are other, sometimes conflicting, ways by which parasites can affect network stability, defined as the networks ability to remain approximately in its present state or else return to that condition following a disturbance (Kratina *et al.*, 2012). Due to the close, dependent relationship that they have with their hosts, parasites are often highly vulnerable to secondary extinctions (Allesina *et al.*, 2009; Lafferty & Kuris, 2009). For example, the extinction of one snail species in the Carpinteria salt marshes would result in the subsequent extinction of 17 trematode parasites (Lafferty & Kuris, 2009). This vulnerability results in an overall decrease in the robustness of a food web to species loss.

Incorporated as single, species-specific nodes in the fine sand communities in the German Bight, most parasites do not appear to be particularly vulnerable to secondary extinction. Perhaps the main exception to this rule is the parasitic copepod *Clavella adunca*, which infests only whiting in the food webs. However, by disaggregating each parasite into ontogenetic, niche-shift nodes, further vulnerabilities are revealed. For example, adult life stages of the parasitic trematode *Stephanostomum baccatum* rely on the teleost *Eutriglia gurnardus* as their sole viable host in the food web. Adults of another trematode, *Zoogonoides viviparus*, infest only three species in the food web and adult life stages of the copepod *Lernaeocera branchialis* have only two viable hosts in the web. Although the negative effects of secondary extinction would likely be significantly less than those described in the Carpinteria salt marshes (Lafferty & Kuris, 2009), there is some evidence

that the low host-specificity of some parasite life stages may reduce the robustness of the food web, partially supporting the first hypothesis of this study. This also highlights the need for parasites to be appropriately incorporated into food webs, since these vulnerabilities would not have been revealed had the parasites been included only as single, species-specific nodes in the food web. Incorporated into the fine sand communities of the German Bight as species-specific nodes, parasites substantially increased the proportion of omnivorous species in the web, particularly so when included in their role as both consumers and resources (see Table 3.5; section 4.2.2). The relationship between omnivory, defined as feeding over more than one trophic level (Pimm & Lawton, 1978) and food web stability has long been debated. Perhaps the primary way by which omnivory can affect food web stability is through its association with network complexity (Kratina *et al.*, 2012). An omnivore is likely to have a greater selection of prey species than a species feeding from only one trophic level. This weakens the interaction between the omnivore and each of its prey items and these “weak links” typically have a stabilizing effect on the food web. This is because the omnivore is able to adapt its diet in response to fluctuating abundance of different prey species, preventing a single species from becoming dominant (McCann *et al.*, 2005) and itself from becoming locally extinct (Dunne *et al.*, 2002). The same can be said for non-omnivorous species that feed from a broad niche. Generalist species and omnivores with more general diets may, on average, be characterised by many, weak interactions and are therefore likely to have a stabilizing effect on food webs. The strength of those interactions can be subject to high levels of variance and at those times when a particular interaction is strong, exaggerating the effects of predator-prey fluctuations (Berlow, 1999). Overall, however, more general and omnivorous feeders are likely to stabilize a food web (Namba *et al.*, 2008; Kratina *et al.*, 2012).

Therefore, it may appear that the already complex and relatively stable fine sand communities of the German Bight (Dannheim 2007, Shojaei *et al.*, 2016; Steger *et al.*, 2019) would be made more stable by the drastic increases in omnivory, that were a result of the parasites' inclusion. However, since parasites were modelled as single, species-species nodes in the food web, a vital part of many of the parasites' ontogeny has been neglected. Parasites with complex life histories, such as many of those included here, can be seen as a series of host-specific life stages, without overlap between the hosts of each life stage (Sukhdeo, 2012) as opposed to a classically "general" consumer. As mentioned previously, some parasite life stages can in fact be highly host specific. Most parasites in the Carpinteria salt marshes depend on a single host species at some point in their life cycle (Lafferty *et al.*, 2006b). Therefore, individual parasites are not able to adapt their diet in response to environmental conditions in the same way as a general, omnivorous free-living species can. Disaggregating parasites into separate ontogenetic niche shift nodes reduces both omnivory and complexity in the web and likely also reduces the apparent food web stability as much of the increased stability associated with omnivory is confounded by complexity. Whether this is a more ecologically realistic manner for parasites to be portrayed in food webs remains unresolved. Separate life stage nodes appear to represent the parasites' susceptibility to secondary extinction more accurately and the basis of its omnivory and complexity. However, disaggregating parasites whilst maintaining discrete species-specific nodes for free-living species may overstate the impact of parasites on topological indexes such as connectance and linkage density and overestimate their effect on food web functioning. It remains that the manner in which parasites are incorporated into a food web can fundamentally alter their apparent impact on complexity and stability (Rudolf & Lafferty, 2011).

### 4.3 The effects of parasites on trophic levels

#### 4.3.1 Parasites and trophic level “stretch”

Both the mean and maximum short-weighted trophic level of species in the fine sand communities of the German Bight were increased after parasites were included in their role as consumers, regardless of whether they were represented by species-specific or ontogenetic niche shift nodes. Only a slight increase occurred in the mean trophic level of the dab-specific food web, due to its limited richness of parasites, however maximum trophic level was increased to a similar degree as the more parasite-rich whiting-specific food web and the whole station food web. The maximum trophic level was occupied by a parasite in every food web from the FSd station in which they were included. Larger increases in mean trophic level occurred in the whiting-specific food web and the whole station food web than occurred in the dab-specific after parasites were included in their role as consumers only, however this does not appear to constitute trophic level “stretching”, defined here as an inflation of short-weighted trophic levels beyond ecologically realistic limits. An analysis of 9 highly resolved food webs undertaken by Williams & Martinez (2004) detected a maximal short-weighted trophic level of 4.3 for any species. However, the authors concede that the inclusion of parasites may increase the maximum short-weighted trophic level in a food web, up to but never exceeding a short-weighted trophic level of 5. Therefore, the parasites’ maximum trophic levels of 4.41, 4.52 and 4.5 in the dab-specific, whiting-specific and whole station food webs respectively, that were analysed here, are acceptable and do not appear to represent trophic level “stretch” when parasites are included in their role as consumers alone.

Despite their conformity to the bounds of ecological realism, it is possible that the trophic levels of some parasites in the current case study food webs have been erroneously inflated due to the exclusion of some intermediate hosts. For example, two trematode parasites, *Hemiurus communis* and *Derogenes varicus*, that are included in the current food webs are obligate parasites of gastropods as their first intermediate host (Koie, 1979; 1995).

However, despite their presence at the station, no gastropods are included in any of the food webs described by the current study. In the whole station food web, this is due to the gastropods' restricted contribution to the station's energy flow (Steger *et al.*, 2019), no species of gastropod are included in the 90 % cumulative cut-off. One species of gastropod, *Euspira nitida*, was included in an expanded food web which included 97 % of the cumulative energy at the station (see section 3.3), however, the species was excluded from the dab and whiting-specific webs due to their methods of construction. *Euspira nitida* had no direct link to or from either whiting or dab and was therefore excluded from both target fish-specific food webs. This was not limited to *E. nitida* and the process applies to any intermediate host from whom the parasite is not trophically transmitted to dab or whiting or to an intermediate host that occurs outside of the food webs boundaries (see section 4.2.1). Of the 12 species that comprise 97 %, but not 90 %, of the cumulative energy at the station, ten served as intermediate host to one or more parasites (mean =  $2.3 \pm 0.9$  SD). All of these intermediate host species occupied lower trophic levels than the mean trophic level of their parasite's prey. As such, including these species in the web would have resulted in a decrease in the eight parasites' trophic levels. In order for parasites to be accurately included in a food web situated in the fine sand communities of the German Bight, the food web must include species comprising 97% of the cumulative energy at the station and intermediate host species should be included to more accurately represent the short-

weighted trophic level of parasites with complex life histories that include one or more non-trophic transmission infection pathways. The short-weighted trophic level of parasites with obligate hosts that occur outside of the food web would also be more accurately represented by extending the bounds of the food web to include the other habitats, as discussed in section 4.2.1.

After including parasites in their role as consumers and resources in the dab and whiting-specific food webs, parasites again occupied the highest short-weighted trophic levels of 4.42 and 4.6 and all trophic levels remained within ecologically realistic boundaries (Williams & Martinez, 2004). However, as hypothesised, when parasites were aggregated into single, species-specific nodes and included in the whole station food web, trophic levels were stretched beyond the realistic limits outlined by Williams & Martinez (2004). All parasites included in that food web occupied trophic levels exceeding the maximal short-weighted trophic level of 5 (Figure 3.22). The inclusion of species-specific parasite nodes in their role as consumers and resources stretched the short-weighted trophic level of 15 free-living species in the web beyond the theoretical upper limit of 5 and all but 12 nodes beyond the maximal observed trophic level of 4.3. Parasites in these food webs occupy the highest trophic levels and therefore including outgoing links from parasites to their consumers will raise the trophic level of the free-living consumer. For example, some suspension feeding bivalves, such as the striped Venus clam *Chamelea gallina*, may consume a significant amount of trematode cercaria (Lafferty *et al.*, 2006b). This link considerably raises the striped Venus clam's trophic level (Figure 3.22) as the cercarial life stages are aggregated with the parasite's adult life stages, which occupy the highest trophic levels. The non-feeding cercarial life stages will not contribute the parasite's overall trophic level calculation, which is based on the average trophic level of the parasite's resources.

Therefore, in order for parasites to be accurately included in food web trophic level calculations, disaggregation of the parasites into ontogenetic niche shift nodes (Preston *et al.*, 2014) might be required.

Outgoing links from parasites to their consumers have been excluded from previous TL calculations on the basis that they may not be energetically significant links (McLaughlin, 2018), further parasites have also been excluded completely from trophic level calculations (Lafferty *et al.*, 2006a). However, this is a problem when trying to represent the parasites visually in a food web, which are often structured according to TL (Williams & Martinez, 2004). Including parasites in visual representations of a food web can shed light on their role and position in the web and elucidate their indirect impact on free-living species and the food web at large. A novel calculation for parasite trophic level, which incorporates the trophic level of their “basal” life stages, might also be a useful tool for informatively representing parasites with complex life histories in food web diagrams and assigning them to ecologically realistic trophic levels. In cases where the parasite also infests its consumer, a trophic loop is produced, which raises the parasite’s own trophic level and the mean trophic level of the food web as a whole. As was observed in the current case study, including parasites in their role as consumers and resources will increase the prevalence of mutual predation, or double link motifs, (see section 3.7.2) which produce the trophic loops (Lafferty *et al.*, 2006b) and inflate short-weighted trophic levels in turn (Williams & Martinez, 2004). In these ways, including species-specific parasite nodes in their roles as both consumers and resources into food webs can inflate short-weighted trophic levels beyond ecologically realistic bounds. Whilst disaggregating the parasite into separate life stage nodes will prevent much of the trophic level stretching, there are problems associated with the method. For example, disaggregating parasites can produce artificial changes in

food web measures of complexity, which produces error in the subsequent quantification of stability (see sections 4.2.1 & 4.2.4). It is also unclear whether the disaggregated, free-living, non-feeding life stage nodes of some parasites with complex life histories are accurately labelled as basal nodes. Whilst this appears to be appropriate, as they have no incoming links from their resources, they are neither dead nor autotrophic, and there is no indication in the food web as to where they obtain their energy. It has been suggested that a link from each parasite life stage to the subsequent node in its life cycle should be included if parasites are disaggregated ontogenetically (Huxham *et al.*, 1993; Sukhdeo, 2012). This type of link was excluded in the current case study on account of ecological realism, in that the previous life stage is not exactly consumed by its subsequent stage. If these links were included, the free-swimming, non-feeding life stages of some parasites in the current food web would not occupy the basal trophic level of 1, but the trophic level of the previous life stage + 1, weighted by the life stage's shortest chain length to a basal node (Williams & Martinez, 2004). Therefore, when links from those life stages to their direct predators are included, the predator's trophic level would also be increased and it would also then be considered an omnivorous species. This negates some of the method's ability to prevent trophic level stretching, though the extent of this would likely be mitigated by the typical collection of all cercaria, nauplii or another taxon's free-living life stages, into trophic species. Taking this into account, disaggregating parasites into ontogenetic niche shift nodes (Preston *et al.*, 2014) and excluding links between subsequent life stages appears to be the most reasonable method for calculating parasite short-weighted trophic levels in the fine sand communities of the German Bight.



#### 4.3.2 The new concept of trophic efficiency-weighted trophic levels

When species-specific parasite nodes were incorporated into the current case study food web, in their roles as both consumers and resources, trophic levels were inflated beyond the realms of ecological realism (Williams & Martinez, 2004), which is referred to here as trophic level “stretch” (see section 4.3.1). A novel method was developed here for weighting flow-based trophic levels by the mean trophic efficiency of each interaction in food webs that do not include information on link strength or the energetic significance of each interaction. Trophic efficiency is based on the 10 % rule (Lindeman, 1942), which states that 10 % of the total energy present in one trophic level of a food web will be transferred to the next.

The trophic efficiency-weighted trophic levels of species-specific parasite nodes included in their roles as consumers and resources, in the fine sand communities in the German Bight, conformed to ecologically reasonable boundaries set out by Williams & Martinez (2004). The greatest reductions in trophic level, compared to short-weighted trophic levels, were observed in suspension and interface feeders that had direct predative links to trematode cercaria, supporting the initial hypothesis that the influence of parasites in trophic level calculations would be less in trophic efficiency-weighted trophic levels. Using flow-based trophic levels, based on the trophic efficiency of each interaction in a food web; single, species-specific parasite nodes, and both their incoming and outgoing links, can be represented in food webs without resulting in trophic level stretch. Whether this represents a more ecologically realistic portrayal of parasites’ places in food webs is debateable. No evidence could be found that species in general will proportionally feed from each trophic level, according to the sum of its available energy. Amongst other factors, trophic level

feeding selection in omnivorous species has been linked to temperature (Yako *et al.*, 2011), assimilation efficiency (Gherardi *et al.*, 2004) and nutritional quality and the species' ability to recognise nutritional quality (Prado & Heck, 2011). These and other factors affecting prey selection in any species (Greene, 1986) make it impossible to state with confidence that species in the fine sand communities of the German Bight will feed proportionally from trophic levels according to trophic efficiency.

Implicit in the method is an assumption that parasites will gain more energy from their lower-trophic-level, intermediate hosts. This assumption has some support. At a population scale, the rate of successful transfer between hosts has been suggested to be 30 % in some parasites (McLaughlin, 2018). If the majority of individuals of a particular parasite species were lost between its consecutive life stages, it could result in a reduction of the adult population's ability to assimilate biomass. Furthermore, the limited literature on parasite biomass in ecosystems suggests that in some taxa, specifically in trematode helminths, the intermediate life stages are by far more abundant than their adult life stages (Kuris *et al.*, 2008). This suggests that those parasites would assimilate more energy from their lower-trophic-level, intermediate hosts, supporting one assumption of the trophic efficiency-weighted trophic levels. On the other hand, the temporal span of each life stage should be also be considered. Adults of the human-infesting trematode *Clonorchis sinensis* can persist for up to 30 years (Ortega, 2006). Longer spans of infection increase the proportion of an individual parasite's total lifetime energy that is obtained from that life stage's host.

Insufficient information on the timeframe of infection for each life stage in the current case study food web's parasites and an absence of data quantifying parasite biomass at the station means that we are unable to assess the validity of the assumption that parasites gain more energy from their lower-trophic-level hosts. This information would be extremely

beneficial for the reasons discussed above and in order to augment the current topology food web with an energetic component, allowing for more detailed and ecologically representative analyses. However, it is noted that this would require a substantial investment of time and resources.

On balance, trophic efficiency-weighted trophic levels provide a potential solution for the problem of trophic level stretching when parasites are included in topological food webs that implicitly lack information on the interaction strength and energetic contribution of each species and link in the web. However, some improvements are possible. For example, the trophic efficiency of each link here is based on the mean trophic level of the two interacting species (see section 2.5.2). It is possible that another measure would compare more suitably with the exponential graph that describes the loss in energy at each trophic level. The 10 % rule could also be adapted for the particular target habitat and scaled between 5 and 20 %, which have been put forward as more encompassing bounds of trophic efficiency (Trites, 2003).

## 4.4 The erroneous label of parasites as “top predators”

### 4.4.1 Species-specific parasite nodes

Top predators occupy the highest trophic levels in a food web and have no natural enemies.

As such, when parasites are included in their role as consumers only, they are necessarily modelled as top predators, as was the case in the current case study (Figure 3.15; 3.23).

However, nearly all parasite species will be concomitantly consumed by a predator of their host at some point in their life cycle. Therefore, including parasites in their role as resources will negate the label of top predator for most parasites. However, even when parasites are included in their roles as consumers and resources, they still occupy the highest trophic levels in the current case study food web. Traditionally, the highest trophic levels in a food web have been occupied by true top predators and therefore replacing them with parasites is a significant departure from the general comprehension of food web composition and function (Preston & Johnson, 2010). This can also be problematic as some free-swimming, non-feeding, parasite life stages will effectively occupy the highest trophic levels in a food web, significantly mis-representing their role as resources and can result in trophic level stretch, when direct links to their consumers are included (see section 4.3.1). Disaggregating parasites into separate, ontogenetic nodes will more accurately represent the position of each life stage in a food web diagram. However, increasing the number of parasite nodes will superficially alter topological metrics of complexity (see section 4.2.1) and overstate the importance of parasites on inferences pertaining to stability and persistence. Further, as was the case in the current food web, many parasite life stages will still occupy the highest trophic levels of the food web.

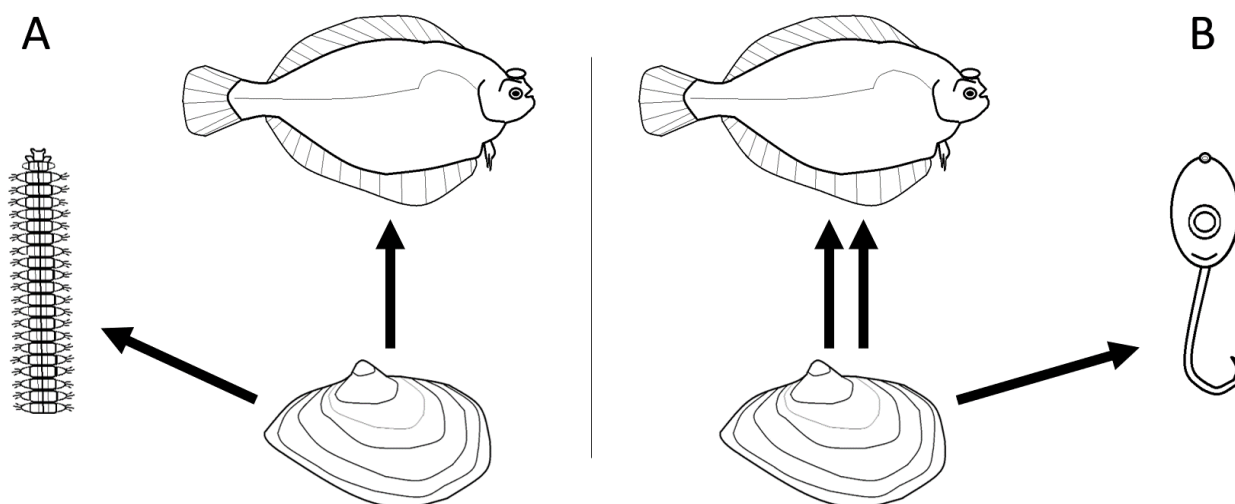
#### 4.4.2 Combined host-parasite nodes

Some parasites form a substantial proportion of the total biomass in ecosystems (Kuris *et al.*, 2008) whilst others do not, and most have never been quantified. However, even a parasite that does not comprise a significant contribution of the total biomass of an ecosystem can modify the flow of energy through it. Parasites can augment and redirect the flow of energy through the modification of their host's behaviour, augmenting or diminishing the energy that flows along a particular link between the host and another free-living species (Lafferty *et al.*, 2006b) and even creating or removing links between them (Mouritsen & Poulin, 2003). Following these observations, it has been suggested that parasites could be included in an "energy-modifier" food web (Sukhdeo, 2012). Parasites would there be incorporated into an energy flow food web, in which each link is quantified by the amount of energy that passes between the interacting consumer and resource. Parasites would not be included as discrete nodes, rather they would be combined into a single node with their host, alongside an uninfected version of the same host species. Only combined host-parasite nodes that differed from the uninfected host node in terms of the energetic strength of their interactions would remain in the energy-modifier web and the rest collapsed into a trophic species with the uninfected node.

Unfortunately, it was not possible to explore the viability of an energy-modifier web in the *Tellina fabula* community characteristic of fine sands in the German Bight because no information on the energetic strength of the links between free-living species was available, nor was it within the reach of this study to derive such information. Therefore, the energy modifier web is modified here to explore the usefulness of a novel "link modifier" web. As in the energy-modifier web, discrete parasite nodes were removed from the food web and

replaced with combined host-parasite nodes. This produced substantial increases in the number of nodes and links in the web, as every parasitic interaction now formed a new node. Similarly to the energy-modifier web however, any combined host-parasite node that did not differ from the uninfected node was reduced into a trophic species with the uninfected node. As such, only behaviour-changing parasites that add or remove a link from their host are represented in the link-modifier web.

No evidence of link modification was found in the fine sand communities of the German Bight food web. Therefore, a speculative case study was produced in order to test the model theoretically. New Zealand cockles (*Austrovenus stutchburyi* (W. Wood, 1828)) with encysted metacercariae of the trematode *Curtuteria australis* Allison 1979 are prevented from burrowing, by mechanical obstruction of the foot muscles and hydrostatic skeleton (Mouritsen & Poulin, 2003). Whether New Zealand cockles are actually suitable hosts for the trematode is disputed, since cysts rarely contained active, moving metacercariae, but often contained dead cercaria. However, the cysts do not appear to be destroyed by the bivalve's tissue and this could stimulate link modification in the cockle. Five, burrowing, bivalves in the current case study are similarly infected with the metacercariae of another trematode helminth, *Zoogonoides viviparus*. It is possible that the infestation of these bivalves by *Z. viviparus* similarly prevents the host from burrowing. It is speculated for this theoretical exercise that infaunal predators of those infected bivalves, such as the catworms *Nephtys* spp., are excluded because of the stranding and therefore all links from the bivalves to its infaunal predators may be removed (Figure 4.3).



**Figure 4.3:** Speculative exclusion of predatory links from bivalves to infaunal predators, included in the combined host-parasite node link modifier web FSd.Co and FSd.Co.X. Arrows = links pointing towards the consumer, showing in A links from the uninfected bivalve to swimming (represented by the dab) and infaunal (represented by the catworm) predators. In B, the infected bivalve and trematode metacercaria retain their link to the swimming predator but the infaunal predator has been excluded.

By constructing a combined, link-modifier food web, parasites were incorporated into the fine sand community food webs of the German Bight without being represented as top predators, without stretching trophic levels and without producing marked effects on the topology of the web. In a visual representation, the parasites occupy reasonable positions in the food web and true, free-living top predators occupy the highest trophic levels (Figure 3.30). However, many parasites are excluded from the link-modifier web, as demonstrated by the need for the speculative model explored here. Link modification is difficult to identify in real ecosystems and represents an extreme form of behaviour modification. As such it is unlikely to occur widely in real food webs.

Due to the stratification of host choice in most parasites with complex life histories, the combined node, link-modifier web essentially represents a disaggregated, ontogenetic model of parasite nodes. However, this excludes the free-living, non-feeding life stages of some parasites that form a significant food source for organisms in some ecosystems (Kuris

*et al.* 2008) as these life stages have no host. Another version of the link-modifier food web was constructed to include discrete, parasite nodes for free-living parasite life stages, such as trematode cercariae and copepod nauplii alongside the speculative, combined host-parasite nodes. Assuming that these free-living life stages amount to a significant resource for some species in the food web, as was found in the Carpinteria salt marshes (Kuris *et al.*, 2008), it is reasonable for these nodes to be included separately. Trematode cercaria and copepod nauplii were each reduced into taxon-specific trophic species and the effects of including these nodes on the topology and trophic levels of the food web were subsequently minor. In this way both the parasites' capacity to redirect energy through the food web, by the behavioural link modification of their hosts, and their ability to comprise a significant resource for other species in the network, in their free-living, non-feeding life stages are represented in the web. However, constructing a non-speculative version of this web would require a substantial amount of resources and time and would still perhaps rely on some degree of speculation. Many parasites would be excluded from the web due to likely rarity of link modification in real ecosystems, however this would be mitigated for by constructing a combined node energy-modifier food web. For the purposes of usefully representing parasites' ability to modify the flow of energy through food webs, combined host-parasite nodes appear to be a promising avenue of research.



#### 4.5 Limitations of the approach

The primary limitation of this study is the extent of the host dissections and parasite isolation and identification. Only two species from the BTC food web were dissected, both teleosts, which leaves a large portion of the food web not represented. Therefore, many of the parasites and associated links in the food web were inferred from the literature which spans a timeframe and habitat type quite different from the case study. For example, the nematode *Cucullanus heterochrous* was included on account that it had been recorded to infest plaice sampled in 1965 (Wickens & MacFarlane, 1974). This may have been compounded by the relative scarcity of parasite research, particularly into the identification of intermediate hosts. Intermediate hosts were necessarily inferred at a Class level, which may have resulted in an overestimation. Problems surrounding the identification of the parasites further limited the study, resulting in some damaged specimens and an imperfect identification. The sampling may not reflect seasonal dynamics of the parasite fauna. Furthermore, the selection criteria for including parasites in the whole station food web, setting a lower limit for prevalence, may have introduced a selection bias against some taxa or species that may have a significant impact on the food web as a whole. For example, whilst it did not meet the prevalence limit, the infection intensity of *Cryptocotyle lingua*, a species whose cercaria have been recorded to castrate and cause mortality in their first intermediate hosts (Huxham *et al.*, 1993), was very high and it may therefore have a significant effect on the flow of energy through the food web. This case study was restricted to topological analyses, due to the relative lack of research into parasite-host interaction strengths. In addition, the assessment of the latter in the FSd web was out of scope of this study. A scarcity of research into behaviour modification by parasites included in the current food web limited the applicability of the combined node, link-modifier food web and as such

that chapter was restricted to a speculative exploration of the model. Lastly, the focus of this study is restricted to the fine sand community station in the German Bight. Therefore, only the benthic realm is considered, however many parasites included in the food web have hosts that occur outside of the web (see section 4.2.1). As such it is important to consider the parasites at an ecosystem scale in order to accurately portray their position in a food web.

#### 4.6 Conclusions

This work contributes to understanding of how parasites can be representing in topological food webs without stretching trophic levels and without giving parasites the erroneous label of top predator. A food web describing the fine sand communities in the German Bight (Steger *et al.*, 2019) was expanded to include 12 parasite species, providing the first example of a fully submerged marine food web to include parasites and another case study for future food web analyses.

As hypothesised, including parasites into the fine sand communities of the German Bight produced generic changes in complexity, to be expected when any new species is included, and unique effects on the food webs structure. The proportion of double-link motifs describing mutual consumption was greater after parasites inclusion, which has previously been attributed to concomitant predation (Dunne *et al.*, 2013) but is here due primarily to direct predation on the free-living life stages of parasitic trematodes and copepods. It is therefore important for future studies to make a distinction between the role of concomitant predation and parasites role as resources on a whole when discussing the unique changes that they produce in trophic networks. Parasites appear to be relatively less

connected in the current case study food web, compared to free-living than in other food webs, which may be a result of its different habitat but is more likely a result of the networks small size, the inverse relationship between network size and complexity and the food webs highly connected free-living species. Habitat may play a more critical role here than in other food webs that include parasites as a result of its limitations, however. The fine sand communities of the German Bight are restricted to the benthic realm, however, many of its parasites' obligate hosts occur exclusively outside of the food webs parameters. This highlights the need for food webs to be examined at an ecosystem scale (Smith *et al.* 2007) in order to fully assess their composition and functioning. Due to the absence of some parasite species' intermediate hosts in the 90 % cumulative energy flow (Dannheim *et al.*, 2014) cut-off point, it may also be important for parasites to be included in a 97 % energy threshold web at the fine sand communities in the German Bight. This re-emphasizes the importance of scale and framing in food web analyses.

As hypothesized, trophic levels were stretched beyond ecologically realistic limits (Williams & Martinez, 2004) after parasites were included in as single, species-specific nodes in their role as both consumers and resources. This could be counteracted by disaggregating parasites into separate ontogenetic nodes, though that produced superficial changes in topology and overestimated parasites impact on inferences regarding stability. By calculating flow-based trophic levels, based on the 10 % rule of trophic efficiency (Lindeman, 1942), this stretch could be compensated for. Whilst this appears to be a broadly reasonable method for calculating flow-based trophic levels, without the challenge of collecting information on the interaction strength or energetic component of each link in the food web, it does come with its own complications. The method could be improved with more habitat or biological component-specific calculations of trophic efficiency (Trites, 2003) and

this could be a useful direction for study. Most parasites' erroneous label of "top predator" can be peeled off by including outgoing links to their direct and concomitant consumers in food webs. Calculating trophic efficiency-weighted trophic levels will not reduce their trophic level relative to that of free-living species in the web, however, disaggregating them into ontogenetic niche-shift nodes will provide more resolution on each life stages' position in the food web. Including them in combined nodes with their hosts will prevent parasites from erroneously occupying the food webs highest trophic levels, however it may also reduce many parasites into trophic species with their uninfected host, effectively removing those species from the network and require a substantial amount of resources.

Food webs remain important heuristic tools for the teaching and understanding of ecology, but they represent gross simplifications of the dynamic flows of energy and matter in ecosystems. Excluding parasites from them exacerbates this distortion. This work shows a range of methods by which parasites can be included and demonstrates the advantages of doing so. It also highlights the significant gaps in knowledge that remain, such as the very limited information on energetic flows mediated and modified by parasites. These must be priority areas for future research.

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S=number of nodes/species, L=number of links, Connectance=  $L/S^2$  in the LL.F, LL.X and  $L/S_f(S_f+S_p)$  in the LL.P.  $TL_{sw}$ =short-weighted trophic level.

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Parasites are disaggregated into ontogenetic niche shift nodes after Preston *et al.* (2014).

Short-weighted TL is indicated by the numbers on the vertical axis. The name of the heart urchin *Echinocardium cordatum* has been shortened to “*Echinoc. cordatum*” for space.

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