Universität Bremen

Effects of food quantity on growth and condition of *Trachurus* spp. larvae (horse mackerel) in the northern Benguela upwelling system.

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GENUS

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DECLARATION

Statement according to §10 (11) Allgemeiner Teil der Masterprüfungsordnungen der Universität Bremen vom 27. Oktober 2010:

Hereby I declare that I have written this Master's Thesis by my own and without any assistance from third parties. Furthermore, I confirm that no other sources and resources have been used than those indicated in the thesis itself and that all quotations are marked.

Bremen, _____ _____

Place and date Signature

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ABSTRACT

During the last decades, a tremendous decline of economically important fish stocks grabs attention of politics, fisheries and science. Recruitment success, identified as a major factor for a healthy and stable population, is generally caused by a high survival rate during the planktonic larval stage of fish. In order to draw conclusions about the effect of food availability on the condition of early life history stages of horse mackerel (*Trachurus* spp.) in the northern Benguela upwelling system, wild larvae and juveniles were caught during expedition with RV Meteor ME 103 (1/2) and utilized for feeding and starvation experiments. Food uptake, its digestion time, and proxies for larval growth and condition (CF, otolith increment readings, sRD) were investigated. The effect of prey quantity on growth and condition of *Trachurus* spp. was strongly influenced by developmental stage and the coupled foraging and digestion efficiency. Feeding, growth and condition of transformation larvae (16-20 mm) increased exponentially with prey density until a saturation point was reached at around 10 *Artemia* nauplii ml^{-1}. A further enhancement of food concentration resulted in a decline of condition proxies. In contrast, food scarcity for 65 hours resulted in a decline of larval condition (CF, sRD). However, the species-specific critical threshold level (sRD = 0.84) was by far not reached. Interestingly, an increase in weight and body size was only marginally affected by starvation. Our data stresses the importance of developmental stage, maternal effects and environmental condition to withstand periods of food scarcity in a rapidly changing environment such as the Benguela upwelling system. The gained knowledge contributes to a better understanding of the feeding ecology of early life history stages of *Trachurus* spp. It may help to develop new guidelines (*e.g.* TAC regulations) supporting a sustainable management of the adult fish stock.

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ABBREVIATIONS

ABF	Angola Benguela Front
BCLME	Benguela Current Large Marine Ecosystem
BGR	Biomass Growth Rate [mg/day]
BOFFFF	Big Old Fat Fecund Female Fish- hypothesis
CET	Central European Time
CF	morphometric Condition Factor
CTD	Conductivity, Temperature, Depth- measurement device
DEPC	Diethyldicarbonat ($C_6H_{10}O_5$)
dpc	days post catch [n]
dph	days post hatch [n]
e.g.	*exempli gratia* (Latin for ‘for example’)
EB	Ethidium bromide ($C_{21}H_{20}BrN_3$)
EBUE	Eastern Boundary Upwelling Ecosystems
EEZ	Exclusive Economic Zone
EHL	Early Life History
ESACW	Eastern South Atlantic Central Water
et al.	*et alii* (Latin for ‘and others’)
etc.	*et cetera* (Latin for ‘and other things’)
flex	flexion stage of fish larvae (5-7 mm)
GDM	Gutted Dry Mass [mg]

GENUS	Geochemistry and Ecology of the Namibia Upwelling System
Gi	Instantaneous Growth Rate [mm/day]
HCL	hydrogen chloride (HCL)
i.e.	*id est* (Latin abbreviation for ‘that is’ or ‘that means’)
juv	juvenile fish (21-40 mm)
MNo	oblique MultiNet
M. Sc.	Master of Science
MSY	Maximum Sustainable Yield
n	amount
n/d = n d^{-1}	*Artemia* nauplii per day
n/ml = n ml^{-1}	*Artemia* nauplii per ml
NatMIRC	National Marine Information and Research Centre
NatMIRC	National Marine Information and Research Centre, Swakopmund, Namibia
NBCE	Northern Benguela Current Ecosystem
ODV	Ocean Data View
PNR	Point-of-No-Return
postf	postflexion stage of fish larvae (8-15 mm)
pref	preflexion stage of fish larvae (3-4 mm)
rpm	revolutions per minute
RT	Ring Trawl
SACW	South Atlantic Central Water

SD	Standard Deviation
SDS	Sodium Dodecyl Sulphate ($NaC_{12}H_{25}SO_4$)
SET	Southeast Trade
SL	Standard Length [mm]
spp.	*species pluralis* (Latin abbreviation for ‘multiple species’)
sRD	standardized RNA/DNA ratio
SST	Sea Surface Temperature [°C]
st.	station
TAC	Total Allowable Catches
trans	transformation stage of fish larvae (16-20 mm)
UTC	Universal Time Coordinated
ZMT	Leibniz- Zentrum für Marine Tropenökologie (German abbreviation for ‘Centre for Tropical Marine Ecology’)

1 INTRODUCTION

1.1 Scientific background

The coastal upwelling ecosystem off Namibia supports large fish stocks. The most important species are costal pelagics such as horse mackerel (*Trachurus* sp.) (Fréon *et al.*, 2009) and demersal, gadoid species such as hake (*Merluccius* sp.). Environmental changes and heavy fishing pressure resulted in a tremendous decline or even collapse of economically important fish stocks during the last decades (Hutchings *et al.*, 2009; Perry *et al.*, 2010). Since the 1980s horse mackerels, although of relatively low value, were targeted by midwater trawling and dominated the fish landings in Namibia (Hutching *et al.*, 2009). Consequently, catches declined (Hutching *et al.*, 2009). Since the independency of Namibia in 1990, strictly enforced management tools (*e.g.* limited Total Allowable Catches (TAC)) have encouraged the regeneration of depleted stocks (Boyer *et al.*, 2000). In order to stabilize fish stocks, fisheries biologists focus on factors that determine the size of a cohort (Houde, 2008). Recruitment, which is defined as the number of fish of a year class reaching a certain age and adding to exploitable stock, is considered one key parameter (Miller *et al.*, 1988; Grote, 2010). The recruitment success is one major factor for a healthy and stable population. It is regulated by diverse processes during the early life stages and leads to a high variability in populations (Lasker, 1981; Miller *et al.*, 1988). The recovery potential of a collapsed stock is also determined by the intensity of the recruitment potential (Hilborn, 2010). Therefore, there is an urgent research need to examine and understand the underlying processes and parameters of such environment-stock-recruitment.

1.1.1 Recruitment

Recruitment variability can mainly be explained by tropho- and hydrodynamic processes, influencing early life stages from egg to juvenile phase (Houde, 1978; Lasker, 1981; Houde, 2008). The processes affect larval survival and mortality rates, thus determine recruitment strength and consequently the size of the adult population (Hutsching, 2000; Hutchings and Reynolds, 2004; Geist, 2013). May (1974) identified predation and starvation as major causes for mortality of larval fish. Although predation, as a top-down regulator, is thought to be the more important factor (Bailey and Houde, 1989; Bakun, 2010), some studies pointed out that starved larvae are more susceptible to predation than non-

starved fish, by diminishing escape responses and by extending vulnerable larval stage to predation (Buckley *et al.,* 1999; Rice *et al.,* 1987). Consequently, although predation may be a key regulator of mortality, starvation (a bottom-up regulator) can be considered a contributing factor. A separation of the two interrelated components of mortality seems to be challenging (Miller *et al.,* 1988).

Stage duration of fish larvae, as a life-history character, is critical for the recruitment success. The faster the larvae overcome the vulnerable early life history stage due to high growth rates, the more reduced is the risk of mortality by starvation and predation (Houde, 1978; Bailey and Houde, 1989; Leggett and Deblois, 1994; Houde, 2008). An increase in body size implies more effective foraging and escape from potential risks by enhanced swimming capacity (Houde 1978, 2008). As proposed in the growth-mortality conceptual framework (Anderson, 1988), any factor (*e.g.* prey availability (Cushing, 1975)) modifying the growth rate of larvae cohort is expected to generate recruitment variability. Several hypotheses were developed to explain the interaction of (a-)biotic factors and reduction of larval growth as a consequence of a net decrease in feeding success or reduction in the energy allocation to growth even if food intake remains constant (Jobling, 1993; Buckley and Durbin, 2006).

The "Ocean Triad Hypothesis" (Bakun, 1996) states that an advantageous recruitment habitat is defined by three physical processes: a) enrichment (upwelling, mixing), b) concentration (convergence, fronts, water column stability) and c) retention mechanisms preventing offshore transport. Additionally, environmental factors, such as variations in temperature, turbulence or currents, should not be underestimated in terms of larval survival (Houde, 2008). For instance, temperature affects processes such as: time of spawning, larval feeding rates and success, growth, distribution, natural mortality and swimming activity (Pörtner *et al.,* 2001; Geist, 2013). In contrast, the "Match-Mismatch Hypothesis" (Cushing, 1990) deals with biotic factors of bottom-up regulation. An overlap of spawning period of fish and period of high prey abundance are a prerequisite for recruitment success and hence a stable population. Limited food resources may lead to competition for prey and negatively influence growth rates. Once larvae do not find adequate food sources within a species-specific time frame, larvae are in a stage termed "point-of-no-return" (PNR) (Blaxter and Hempel, 1963). Starved larvae do not sink out of the water column, but become neutrally buoyant and less active (Ehrlich *et al.,* 1976). Even if starving fish are provided

with adequate food, they can not contribute to recruitment success of the population (Johnson and Dropkin, 1994). The PNR differs among species, and it increases with age because of greater body reserves (Blaxter, 1988). Consequently, mismatch of fish larvae and food availability is a principal cause of high larval mortality and poor year class strength (Hjort, 1914; Hunter, 1976; Clemmesen and Doan, 1996). Hjort (1914) proposed that recruitment was determined during the period of first feeding when yolk-sac larvae are forced to feed exogenous. However, the work of Bradford and Cabana (1997) and Myers and Cadigan (1993) indicated that in addition to first-feeding larvae, late larvae and metamorphose stages are also vulnerable to starvation; hence having a profound impact on shaping year-class strength as well (Cushing, 1996). Besides the bottom-up and top-down regulation, recruitment success is influenced by adult fish via quantity and quality of their offspring. "The Big Old Fat Fecund Female Fish (BOFFFF)" hypothesis focuses on maternal effects, resulting in a high variance in the ability to withstand short-term food deprivation (May, 1974). Hart and Werner (1987) as well as Hunter and Kimbrell (1981) suggested that large eggs contain more energy reserves enabling larvae to withstand deleterious effects of short term food deprivation better. Even differences among individuals within a single stock in terms of response to starvation were observed (Navarro and Sargent, 1992).
However, no single hypothesis explains the recruitment success and variability of a fish stock, since multiple factors and mechanisms act together causing variances in the survival of early life stages (Grote, 2010).

1.1.2 Research area

There are four major eastern boundary upwelling ecosystems (EBUE) in the world. The Benguela system is the major eastern boundary upwelling system in the South Atlantic Ocean (Hutchings *et al.,* 2009). It is located off the west coast of the African continent and extends from the Angola Benguela Front (ABF) (17°S) to Cape of Good Hope (35°) (Figure 1). The tropical Angola Basin in the north and the southerly flowing Angola current as well as the Agulhas Current in the south enclose the Benguela system by warm water currents, which is a unique characteristic (Shelton *et al.,* 1985). Hence, the Benguela upwelling area exhibits strong thermal fronts (Boyer *et al.,* 2000). The system is separated by strong perennial upwelling of Lüderitz (27 ± 28°S) into a northern and a southern Benguela upwelling system (Shelton *et al.,* 1985). The Lüderitz cell is one of five major

upwelling cells existing in the Benguela system and at the same time the strongest worldwide. Lüderitz upwelled, turbulent water with little vertical stratification, moves northwestwards and acts as a semi-permanent environmental barrier to the longshore transport of pelagic fish eggs as well as larvae (O'Toole, 1977; Boyer *et al.,* 2000).

The bathymetry of the targeted Northern Benguela Current Ecosystem (NBCE) is characterized by a broad shelf around Walvis Bay (23-21°S) and Walvis Ridge (20°S). Additionally, a narrow shelf and a steep slope at the Kunene River Mouth (17.5°S) can be found further north (Geist, 2013). A distinct seasonal variability of South Atlantic central water (SACW) ascertained over the Namibian shelf is regulated by basin scale dynamics (Mohrholz *et al.,* 2008). During the austral summer hypoxic, nutrient rich SACW is transported by southward undercurrents into the northern Benguela, mainly on the shelf, whereas during the upwelling season the oxygen rich Eastern South Atlantic central water (ESACW) moves northward and contributes in a large extent to the water mass composition (Mohrholz *et al.,* 2008). In general, the wind-driven upwelling occurs year-round with maximum intensities in winter and early spring (June-October), and quiescent periods during summer (January-April) (Shelton *et al.,* 1985; Bartholomae and van der Plas, 2007). Nevertheless, upwelling in the northern Benguela current ecosystem (NBCE) is far from uniform and exhibits tremendous spatio-temporal variabilities. High levels of short-term upwelling variability, which are superimposed onto seasonal and inter-annual trends, are driven by diurnal and "event" scale pulsing (Boyer *et al.,* 2000). Seasonal variation in upwelling is greatest off northern and central Namibia due to latitudinal differences (Boyer *et al.,* 2000).

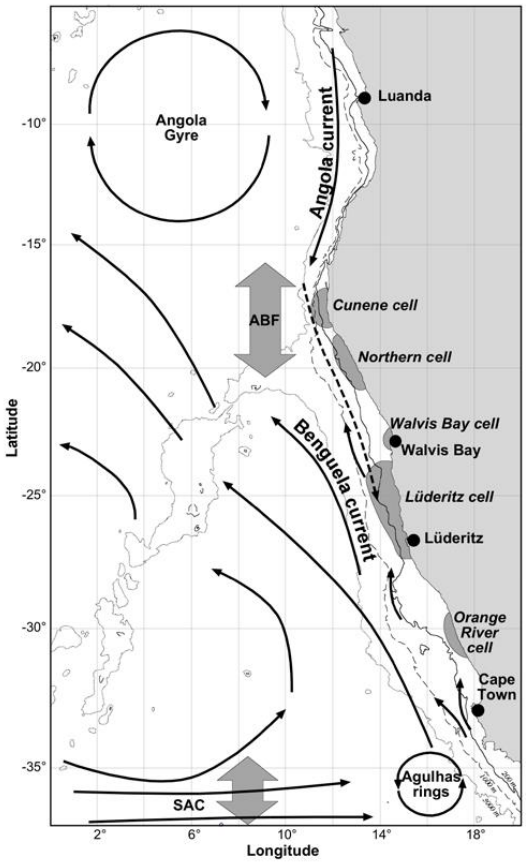

Figure 1: Map of the Benguela Current Region.
Arrows indicate ocean currents. Important cities and the five major upwelling cells (grey areas near the coastline) are shown. Abbreviations: SAC = South Atlantic Current, ABF = Angola Benguela Front (Ekau *et al.,* 2010)

The pre- dominantly equatorward flowing system, mainly driven by Southeast Trade (SET) winds (Ekman-transport) (Defant, 1936), are the driving force behind the strong coastal upwelling and promotes primary production, which in turn contributes to a highly productive coastal ecosystem with a high zooplankton production and small pelagics' fishery (Boyer *et al.*, 2000; Skogen, 2005). However, during the last decades hydrographical changes have been noticed which had tremendous impact on the ecology of the Benguela upwelling system. Although the extent of the annual southward intrusion of warm Angolan water into the northern Benguela varies between years, an increased frequency of deeper southward penetrations was observed in the recent past (Bartholomae and van der Plas, 2007). These thermal anomalies were recorded four times in the Benguela upwelling system: 1934, 1963, 1984 and 1995 (Gammelsrød *et al.,* 1998; Boyer *et al.,* 2000; Bartholomae and van der Plas, 2007). The so called Benguela Niño causes anomalous atmospheric conditions in the western tropical Atlantic (Boyer *et al.,* 2000). Intrusions of waters of the Angola Current are extraordinarily strong near the shore, lasting from austral summer to winter and resulting in the advection of warm, highly saline water as far as 25°S (Shannon *et al.,* 1986; Boyer *et al.,* 2000; Lutjeharms *et al.,* 2001). This contributes not only to a tremendous increase in water temperature off the Namibian coast (1963 event: increase of 2-4 °C), but also to considerable modifications of the biological productivity and causes large-scale death of organisms in the coastal zone (Lutjeharms *et al.,* 2001).

Furthermore, it can be expected that climate change affects the physical processes and hence the biochemical and ecological environment of the Benguela upwelling system. The

increased wind stress over the South Atlantic Ocean will cause an advection of cold upwelled water further offshore (Lutjeharms *et al.,* 2001). However, the intensification of the South Atlantic Anticyclone associated with increased atmospheric subsidence, enhanced insolation, less clouds and higher temperature will counteract the offshore transport of cooler water by warming of the surface water (Lutjeharms *et al.,* 2001). The upwelling cells may intensify with persistently greater wind stress, but there will be a limit of the minimum water temperature of a cell (Lutjeharms *et al.,* 2001). The depth from which upwelled water derives depends on the depth of the continental shelf edge, which consequently imposes a limited temperature likely to be reached in an upwelling cell (Lutjeharms *et al.,* 2001). It is uncertain which of the two processes (surface warming *versus* enhanced upwelling) will be permanently predominant. But both wind and sea surface temperature (SST) data of recent studies (Bailey *et al.,* 2009; Hutchings *et al.,* 2009) revealed an increase of quiescent upwelling periods in the NBCE during the last two decades.

In Addition to the hydrodynamic condition of the Benguela upwelling system, trophodynamic processes need to be considered in order to outline the environmental condition of early life history stages of fish in this system. The ratio of new and regenerated primary production is relatively low compared to other EBUE, indicating that the food web is supplied only with a small, available proportion of the total production (Lutjeharms *et al.,* 2001). Consequently, the system is vulnerable to reduced nutrient supply during periods of quiescent upwelling (Lutjeharms *et al.,* 2001). The zooplankton community of the tropical Angolan waters north of the ABF, the northern and southern Benguela system can be clearly separated (Shannon, 1985; John *et al.,* 2004; Lett *et al.,* 2007). Copepods are the dominant mesozooplankton group in terms of abundance and biomass (Timonin *et al.,* 1992) followed by euphausiids (Olivar and Barangé, 1990). Especially, the order Calanoida is richer in species and more diverse in terms of body size and ecological characteristics than orders such as Cyclopoida, Poecilostomatoida and Harpacticoida (Loick *et al.,* 2005; Schukat, 2012). However, Verheye and Kreiner (2009) observed positive anomalies of small cyclopoids (e.g. *Oithona* sp.) in their densities parallel to a warming of the system during the last two decades.

In conclusion, not only changes in physical processes, driven by climate change or by anomalies, affect the habitat of fish population, but also biotic variables (*e.g.* zooplankton availability) contribute to the survival of fish population in the Benguela upwelling system.

1.1.3 Biology of *Trachurus* spp.

The biology of *Trachurus* (horse mackerel, order Perciformes) has been examined over the last decades; nonetheless important gaps in terms of feeding ecology still exist. Horse mackerels are widely distributed in the marine environment. The geographical distribution of *Trachurus* (Linnaeus, 1758) includes the North-eastern Atlantic from Iceland to Senegal, the Mediterranean Sea, Marmara Seas and Black Sea (FAO, URL 1). Additionally, *Trachurus* is an important component of the Benguela ecosystem (Crawford *et al.,* 1987) (Figure 2). Taxonomical research confirmed that two distinct species of horse mackerel occur in Namibian and Angolan waters namely the Cape horse mackerel (*Trachurus capensis*, Castelnau, 1861) and the Cunene horse mackerel (*Trachurus trecae*, Cadenat, 1949). *T. capensis* larvae are widely distributed; being found in cold water masses (< 20 °C) from the Lüderitz upwelling cell to southern Angola, but mainly occur between 17°S and 21°S (Hecht, 1990; Naish, 1990). *T. trecae* larvae prefer warmer water (> 20 °C) and occur especially in northern Namibia and southern Angola. The distribution of these two species overlaps between 16°S and 17°S, depending on the position where the cold (Benguela Current) and warm (Angola Current) water masses meet. Morphologically both species are very similar and are not distinguishable by the outer appearance (Boyer *et al.,* 2000).

In general, larval shape can be used as an indicator for the different growth strategies of fish larvae (Froese 1990). Estensoro (2006) and Froese (1990) classified the shape of *Trachurus* as tadpole-like with a short body and large head. Hunter and Kimbrell (1981) characterized mackerel larvae as fast growing and efficiently metabolizing larvae which have high food requirements. Larval development is rapid resulting in high energetic demands, but simultaneously enabling access to a broader food spectrum. *Trachurus* larvae exhibit a hatching length of around 2 mm (Ahlstrom and Ball, 1954). Notochord flexion of *Trachurus* spp. takes place at around 6 mm (Díaz *et al.,* 2009), followed by fin development starting at around 7-10 mm (Haigh, 1972; Artüz, 2000). High feeding incidence is associated with a looped gut, reducing the amount of regurgitation at catch (Arthur, 1976). In *T. de-*

clivis the gut loops at about 3.5 mm SL (standard length), which is approximately the size at which the larvae begin to feed (Young and Davis, 1992). *Trachurus* larvae benefit from their fast development compared to other slow-growing specimen. In fact, Perciformes larvae reach developmental milestones at smaller sizes than clupeoids (Díaz *et al.*, 2009). The greater swimming ability of horse mackerel results in a higher efficiency in capturing prey and in escaping from predators compared to clupeoid larvae of the same body size. High feeding indices contributes to a high daily biomass growth rate and good nutritional condition (Geist, 2013). Therefore, larval *Trachurus* offer much greater predation avoidance ability than clupeoid larvae (Lenarz, 1973). Additionally, horse mackerel larvae exhibit big mouth gaps, enabling to prey on a broader food spectrum and to consume large, energetically profitable prey items (Díaz *et al.*, 2009).

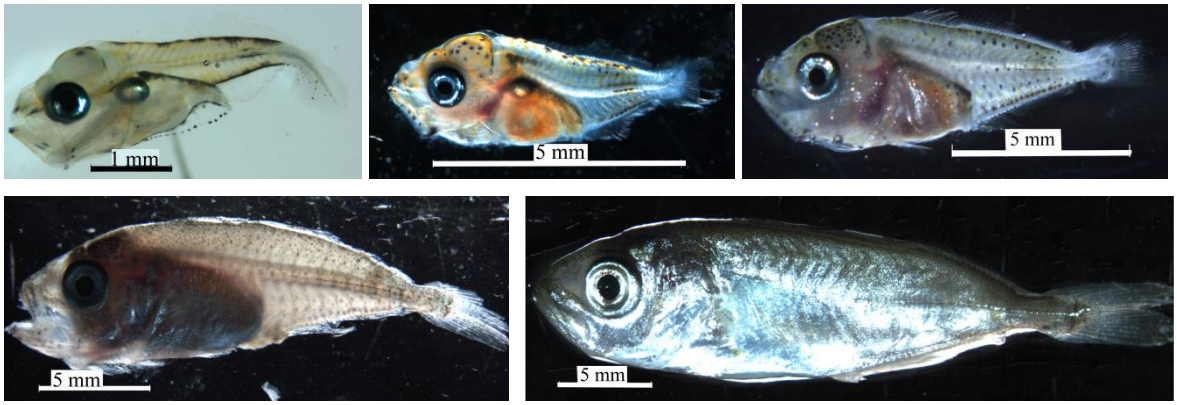

Figure 2: Early larval stages of *Trachurus* spp. caught in the northern Benguela upwelling system.
a) 3 mm larvae b) 6 mm larvae c) 10 mm larvae d) 19 mm larvae e) 30 mm juvenile. Images were taken by Dr. Geist.

Larval *Trachurus* prey on a wide range of copepod species varying in size and stage, including small *Oithona* sp. and *Oncaea* sp. (Westhaus-Ekau, 1988; Young and Davis, 1992; Pillar and Barange, 1998; Robert *et al.*, 2009; Sassa and Tsukamoto, 2012; Geist, 2013). Horse mackerel can be classified as an opportunistic daytime feeder, adapting to prevailing food availability (Westhaus-Ekau, 1988; Young and Davis, 1992). Nonetheless, a dietary shift during the early ontogeny of *Trachurus* towards larger prey items combined with higher trophic levels takes place (Westhaus-Ekau, 1988; Diaz *et al.*, 2009). This indicates a change in their position in the planktonic food web (Diaz *et al.*, 2009; Geist, 2013). Early life history traits suggest a good adaptation of *Trachurus* larvae to unstable environmental condition (*e.g.* upwelling system). The tolerance of wide temperature ranges (*e.g.* thermal window: 12.8 °C-25.7 °C; O'Toole, 1977; Sassa and Konishi, 2006; Geist, 2013), as well

as hypoxic conditions, characterize the larvae of *Trachurus* as eurypotent. Traits of early life history of *T. capensis* enable the larvae to prolong retention time in coastal regions with good food supply, but also deal with periods of food scarcity. Consequently, survival and recruitment success of *Trachurus* larvae increase (Geist, 2013).

Trachurus is not only an important food source for fish (*e.g.* hake) and marine mammals (*e.g.* seal) (Diaz *et al.,* 2009), but also essential for fisheries off the coast of South-West Africa (*T. capensis*), North Atlantic (*T. capensis*), New Zealand (*T. declivis*), Chile (*T. murphyi*) and Japan (Xie *et al.,* 2005). Since 1975, *T. capensis* has been the major contributor to landings made within the Exclusive Economic Zone (EEZ) of Namibia. In the 1980's the catches exceeded 600 000 tons per annum (Figure 3) (FAO, URL 2). It is assumed that the increasing abundance of horse mackerel was associated with the collapse of the pilchard (*Sardinops sagax*) stock at end of the 1960's and also the decline of the hake (*Merluccius capensis*) stock over the past two decades (FAO, URL 2). In 2000, the most northern representative of the trachurid family, *T. capensis* (Linnaeus, 1758) has ranked second in catches (275 000 tons, > 10 % of total catch) (Abaunza *et al.,* 2003). Nevertheless, landings decreased between 2005 and 2008. According to research surveys, the reduction was caused by a decline in both, biomass and an overall reduction in size of captured fish, indicating that the fishery was under pressure (FAO, URL 2). In 2010, global capture production exceeded 250 000 tons. The most recent increase in abundance proxies indicates a good condition of the *Trachurus* stock. According to the 'State of stock Report 2012' by the Benguela Current Large Marine Ecosystem-project (BCLME, URL 3), the stock is presently estimated to be around the maximum sustainable yield (MSY) level of between 280 000-300 000 tons. Caught *Trachurus* are mainly used as fish meal and fish oil in aquaculture and as fresh, dried salted, smoked and canned food fish for the Namibian and South African market (FAO, URL 4). In order to stabilize the catch and to establish more effective and sustainable fishery management tools, it is necessary to understand the early life history and recruitment processes of *Trachurus* as an economically important target species in the Benguela system. In addition, behavior and availability of horse mackerel affects not only the commercial horse mackerel fisheries but also other sectors such as hake fisheries (FAO, URL 4).

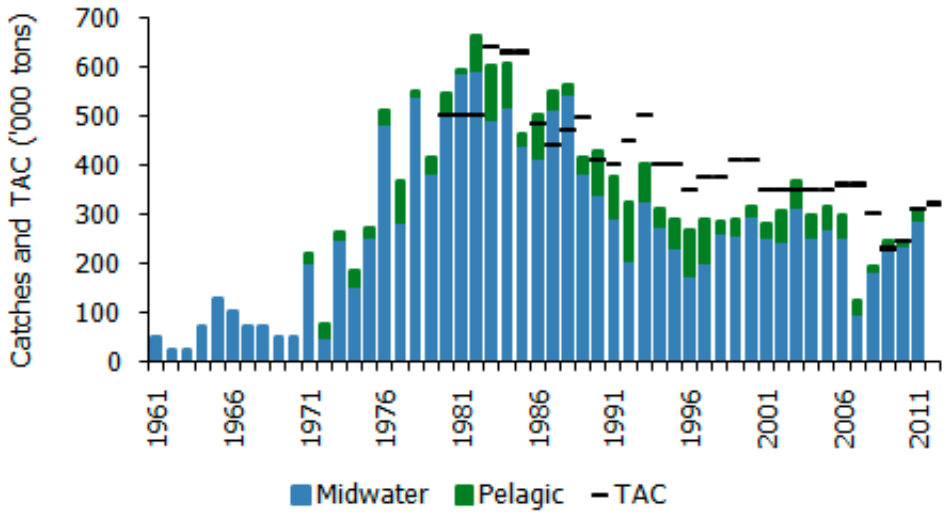

Figure 3: Variability in annual landings of *Trachurus capensis* in Namibia (1971-2011).
Landings of horse mackerel were taken by the pelagic and midwater fleets. Total Allowable Catches (TAC) is indicated as black line (BCLME State of stock Report 2012, URL 3).

1.2 State of the art and justification of the research project

As outlined above, processes during the early life history (ELH) stages of fish (egg, larva, and juvenile) were identified as key regulative mechanisms for survival and recruitment success (van der Lingen *et al.*, 2006; Ekau *et al.*, 2010). Early life stages, offering a planktonic lifestyle, are very sensitive to environmental changes (biotic and abiotic) due to their restricted movement potential and their fragile morphology (Geist, 2013). Recruitment success is influenced by various factors such as prey composition and availability (Cushing, 1975). Nutritional condition and a rapid growth rate, essential to overcome the vulnerable larval phase, depend on prey quantity and quality (Cushing, 1975). ELH is considered a potential bottleneck for population development. However, just a few studies (*e.g.* Geist, 2013) dealt with the condition of early life history of pelagic species, such as *Trachurus* spp., in spite of being an economically important target species in the Benguela system. Most studies deal with general investigations in order to gain better knowledge about the underlying processes of recruitment and early life history traits, influencing the survival of fish larvae. Since nutrition is a key stone regarding larval survival, several studies (MacKenzie *et al.*, 1990; Ferron and Leggett, 1994; Grote, 2010; Geist, 2013) concentrate on ingestion, growth and nutritional condition of fish larvae.

MacKenzie *et al.* (1990) estimated the ingestion rates of different fish larvae in the wild and compared the generated model-results to laboratory derived values. The literature-model based study revealed that body size is a powerful intra-specific indicator of ingestion rates (MacKenzie *et al.,* 1990). Life-history traits as well as a major part of the ecology of the fish depend on the larval body size (Miller *et al.,* 1988). MacKenzie *et al.* (1990) assumed that environmental changes (*e.g.* temperature) and/or behaviour affecting local distribution of larvae and their prey, are expected to have a dramatic effect on larval feeding rates in the marine environment (MacKenzie *et al.,* 1990). Additionally, evacuation rates can be adduced to draw conclusions regarding fish feeding rates, energy budgets, and the trophic dynamics of aquatic systems (Sweka *et al.,* 2004; Kawaguchi *et al.,* 2007). Several factors, of both biological and physical nature, influence the evacuation rate in fish, but temperature and food type seemed to have the greatest impact (Westhaus-Ekau, 1988; Pillar and Barange, 1998). Changes in feeding rates and the processing of the consumed food generally accompany modifications in condition and growth of the fish larvae.

The determination of growth and age based on back calculations from growth increments readings of sagittal otoliths is a common research procedure and enables investigations about the life history of larval fish (Geist, 2013). Previous studies validated a daily formation on growth increments of *Trachurus* larvae (Xie *et al.,* 2005). Readings of sagittal otoliths indirectly reveal information about nutritional condition of larvae, since fish larvae invest a surplus of energy mainly in somatic growth (Houde, 1978). In the past, otolith increment width (= larval growth rate) has been used by different investigators as an indicator for variations in certain environmental factors, including temperature, salinity, light, upwelling intensity and oxygen deficiency (Morales-Nin, 1987; Folkvord *et al.,* 2004; ICES, 2004). Additionally, several scientist (Checkley, 1984; Wright and Martin, 1985; Morales-Nin and Aldebert, 1997; Shoji and Tanaka, 2004) investigated growth rate based on otolith readings in relation to food availability and confirmed their dependency.

Nutritional condition of larvae, which is a measure of their ability to withstand starvation, greatly affects the recruitment success of the fish larvae (Ehrlich *et al.,* 1976). Hence, an assessment of larval nutritional condition is clearly of critical importance. Several scientists suggested that differences in larval body form between fed and starved larvae can be consulted for identification of the nutritional status of the larvae (Theilacker, 1978). Hence,

a morphometric condition factor was developed. It is considered an important biological parameter for fishes, from which the condition of stocks' health of fish populations can be deduced (Bagenal and Tesch, 1978). Nucleic acid analysis, as a proxy for nutritional condition and protein growth potential of the near past, has been used for more than two decades (Meyer *et al.*, 2012). The nucleic acid determination has undergone a great development in recent years (Ferron and Leggett, 1994; ICES, 2004). The amount of DNA is considered to be constant in somatic tissues, whereas the amount of RNA in cells is directly proportional to the protein synthesis rate (Clemmesen, 1994). Hence, the RNA/DNA ratio is an eco-physiological index of the metabolic rate in cells and consequently has been proven to be a useful indicator of nutritional condition and growth rate in fish larvae (Buckley *et al.*, 1984; Clemmesen, 1994; Westerman and Holt, 1994; ICES, 2004; Chícharo and Chícharo, 2008).

Well-fed larvae and fast growing larvae offer higher RNA/DNA ratios and a wider daily increment deposition than starving larvae (Ramírez *et al.*, 2001; ICES, 2004). A joint investigation of larval otolith microstructure and biochemical condition indices is a promising methodical approach to research processes affecting recruitment variability. So far, only a few studies conducted RNA/DNA ratio as well as growth rates analyses in the same larvae (*e.g.* haddock *Melanogrammus aeglefinus* (Caldarone, 2005), cod *Gadus morhua* (Clemmesen and Doan, 1996) and hakes *Merluccius paradoxus* and *Merluccius capensis* (Grote, 2010)). Several studies of different fish species successfully related RNA/DNA ratios with food density and somatic growth (Clemmesen, 1994; ICES, 2004). However, Grote (2010), who investigated the early life strategy and the factors affecting recruitment of cape hakes (*Merluccius paradoxus* and *Merluccius capensis*) in the Southern Benguela upwelling system off South Africa, did not find a correlation between RNA/DNA ratio and growth rate. Grote (2010) concluded that no single factor is responsible for survival of fish larvae, a combination of factors seem to be essential to increase recruitment success. Besides, the mentioned growth and condition indices reveal different information on the physiological status of individual larvae, recommending a combination of all methods to gain a detailed insight into the nutritional condition of larvae (Ferron and Leggett, 1994).

Throughout the 20th century, the specific contribution of food quantity to variability in larval growth, survival and how this may be translated into fisheries recruitment has been

debated, but without resolution (Buckley *et al.*, 2004). In particular, estimation of prey availability in nature remains problematic as it encompasses many diverse factors, such as the density, quality, distribution and vulnerability of planktonic prey, larval feeding behaviour, and physical factors including light and turbulence levels (Dower *et al.*, 1998; Fiksen and MacKenzie, 2002). There is an urgent need to address questions concerning the effect of food density, food scarcity and surplus on growth and condition in the early life history of larvae using different approaches. Additionally, as previously mentioned, depending on the degree of mismatch between fish larvae and prey availability, food-deprived larvae may die or weakened larvae may be more vulnerable to predation (Skajaa *et al.*, 2004). Therefore, there is an essential need not only to assess the degree of food limitation in the sea, but also to understand how the physiological process of starvation affects early life stages to gain a mechanistic understanding of the role that prey deprivation plays in the recruitment process.

The present study addresses these open questions. The novelty of this project is that the food uptake, digestion and the underlying biochemical processes of *Trachurus* spp. are in focus. The effect of food quantity (from food scarcity to elevated food concentrations) on growth and nutritional condition of *Trachurus* spp. larvae is determined by means of different methods (*e.g.* ingestion and gastric evacuation rate determination, sagittal growth readings, RNA/DNA analyses). Almost all methods are conducted on the same *Trachurus* specimen, so a detailed data set is generated. To my knowledge based on recent literature, these important parameters regarding early life history and the recruitment success of horse mackerel as an economical important fish species, have not been determined yet. The gained knowledge contributes to a better understanding of the feeding ecology of *Trachurus* spp., its recruitment success and population dynamics over relatively short periods of time. This short time scale is important due to the dynamic nature of the marine environment and the rapid response of fish larvae to environmental changes. The generated results can also be incorporated in ecosystem models. Such models lead to a better understanding of the marine environment and natural processes which control the population dynamics of fish. In future, new management tools (*e.g.* TAC regulations) for the exploited environment can be developed based on the data gained here.

1.3 Objectives

This study is part of the GENUS project (Geochemistry and Ecology of the Namibia Upwelling System), and different research questions regarding the upwelling system off Namibia are addressed. GENUS aims to examine and model relationships between climate change, biogeochemical cycles, and ecosystem structure in a large marine ecosystem: the upwelling system of the northern Benguela/Namibian Coast (GENUS, URL 5). The present study aims to gain knowledge about the early life history and the nutritional factors influencing the recruitment success of *Trachurus* spp. in the Benguela upwelling system off Namibia. The focus lies on the effects of food quantity as well as starvation on growth rates and nutritional condition of *Trachurus* spp. larvae. Besides, food uptake and processing of food are investigated. Almost all methods are conducted on the same *Trachurus* specimen, so a detailed data set is generated. The results can be consulted to develop new realistic ecosystem models helping to understand complex processes in the marine environment. This work in particular addresses two objectives which are summarized below:

Objective 1

Prey quantity is used as a proxy to estimate mortality and assess recruitment success. *Trachurus* spp. was selected as a model organism in this study. Morphological (increment readings of otoliths, morphometric condition factor) and biochemical (RNA/DNA) characteristics are used to test the following two hypotheses:

Hypothesis 1: Ingestion rate of *Trachurus* larvae increases proportionally to food quantity up to a saturation point.

Hypothesis 2: High prey quantity correlates positively with growth and nutritional condition of *Trachurus* spp. up to a saturation point. A prey density, at which larvae exhibit the best condition, can be determined.

Objective 2

Incidences of starvation stress are detected by morphological and biochemical analyses such as decreasing morphometric condition factor, growth rates and RNA/DNA ratios. *Trachurus* larvae were used in experiments in order to estimate critical durations of starvation times. Above mentioned condition parameter are tested to verify following research hypothesis:

Hypothesis 3: Starvation stress negatively affects the nutritional condition and growth rates, reflected first in stagnation and later a decrease in the condition parameters.

2 MATERIALS AND METHODS

2.1 Sampling

Fish larvae and juveniles for experiments were caught during an expedition on the research vessel Meteor cruise ME 103 from December 25th 2013 until February 21st 2014. The expedition was separated into two parts: ME 103-1 and ME 103-2. One aim of ME 103 was to collect live larvae for feeding and starvation experiments in order to investigate feeding ecology of horse mackerel larvae and juveniles (*Trachurus* spp.). The sampling was conducted in the Benguela upwelling system from Kunene river at the border to Angola (17° 15.00' S/ 11° 10.01' E) down to the Lüderitz upwelling cell (28° 38.17' S/ 15° 59.98' E) (Figure 4). Living *Trachurus* were caught at 14 out of 58 stations (appendix, A-Table 1). Collection of living *Trachurus* specimen was particularly successful at stations located north of 23°S. Temperature data obtained from CTD rosette were available to most of the ichthyonplankton hauls. In case CTD-data did not exist, required temperature was taken from the closest station offering the same hydrological conditions.

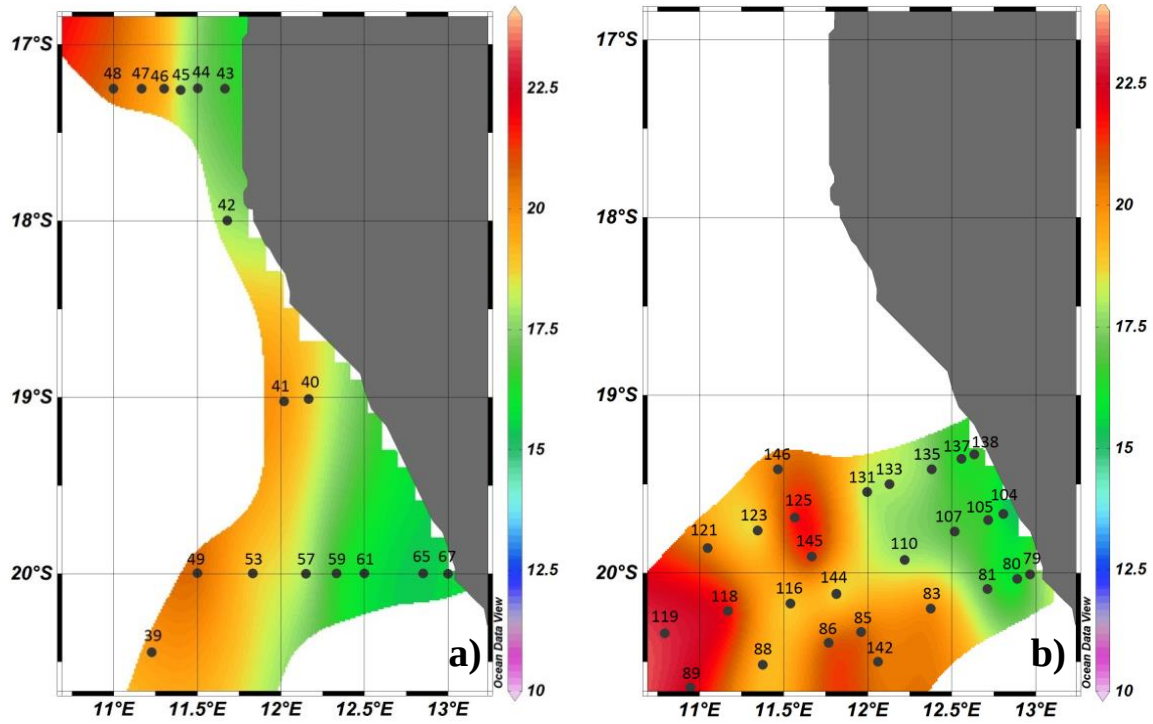

Figure 4: Map of sampling stations in the northern Benguela upwelling region.

a) ME 103-1 b) ME 103-2. Only stations between 20.5°S and 17°S are displayed. At stations further south, no live *Trachurus* spp. larvae were caught. The color code represents the different temperatures [°C] at 20 m depth.

Two different net types were deployed to catch live *Trachurus* spp.: an obliquely towed Multinet (HYDROBIOS, type Midi: 0.25 m^2 mouth area, mesh size of 500 µm) (Figure 5 a) and a Ring Trawl (RT) (diameter of mouth area: 1.6 m, mesh size of 1000 µm) (Figure 5 b). The Multinet was towed at a ship speed of 1.5 knots and the RT was towed at 0.5-1 knots over ground. The RT was mainly lowered down to 20-30 m of the water column due to the assumption that over 50% of *Trachurus* larvae concentrate in the top 20 m (Geist, 2013). Furthermore, RT tow duration was short in order to increase the chance of catching fish larvae alive.

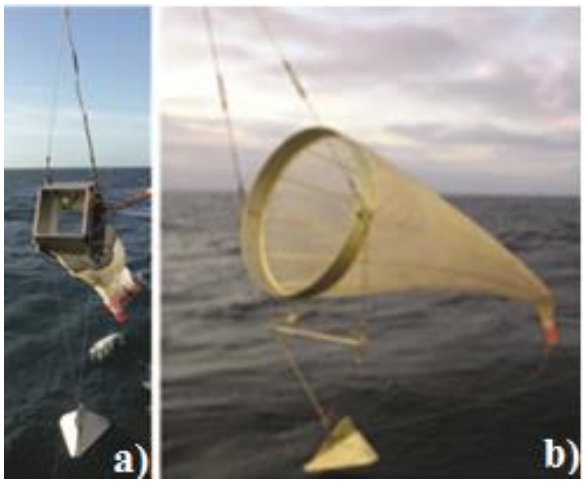

Figure 5: Different net types which were used to sample living *Trachurus* larvae.
a) obliquely towed Multinet (HYDROBIOS, type Midi: 0.25 m^2 mouth area, mesh size of 500 µm) b) Ring Trawl (RT) (diameter of mouth area: 1.6 m, mesh size of 1000 µm).

The cod end of one of the nets was retrieved without previous washing of the net in order to avoid damaging the larvae. Living fish larvae were immediately sorted out, identified according to Olivar and Fortuno (1991) and Bianchi *et al.* (1999) and finally transferred in previously prepared water tanks. Dead *Trachurus* individuals were measured (SL = distance from the tip of the snout to the posterior end of the last vertebra) to the nearest of 1 mm under a stereomicroscope. Afterwards the dead larvae were immediately preserved in liquid nitrogen and finally stored at -80 °C.

Due to the sampling region of this study, it was assumed that the sampled *Trachurus* species belonged to the species *T. capensis* and not to *T. trecae*. However, genetic analyses were required for confirmation, which could not be conducted in the framework of this study. Henceforth, the presumable *T. capensis* larvae were termed "*Trachurus* spp.".

2.2 Fish keeping on board of RV Meteor ME 103

Living *Trachurus* were kept separately in 0.5-1 l translucent Kautex beakers (depending on the larval size) and were fed once a day with cultured brine shrimps (*Artemia salina*) nauplii. *Artemia salina* was cultured on board to guarantee a constant provision of food. The nauplii reached a maximum age of 48 hours. The water quality of the fish tanks was guaranteed by constant cleaning and by replacing 75 % of the water with pre-filtered seawater every day. The larvae were kept in a temperature-controlled refrigerator, which was set to the ambient temperature at sampling depth (18 °C ± 1 °C) (Figure 6). Photoperiod was regulated at 12 light-hours cycle, since fish larvae are visual feeders (Hunter and Kimbrell, 1981, Blaxter, 1988).

In order to establish the experimental design for subsequent feeding experiments planned for ME 103-2, a pre-study concerning feasible food concentration levels was conducted. Larvae (8-10 mm), sampled during ME 103-1, received 5 different prey concentrations for 24 hours: 1 nauplia ml^{-1}, 5 nauplii ml^{-1}, 10 nauplii ml^{-1}, 15 nauplii ml^{-1} and 20 nauplii ml^{-1}. The set prey concentrations were defined based on past results (Houde, 1972; Klumpp and Westernhagen, 1986; Garrido *et al.*, 2012). At the end of the pre-study, remaining nauplii were counted in the keeping facilities. Based on these results, four prey quantities were chosen for the subsequent feeding experiment. Larvae utilized in the pre-study were preserved in liquid nitrogen and finally stored at -80 °C.

Figure 6: Temperature-controlled refrigerator utilized for keeping *Trachurus*.
Temperature was adjusted at 18 °C ± 1, light cycle was set to 12 hours and aeration could be provided if necessary.

In total, 30 live caught *Trachurus* larvae and 8 juveniles survived the catching procedure and the first 48 hours after catch. 47 larvae, which did not survived, were used as base line for further analysis (*e.g.* RNA/DNA ratios).

2.3 Experiments with *Trachurus* spp. larvae & juveniles

2.3.1 Food uptake and digestion

Two different approaches were examined in order to evaluate the food uptake and digestion efficiency of larva and juvenile *Trachurus* spp.: a feeding experiment and determination of gut evacuation rates.

The feeding experiment estimated the effect of different food concentrations on the larval ecology. Ingestion rates were determined with 18 *Trachurus* larvae (7-20 mm) and 3 juveniles (21-40 mm) during ME 103-2. The larvae were kept in the same experimental set up (at 18 °C) as the larvae utilized for preliminary tests (chapter 2.2).

Trachurus larvae were randomly divided into four groups. Each group was fed with different food concentrations of newly hatched *Artemia salina* nauplii: a) 1 nauplia ml^{-1} b) 5 nauplii ml^{-1} c) 10 nauplii ml^{-1} d) 15 nauplii ml^{-1} (Table 1). The chosen prey concentrations based on preliminary results of the pilot test conducted during ME 103-1 (chapter 2.2). *Trachurus* spp. received food at 9:00 UTC (10:00 CET) every day. After 24h the amount of ingested nauplii per fish specimen [n d^{-1}] and the percentage consumption of the received food [% d^{-1}] were calculated. The daily ingestion rate was determined on 8 consecutive measurements. In order to minimize the daily variations, the average ingestion rate of each *Trachurus* specimen was calculated. These average ingestion rate is termed “ingestion rate” in the following analyses. The experiment was stopped after 8 days to guarantee a good condition of larvae and juveniles. Larvae and juveniles were measured (SL), frozen in liquid nitrogen and finally stored at -80 °C.

Table 1: List of *Trachurus* spp. individuals used in the feeding experiment at 18 °C.
The received food concentration and amount of tested individuals are listed in the table.
Abbreviation: postf = postflexion (8-15 mm), trans = transformation (16-20 mm), juv = juveniles (21-40 mm)

developmental stage	prey density [nauplii ml^{-1}]	amount of *Trachurus* [n]
postf	1	1
trans	1	2
juv	1	0
postf	5	0
trans	5	5
juv	5	1
postf	10	3
trans	10	2
juv	10	0
postf	15	2
trans	15	1
juv	15	2

Remaining live *Trachurus* specimens (17-70 mm) were transported to NatMIRC (National Marine Information and research Centre, Swakopmund, Namibia) for a repetition of the feeding experiments at an elevated temperature (22 °C), to investigate the effect of a warming in the northern Benguela System. After recuperation time of 3 days, 16 larvae and juveniles were available for further experiments. The experimental set-up was the same as used onboard of RV Meteor (Figure 6). However, due to the restricted amount of larvae and juveniles, *Trachurus* were randomly separated into only two groups. The first group received 5 *Artemia* nauplii ml^{-1} and the second group 15 nauplii ml^{-1}. The experiment was forced to be stopped after six days, in order to guarantee a healthy condition of *Trachurus* individuals without any influence of stress factors. All specimens were preserved in liquid nitrogen and shipped to ZMT for further investigations.

Gut evacuation rate at 18 °C were estimated of 18 larvae on board of RV Meteor ME 103. The larvae and juveniles did not receive any *Artemia* nauplii for 2.5 h in order to ensure that the guts were completely empty. The measurement of gut evacuation rate started as soon as food was extensively offered and ended once the first formation of feces was noticeable. For each individual, determination was repeated 2-6 times during subsequent days. Mean gut evacuation rate [min] was calculated in order to minimize daily fluctuations of the gut evacuation rate.

Gut evacuation time at 22 °C was ascertained for 16 larvae and juveniles at NATMIRC (Swakopmund, Namibia), where the same experimental set up was adopted.

2.3.2 Starvation experiment

A starvation experiment was conducted with *Trachurus* larvae (3-5 mm) of station 40, 41, 44, 45, 46, 47 (Table 2). Starved fish larvae were frozen in liquid nitrogen at time intervals of 6 hours from 48-76 hours of starvation. To investigate immediate reaction to starvation, the aim of ME 103-2 was to get more detailed information concerning the starvation effect of the first 24 hours on growth and nutritional condition. Therefore, small larvae (3-7 mm) of station 131 were frozen within the first 24 hours (12, 18 and 24 hours) (Table 2). In addition, remaining *Trachurus* specimens were kept for 65 hours of starvation to receive comparable starvation periods with regard to ME 103-1. In total, 78 *Trachurus* larvae were utilized for this starvation experiment. Larvae were frozen immediately in liquid nitrogen and stored at -80 °C for subsequent lab analysis at ZMT.

Table 2: List of *Trachurus* spp. larvae used in the starvation experiment at 18 °C.
The station at which larvae were sampled and the duration of starvation are listed in the table below. Abbreviation: pref = preflexion (3-4 mm), flex = flexion (5-7 mm)

station	starvation time [h]	developmental stage	amount of *Trachurus* [n]
40	76	pref	5
41	48	pref	6
41	48	flex	2
41	55	pref	1
41	55	flex	10
44	66	flex	1
45	60	pref	4
45	60	flex	2
45	66	pref	3
46	60	pref	1
46	60	flex	1
47	48	pref	2
47	48	flex	5
47	54	pref	3
47	54	flex	1
47	60	pref	1

Continuation of Table 2: List of *Trachurus* spp. larvae used in the starvation experiment at 18 °C.
The station at which larvae were sampled and the duration of starvation are listed in the table below.
Abbreviation: pref = preflexion (3-4 mm), flex = flexion (5-7 mm)

station	starvation time [h]	developmental stage	amount of *Trachurus* [n]
131	12	pref	4
131	12	flex	4
131	18	flex	9
131	24	flex	7
131	65	pref	1
131	65	flex	5

2.4 Analytical laboratory work

To estimate the effect of food concentration on nutritional condition and growth of *Trachurus* larvae and juveniles, morphometric condition factor, growth rate and RNA/DNA ratios were investigated. All analyses were aimed to be conducted on the same individual larvae and juvenile obtaining a high resolution data set. For the first time, these morphometric and biochemical analyses were combined to investigate *Trachurus* spp. growth and condition sampled in the northern Benguela upwelling system.

2.4.1 Basic measurements

Body length (SL) of all *Trachurus* larvae and juveniles was measured. Subsequently, larvae and juveniles were staged according to distinctive morphological developments (Geist, 2013; Olivar and Fortuno, 1991; Westhaus-Ekau, 1988): around 4 mm = flexion and looped gut, around 8 mm = dorsal fin readily developed, around 12 mm = distinct differentiation of the intestinal tract and onset of metamorphosis, and at the latest at 18 mm = intestinal tract fully developed. Hence, specimens were categorized into the following size classes: 3-4 mm = pre-flexion larva (pref), 5-7 mm = flexion larva (flex), 8-15 mm = post-flexion (postf), 16-20 mm = transformation larva (trans), and 21-40 mm juveniles (juv) (Figure 2).

In order to scale the gutted dry mass (GDM) using a high-precision balance (Satorius) (± 1 µg), the gastrointestinal tracts of all larvae and juveniles were carefully removed on ice under a stereomicroscope before they were freeze dried. The relationship between GDM and SL are given in the appendix (A-Figure 1).

2.4.2 Morphometric condition factor

The evaluation of the nutritional condition of each *Trachurus* was based, *inter alia*, on the morphometric condition factor (CF) (Heincke, 1908). The applied equation was adjusted for a species-specific length body mass relation:

$$CF = GDM * SL^{-b} * 10^3 \quad (1)$$

where *GDM* is gutted dry mass [mg], *SL* is standard length [mm] and *b* is derived from species-specific potential length-weight regression (appendix, A-Figure 1).

2.4.3 Growth rate determination based on otolith readings

In total, 230 larvae and 22 juveniles of *Trachurus* spp. were analyzed concerning growth rate and age determination. Both sagittal otoliths of all freeze-dried larvae were removed with a dissecting needle under a dissecting microscope and samples were returned to the deep-freezer immediately afterwards. A triange was cut off in the area where sagittal otoliths are located (Figure 7). Particular attention was payed to avoid damage of the specimen. The tissue next to the otoliths were collected in order not to lose tissue and to garantuee a comparison with the subsequnetly RNA/DNA method.

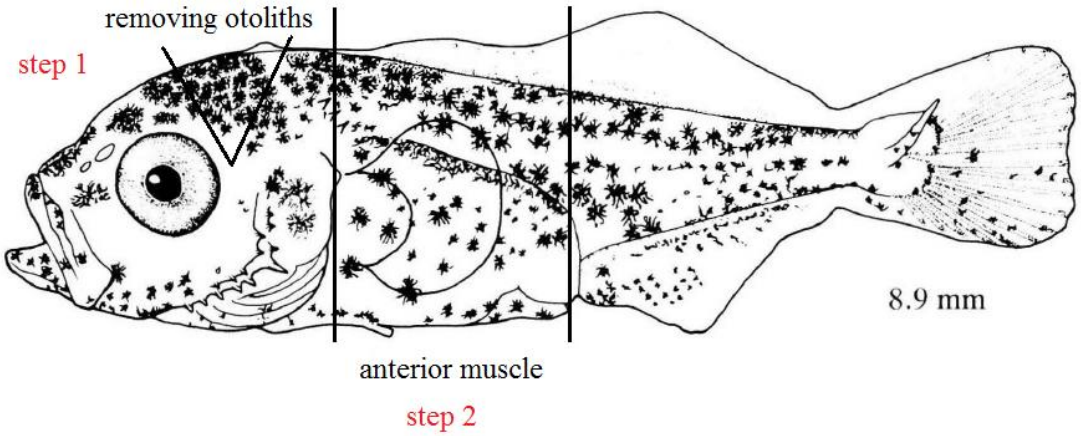

Figure 7: Modified drawing of *Trachurus capensis* (Olivar and Fortuno, 1991).
The areas of which otoliths and the anterior muscle part were dissected are highlighted.

The recovered otoliths were rinsed with destilled water, dried for 48 h and finally mounted on glas sildes with the suculus-side down (glue: Uhu-Plus-Schnellfest 2-K-Epoxikleber). Otoliths of preflexion larvae (3-4 mm) required no further treatment. However, the sagittal

ototliths of larvae > 5 mm and juvenils were grinded with sand paper of 4000 granulation and etched with hydrogen chloride (HCL, 0.02 M, 7.6 pH) (Jones and Brothers, 1987; Jenkins and Davis, 1990) for 5-10 seconds until all increments were within the same plane and the core was clearly visible. The grinding and etching process was monitored by frequent microscopic controls. The otolith increments were counted under 10 to 650 X magnification using a stereomicroscope (Zeiss Axioskop) and Zeiss immersion oil. Digital images were taken by means of a Zeiss Axio Cam ICc 1 and edited using the computer software Axio Vision Release 4.8. (2006-2009). To measure individual width of otolith increments and radius, the computer image-analysis software Image Pro Plus 5.1 was used. The increments were recorded from the core to the edge of the otoliths along the longest axis where the most complete increment sequence was found (Morales-Nin and Aldebert, 1997). Readings of the increments were performed randomly and with no consideration of age, length and feeding regime. 34 readings were checked by a second reader (Stefanie Bröhl, ZMT), when counts differed by more than 10 % of the first count, the otolith was excluded from further analyses. 78 % (n = 198) of the total number of otoliths were used for further analyses.

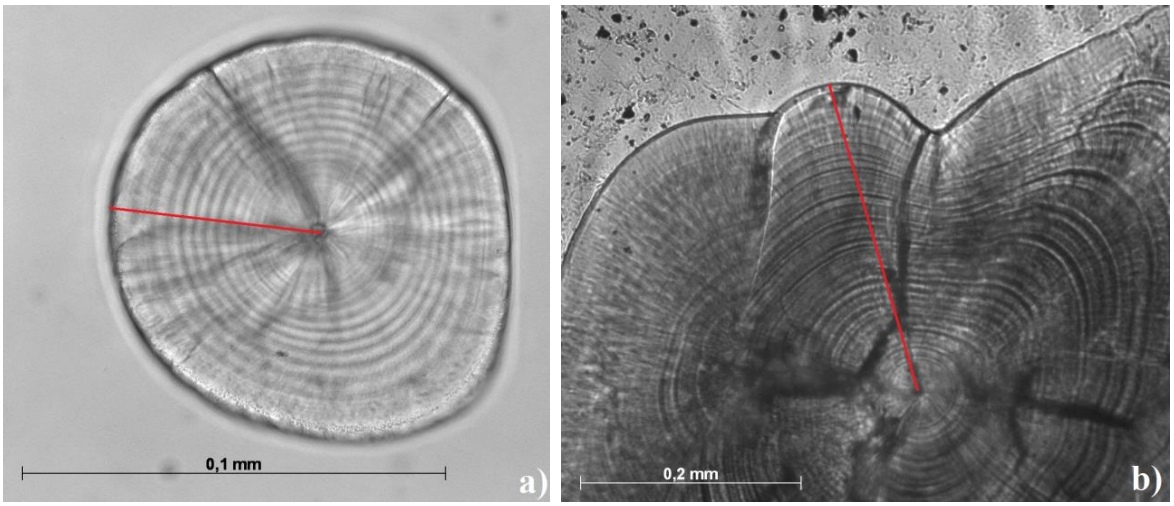

Figure 8: Images of sagittal otolith of *Trachurus* spp.
a) Sagittal otolith of a 15 days old preflexion larvae. b) Grinded sagittal otolith of a 58 days old juvenile. The red line presents the transit line along which increments were counted. Both pictures were taken by Zeiss Axio Cam ICc 1 and edited by the computer software Axio Vision Release 4.8. (2006-2009).

The age in days post hatch (dph) was defined as number of increments counted in sagittal otoliths. The relationship between *Trachurus* larval/juvenile length and age [dph] was analyzed by fitting a linear regression (appendix, A-Figure 3).

A power function was fitted to describe the allometric relationship between larval/juvenile size and otolith radius (Folkvord and Mosegaard, 2002):

$$SL = a * OR^b \quad (2)$$

where *SL* is standard length [mm] measured, *a* and *b* are regression parameters and *OR* is the otolith radius [µm]. The back-calculation of SL_{bci} of *Trachurus* spp. larvae and juveniles is based on this allometric growth function and is conducted to compare growth rates within the first 30 days of larval life:

$$SL_{bci} = a * OR_i^b \quad (3)$$

where SL_{bci} is the standard length back-calculated for the i^{th} increment, OR_i is the otolith radius at increment *i* and *a* and *b* are regression parameters. To minimize daily variations, average growth rates of each larvae/juveniles were separately calculated. Furthermore, average growth rate days post catch (dpc) was calculated, in order to determine particularly the effect of the conducted feeding and starvation experiments. All analyses based on growth rate were related to growth rate dpc, if not explicitly stated otherwise.

Based on the back-calculation of SL_{bci} and GDM, the daily increase in biomass during the larval life was estimated. To define the relationship between GDM and SL with the highest precision possible, data of previous cruises (MSM 07, Afr 258, D 356, MSM 17-3, MSM 19-1b, ME 100) were incorporated (Geist *et al.*, 2014). SL and GDM of *Trachurus* of the same size classes (3-40 mm) and the same sampling region in the Benguela upwelling system were utilized. *Trachurus* larvae from starvation experiments were not included. The length weight relationship is expressed by the following equation ($r^2 = 0.929$, $p < 0.0001$*) (appendix, A-Figure 2):

$$GDM\ [mg] = -5.85617 + 2.9308041 * Ln(SL) \quad (4)$$

where *GDM* is the gutted dry mass [mg] of larave or juvenile and *SL* is standard length [mm] of *Trachurus*.

Subsecently, the backcalculated SL of horse mackerel after catch (dpc), were utilized to determine the GDM (equation 4) during the experiments. Then, daily increase in biomass (BGR = Biomass Growth Rate) was calculated by substracting:

$$BRG\ [mg\ d^{-1}] = GDM_{x+1} - GDM_x \quad (5)$$

where *BGR* ist the biomass growth rate [mg d^{-1}], gutted dry mass (GDM_x) was substracted from the gutted dry mass of the following day (GDM_{x+1}).
For further anlyses, the mean of biomass growth rate was computed for the days post catch, when experiments were conducted.

According to Ivlev (1961), gross growth efficiencies (K_l) of 16 larvae and juveniles were calculated. K_1 is the fraction of ingested food incorporated into tissue and may be computed in terms of material (*e.g.* the weight of dry matter, carbon, or nitrogen) or energy (Checkley, 1984).

$$K_1 = G * I^{-1} \quad (6)$$

where *G* is the growth rate [mm d^{-1}] and *I* the ingestion rate [nauplii d^{-1}].

2.4.4 RNA/DNA analysis

The determined RNA/DNA ratio was used as a proxy for nutritional condition and protein growth potential during the last 3-4 days of early life stages (Clemmesen, 1988; Clemmesen, 1996). The RNA/DNA was determined fluorometrically with ethidium bromide. Samples were prepared and measured according to the protocol developed by Clemmesen *et al.* (2003) and ICES (2004). Depending on the size of the *Trachurus* larvae and juveniles either whole freeze-dried larvae (3-7 mm larvae) or just the anterior part of dorsal muscle tissue (of 8-20 mm larvae and 21-40mm juveniles) were used in these analyses (Figure 7). Olivar *et al.* (2009) showed that nucleic acid ratio can differ depending on muscle tissue position in *Sardina pilchardus* and *Engraulis encrasicolus* larvae. To allow comparison within experiments starvation larvae were analyzed as whole, whereas only anterior muscle tissues were examined for fed larvae. This change in the methodical procedure was required because it was impossible to homogenize whole juvenile *Trachurus* utilizing the same extraction method. The minimum dry mass for which confident fluorescence measurements of *Trachurus* tissue were obtained was 60 µg. All laboratory equipment, consumables, chemicals (*e.g.* flasks, bottles, eppendorf cups, spatula, tips of pipettes, buffer *etc.*) were either rinsed with Diethyldicarbonat (DEPC) and/or autoclaved in order to minimize the possibility of contaminations during the analytical process. DEPC inactivates RNase enzymes in water and on laboratory utensils (Wolf *et al.*, 1970).

For the nucleic acid extraction, samples were rehydrated in Tris-SDS buffer (volume was size-dependent, between 400-2000 µl) (Tris 0.05 mol l^{-1}, NaCl 0.01 mol l^{-1}, ethylenediaminetetracetic acid (EDTA) 0.01 mol l^{-1}, sodium dodecyl sulfate (SDS) 0.01 %) for 30 minutes cooled on ice. Different sized glass beads (0.17-0.34 mm) were added to the rehydrated samples. The disruption of the tissue cells were conducted by means of a cell mill (FastPrep-24 by MP). Homogenization using the FastPrep instrument was conducted for 3 x 40 seconds at a speed setting of 6.0 (maximum speed). The sample tubes were placed on ice for 5 minutes between each run according to manufacturer's recommendation for nucleic acid extraction (MP FastPrep, URL 6). After centrifugation (8 minutes, 6000 rpm, 2 °C; centrifuge 5804 P by eppendorf), the supernatant was transferred in an already prepared eppendorf cup and stored on ice until it was measured.

RNA and DNA content in the homogenate was determined fluorometrically in three steps using a microplate fluorescence reader (Tecan infinite M200 Pro) and the additional software I-control V 2.2.: 1) Fluorescence of the used chemicals was determined. 2) Ethidium bromide (EB) was used as fluorometrical dye, which intercalates with the nucleic acids. Subsequently, total nucleic acid content of the sample was estimated (RNA and DNA content). 3) The enzyme RNase was added to the samples for RNA digestion (30 minutes at 37 °C) and consequently the remaining DNA was measured. The RNA fluorescence was calculated by subtracting the DNA fluorescence from the total RNA/DNA content. The RNA content was calculated from fluorescence readings of a calibration curve using RNA standards (23S rRNA Boehringer). While the DNA content was estimated using the relationship between RNA and DNA fluorescence with a slope ratio of standard DNA to standard RNA of 2.2. This standardization accounts for the fact that DNA calibration curve is steeper than RNA due to double-stranded DNA helices (Le Pecq and Paoletti, 1966). Consequently, the relative fluorescence intensity difference of RNA and DNA was adjusted.

To allow for comparison of RNA/DNA ratios with literature, values were standardized according to Caldarone *et al.* (2006):

$$sRD = \frac{RNA}{DNA} * SF_{Pi}^{-1} \quad (7)$$

where *sRD* is the standardized RNA/DNA ratio and SF_{Pi} a standardization factor. The standardization factor (SF_{Pi}^{-1}) is calculated by dividing the standard curve slope ratio of 2.2 by the slope ratio of the reference protocol (2.4) (Caldarone *et al.*, 2006).

Standardized RNA/DNA ratios were utilized to calculate instantaneous growth rates (Gi) using a multi-species model of larval fish growth (Buckley *et al.*, 2008):

$$Gi[d^{-1}] = 0.0145 * sRD + (0.0044 * sRD * temp) - 0.078 \quad (8)$$

where *Gi* is the instantaneous growth rate, *sRD* is the standardized RNA/DNA ratio, *temp* is the temperature experienced by the larvae [°C].

Based on the Gi, the RNA/DNA threshold level for growth of *Trachurus* larvae were estimated by calculating the turning point from positive Gi to negative Gi. The following back-calculation related the Gi threshold level to the sRD value of this tuning point (Grote, 2010).

2.5 Statistical analysis

Superimposed surface plots of sampling station and water temperatures at 20 m depth (30 ‰ DIVA-gridding) were constructed by means of Ocean Data View 4.5.0 (Schnitzler 2001, http:// odv.awi). In addition, all graphs were post-processed using Adobe Illustrator CC 2014.0.0 Release.

All data were tested concerning normal distribution (Shapiro-Wilk test) and homogeneity of variance (Levene test). Non-parametric multiple comparisons with unequal sample sizes (Kruskal–Wallis test; Zar, 1996) were used to compare morphometric condition factor, average growth rate and RNA/DNA ratio of *Trachurus* spp. larvae and juveniles concerning size classes, stations where the larvae were caught, varying prey density and starvation time. If a significant difference was determined, a post-hoc comparison test was performed. Since group sizes were not equal and all possible pairs needed to be compared, a Dunn test (Dunn 1964) was selected. The criterion for variable selection and retention was always set at $p < 0.05$. The relations between the parameters of condition and prey density and starvation time respectively were analyzed by least-square linear regressions and non-linear regression, respectively. All computations were performed with the statistic software

JMP ® Pro 10.0.0. Data averages were given as mean ± standard deviation, if not indicated otherwise.

2.6 Experiments with animals

As outlined above, during this study experiments with animals were conducted. Especially *Trachurus* spp. larvae were in focus of the experimental set up. In addition, brine shrimps (*Artemia salina*) were cultured and subsequently utilized as diet for the wild caught *Trachurus.* In total, 30 fish larvae were used for feeding experiments. Since 78 *Trachurus* larvae refused the ingestion of food, they were used to conduct a starvation experiment. The rules of animal protection law (§ 7 of the Animal Welfare Act) were followed for each *Trachurus* and *Artemia* specimen, respectively. The project was adhered closely to Article 1 of the Animal Welfare Act: "The aim of this Act is to protect the lives and well-being of animals, based on the responsibility of human beings for their fellow creatures. No one may cause an animal pain, suffering or harm without good reason" (juris, URL 7). According the current state of knowledge, no permits were required.

3 RESULTS

The following analyses focused on *Trachurus* spp. data generated at 18 °C water temperature. Experiments conducted at NatMIRC at 22 °C were only utilized for investigations concerning gastric evacuation rate. All specified results (mean ± standard deviation) and equations of applied functions ($y = a + bx$ or $y = a * x^b$) are listed in the appendix of this study (A-Table 2).

3.1 Feeding experiment of *Trachurus* spp.

3.1.1 Food uptake and digestion

In order to estimate food uptake as well as the processing of the food, ingestion rate and gastric evacuation rate of horse mackerel were investigated.

Ingestion rates of 17 *Trachurus* spp., grouped by size classes, were estimated. Juvenile (21-40 mm) *Trachurus* exhibited the highest ingestion rate [n d^{-1}], followed by the transformation (16-20 mm) and postflexion (8-15 mm) larvae (Figure 9). A Kruskal-Wallis test validated that the ingestion rate was significantly influenced by size ($p < 0.0001$*). In addition, the consumption rate of all size classes depended on offered food density ($p < 0.0001$*) (Figure 9). Postflexion larvae consumed at the lowest mean ingestion rate (Figure 9). It slightly ascended from 591.5 ± 22 n d^{-1} (1 nauplia ml^{-1}) to 1374.83 ± 230.14 n d^{-1} (10 nauplii ml^{-1}), followed by a stabilization of the consumption rate at 10 and 15 nauplii ml^{-1} (Figure 9; appendix, A-Table 3). The ingestion rates of transformation larvae was best described by a parabola-shaped function ($r^2 = 0.59$, $p < 0.0001$*) (Figure 9). Larvae consumed most at a prey density of 10 nauplii ml^{-1} (4114.27 ± 331.44 n d^{-1}). The mean ingestion rate of the juveniles increased linearly from 2462.73 ± 131.94 n d^{-1} at 5 nauplii ml^{-1} to 5931.42 ± 0 n d^{-1} at 15 nauplii ml^{-1} ($r^2 = 0.93$, $p < 0.0001$*).

Summarizing, juveniles ingested as much prey as possible, whereas postflexion and transformation larvae consumed prey at an increasing rate up to a saturation point, assumingly found at around 10 nauplii ml^{-1}. Once the saturation point was reached, the ingestion rate did not increase with enhanced food quantity. It was either followed by a decline (transformation larvae) or a stagnation of ingestion rate (postflexion larvae) (Figure 9).

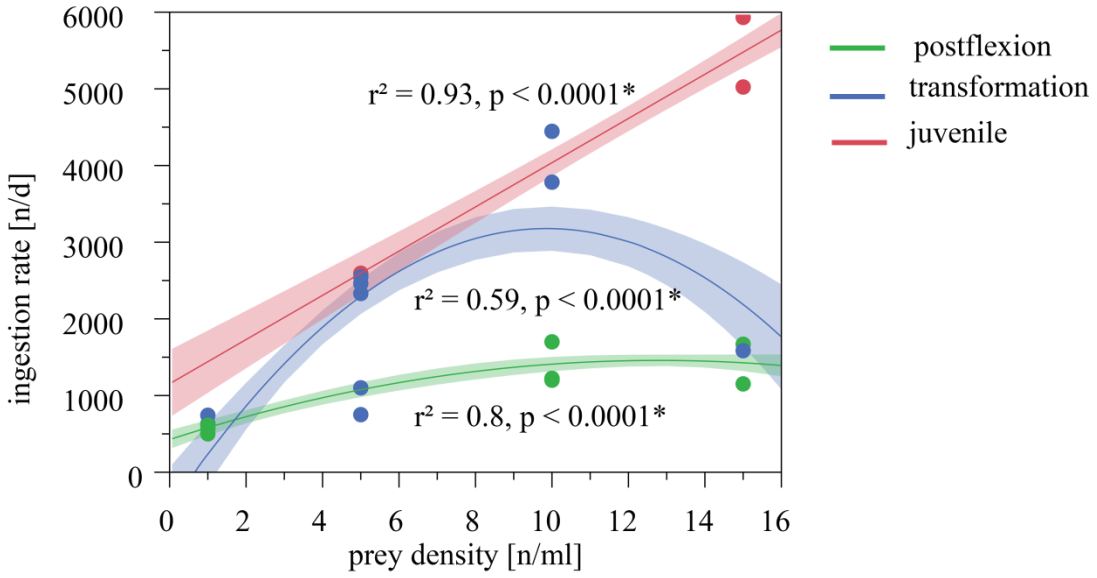

Figure 9: The relationship between ingestion rate [n d^{-1}] of *Trachurus* spp. and food density [n ml^{-1}]. The data were grouped by size classes: postflexion (6 n), transformation (9 n), juveniles (3 n). The ingestion rates of early life history stages and prey density correlated significantly ($p < 0.0001$*). The ingestion rate referred to ingestion rates of each *Trachurus* specimen determined on 8 consecutive days.

In order to remove size-dependent differences, the average ingestion rate was expressed in average ingestion rate [n d^{-1}] per mg GDM of *Trachurus* specimen. In all three size classes the standardized consumption rate increased linearly with nauplii density, however slopes and absolute values differed (Figure 10; appendix, A-Table 3). Nevertheless, the analysis of the data revealed distinct differences between larval and juvenile individuals (Figure 10). Hence, the grouping of data according the size classes was retained. The ingestion rate of all size classes increased linearly with enhanced food quantity, whereby postflexion larvae offered the steepest increase. Postflexion *Trachurus* consumed up to 0.491 n d^{-1} per mg GDM of fish at a prey density of 15 nauplii ml^{-1}. Besides, the highest variance was detected in this larvae group (Figure 10). It was prominent that the variability of ingestion rates between the size classes increased with elevated food quantity. The average ingestion rate of transformation horse mackerels varied between 0.08 ± 0.01 (1 nauplia ml^{-1}) and 1.005 ± 0.475 n d^{-1} per mg GDM of fish larvae (15 nauplii ml^{-1}). Juveniles ingested far less in relation to their body mass (5 nauplii ml^{-1}: 0.27 ± 0.1 n d^{-1} per mg GDM of fish, 15 nauplii ml^{-1}: 0.41 ± 0 n d^{-1} per mg GDM of fish) than larval *Trachurus* (Figure 10).

In addition to the significant size class- differences (Kruskal-Wallis test, $p < 0.0001$*), the ingestion rate of *Trachurus* spp. was significantly influenced by the prevailing environ-

mental conditions when the larvae were caught. Larvae and juveniles of ME 103-1 exhibited a significantly higher mean ingestion rate than specimens caught during ME 103-2 (Kruskal-Wallis test, $p < 0.0001$*) (appendix, A-Table 3). It has to be noted that ingestion rate of postflexion larvae were only investigated during ME 103-1 and not during ME 103-2 due to a lack of living postflexion larvae.

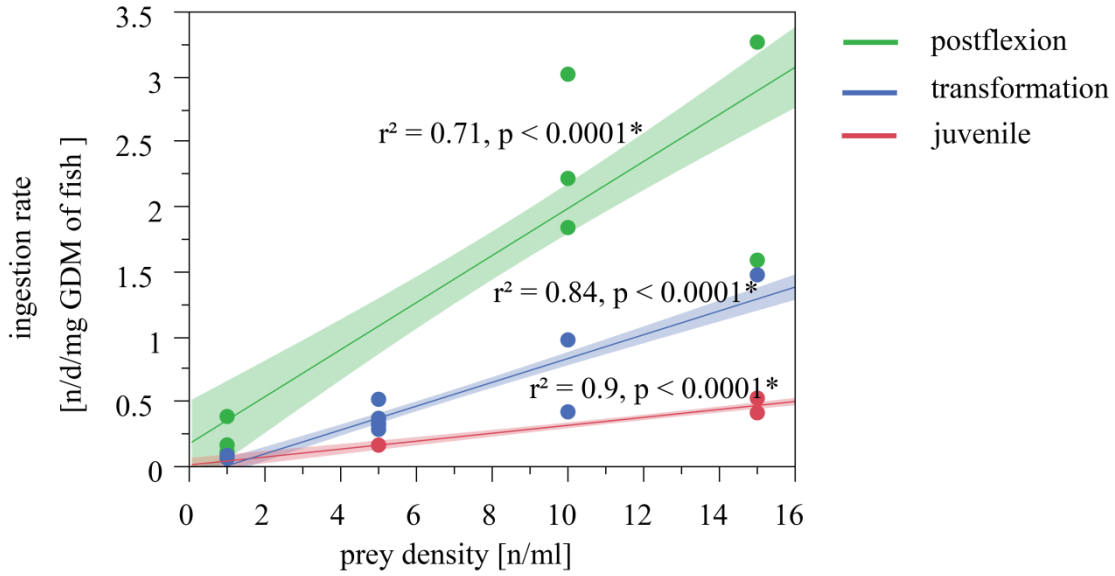

Figure 10: The relationship between ingestion rate [n d^{-1} per mgGDM of fish] of *Trachurus* spp. and food density [n ml^{-1}].
Data were grouped by size classes: postflexion (7 n), transformation (8 n), juveniles (3 n). Both size and origin of *Trachurus* influence considerably the ingestion rate (Kruskal-Wallis test, $p < 0.0001$*). The ingestion rate refers to ingestion rates of each *Trachurus* specimen determined on 8 consecutive days.

Besides ingestion rates of *Trachurus* spp. [nauplii ml^{-1}], investigations concerning food consumption [%] were conducted in order to assess the amount of offered food concentration. No significant size differences were observed (Kruskal-Wallis test, $p = 0.727$), therefore the data of all size classes were integrated for further analysis (Figure 11). At a prey quantity of 1 nauplia ml^{-1}, *Trachurus* individuals consumed 87.59 ± 8.94 % of the received food. The enhanced food density resulted in a decreased foraging efficiency (Figure 11; appendix, A-Table 4). *Trachurus* ingested less than half of the offered food, once prey density was elevated up to 5 nauplii ml^{-1} (42 ± 10.36 %). Horse mackerels caught successfully 28.79 ± 10.73 % at a food concentration of 10 nauplii ml^{-1}, followed by a further decline to 14.1 ± 0.76 % at 15 nauplii ml^{-1} (Figure 11; appendix, A-Table 4).

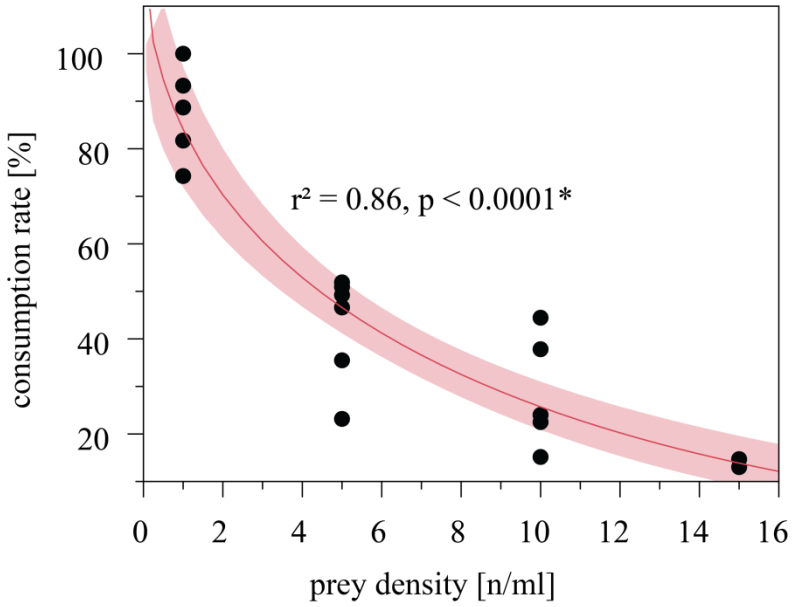

Figure 11: Correlation of consumption rate [%] of *Trachurus* spp. and prey density [nml^{-1}].
The consumption rate (n = 17) refers to consumption rates of each *Trachurus* specimen determined on 8 consecutive days.

Moreover, gross growth efficiency (K_1) was estimates to determine the fraction of ingested food incorporated into tissue and was computed in terms of increase in body size. No size effect on K_1 could be determined (Kruskal-Wallis test, p = 0.427). Therefore, size classes were integrated to calculate K_1. The gross growth efficiency decreased considerably with an enhanced ingestion rate (r^2 = 0.72, p < 0.0001*) (Figure 12). K_1 values of individual larvae ranged between 7.19 * 10^{-4} at an ingestion rate of 750.57 n d^{-1} and 1.01 * 10^{-4} at an ingestion rate of 5023.67 n d^{-1}.

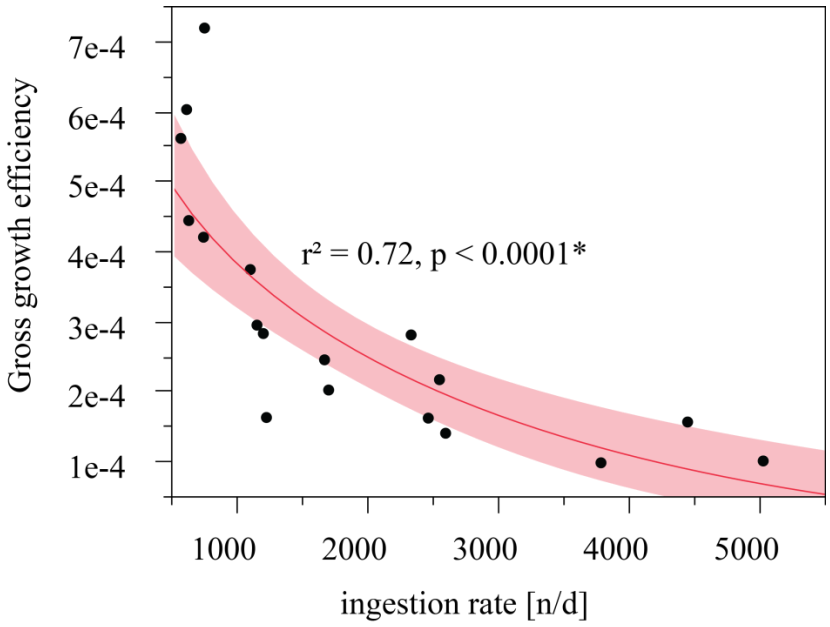

Figure 12: Relationship between gross growth efficiency and ingestion rate [n d^{-1}].
Significant decrease of gross growth efficiency with elevated ingestion rate [n d^{-1}] (r^2 = 0.72, p < 0.0001*). No significant differences between postflexion and transformation stages were determined. Therefore, both size classes were integrated (n = 18).

Drawing conclusions regarding digestion efficiency, gut evacuation rates of 31 horse mackerels at 18 °C and 17 individuals at 22 °C were determined, including several replicates. Data analysis revealed a significant temperature effect on average gut evacuation rate of each size class (Kruskal-Wallis test, p = 0.0474*). For instance, the mean gut evacuation rate of transformation stage larvae was determined to 40.72 ± 18.12 minutes at 18 °C, whereas gastric evacuation rate of transformation larvae declined (36.69 ± 0.69 minutes) with enhanced temperature (22 °C) (Table 3). Besides, gastric evacuation rate were influenced by fish size. Smaller larvae digested slower than transformation larvae and juveniles (Table 3). This size-effect got more prominent when the average evacuation rate was standardized by the average gutted dry mass (GDM) of fish. Statistical tests disclosed differences between size classes (Kruskal-Wallis-test, p = 0.0006*) and thermal conditions (Kruskal-Wallis test, p = 0.0013*). It needs to be noticed, that daily variabilities of the gut evacuation rates resulted in very high standard deviations.

Table 3: Gut evacuation rate of different developmental stages of *Trachurus* spp. at 18 °C and 22 °C. Both, gastric evacuation time [min] and the standardization of the values [min/ mg GDM of fish] are listed. Abbreviation: post = postflexion (8-15 mm), trans = transformation (16-20 mm), juv = juvenile (21-40 mm)

temperature [°C]	developmental stage	amount of *Trachurus* [n]	average gut evacuation rate ± SD [min]	average gut evacuation rate ± SD [min/mg GDM of fish]
18	post	14	47.35 ± 22.88	15.05 ± 12.5
18	trans	12	40.72 ± 18.12	2.98 ± 2.33
18	juv	5	37.64 ± 8.33	1.31 ± 0.32
22	post	2	47.7 ± 10.5	12.95 ± 7.77
22	trans	2	36.69 ± 0.69	2.37 ± 0.8
22	juv	13	30.42 ± 9.09	0.28 ± 0.18

3.1.2 Morphometric condition factor

The CF was determined by means of a species-specific length exponent *b* derived from a power fit function between body length (SL) and gutted dry mass (GDM) (n = 265, $r^2 = 0.93$, $p < 0.0001$*, a = -5.856, b = 2.841) (appendix, A-Table 3). The data analysis concerning CF was conducted with 9 postflexion larvae and 9 transformation larvae. Juveniles were not further analyzed due to the low sample size (n = 2). The nutritional condition of postflexion larvae was not significantly related to offered prey density ($r^2 = 0.14$, $p = 0.4465$), primarily due to the high variability in the CF data (appendix, A-Table 3). The condition of the postflexion larvae ranged between 3.357 ± 1.192 (at 1 nauplia ml^{-1}) and 3.801 ± 0.654 (at 10 nauplii ml^{-1}). In contrast, transformation larvae were significantly affected by enhanced food quantity ($r^2 = 0.62$, $p = 0.0067$*). The CF of the *Trachurus* larvae improved up to a prey density at around 10 nauplii ml^{-1}, followed by a decline at 15 nauplii ml^{-1} (Figure 13). The highest mean CF value of transformation larvae (4.335 ± 0.442) was determined at 10 nauplii ml^{-1}.

The origin of *Trachurus* larvae did not significantly affect the nutritional condition of the larvae (Kruskal-Wallis test, $p = 0.0714$).

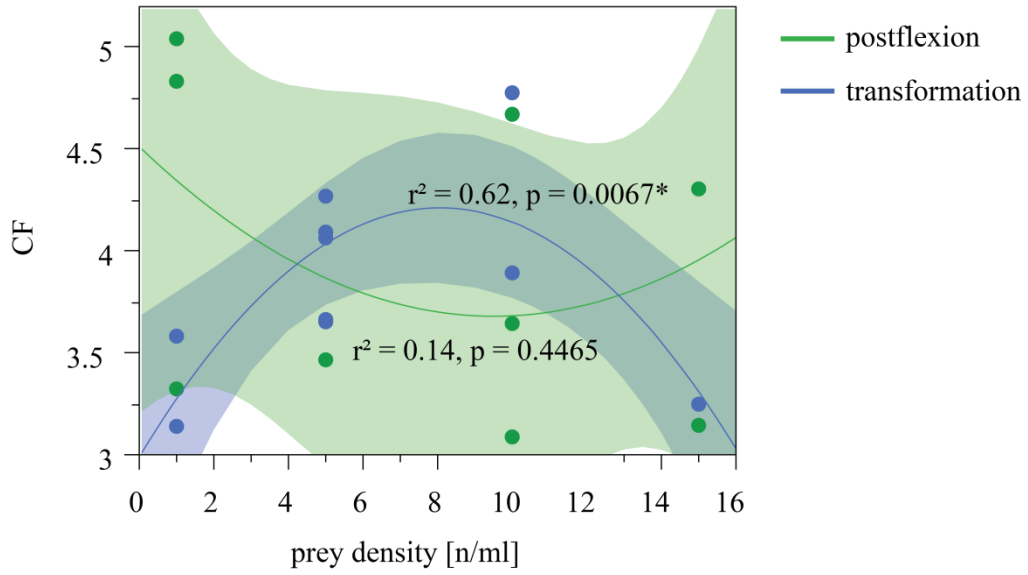

Figure 13: Correlation of condition factor of *Trachurus* spp. and offered prey density.
CF of two different larval stages was analyzed: postflexion (9 n), transformation (9 n).

3.1.3 Growth rate determination based on otolith readings

The mean length at hatch of the analyzed larvae and juveniles was determined at 2.437 ± 1.191 mm. Mean growth rate of larval stages observed during the experiment were related to offered prey density [nauplii ml^{-1}] (Figure 14). The correlation between growth rate of both size classes and prey density was not significant (postflexion: $r^2 = 0.2$; $p = 0.3185$; transformation: $r^2 = 0.47$; $p = 0.2098$). Postflexion larvae grew between 0.293 ± 0.066 mm (10 nauplii ml^{-1}) and 0.375 ± 0.035 mm (15 nauplii ml^{-1}) per day (Figure 14; appendix, A-Table 3). Transformation larvae increased in size with an enhanced prey density (at 1 nauplia ml^{-1}: 0.301 ± 0.023 mm d^{-1} and at 10 nauplii ml^{-1}: 0.535 ± 0.165 mm d^{-1}), after the saturation point was passed the growth rate declined despite an increasing food concentration (15 nauplii ml^{-1}). A high variance in larval growth rates at 5 and 10 nauplii ml^{-1} was observed (Figure 14).

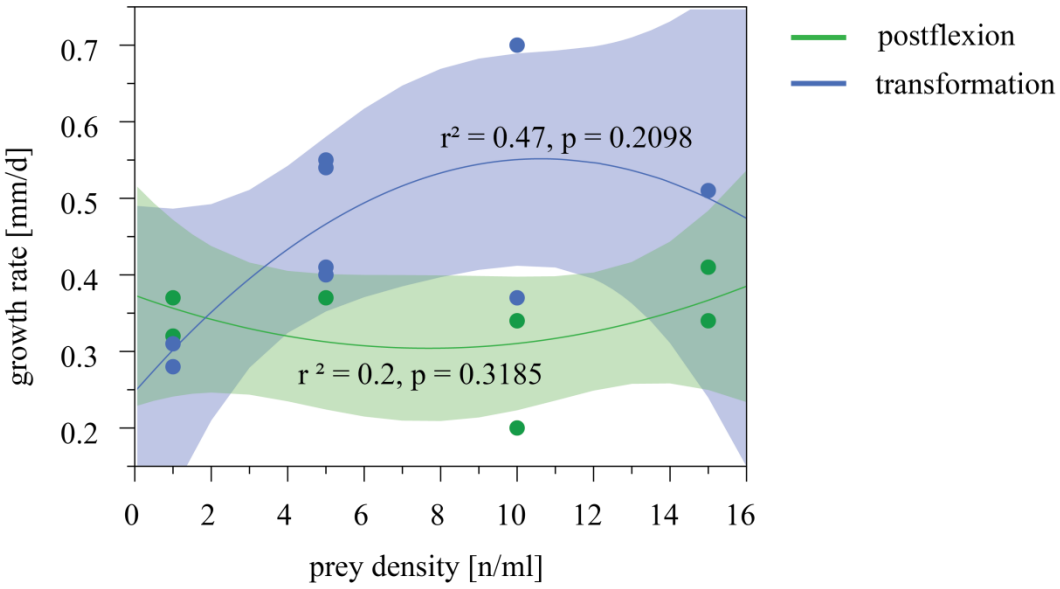

Figure 14: Relationship between growth rate [mm d^{-1}] of *Trachurus* spp. and prey density [n ml^{-1}]. No significant correlation was determined. The larval growth rate (postflexion= 7 n, transformation = 9 n) refers to growth rates of each *Trachurus* specimen determined on 8 consecutive days after catch (dpc).

The generated data of BGR was grouped by size classes due to a significant size effect on BGR (Kruskal-Wallis test, p = 0.0007*) (Figure 15). Juveniles were excluded from the analysis due to the low sample size. The weight gain of postflexion larvae was relatively constant and independent of food concentration ($r^2 = 0.65$, p = 0.0301*) (Figure 15). Despite an enhancement of food quantity, the mean BGR ranged between 0.375 ± 0.025 mg d^{-1} (1 nauplia ml^{-1}) and 0.41 ± 0.04 mg d^{-1} (15 nauplii ml^{-1}) (Figure 15). The increase in body mass with elevated food density was highest in transformation larvae. They ranged between an average BGR of 0.61 ± 0.07 mg d^{-1} at a prey density of 1 nauplia ml^{-1} and 1.11 ± 0 mg d^{-1} at a prey density of 15 nauplii ml^{-1} (appendix, A-Table 3). However, the correlation of BGR and prey density was not significant ($r^2 = 0.30$, p = 0.6735) (Figure 15).

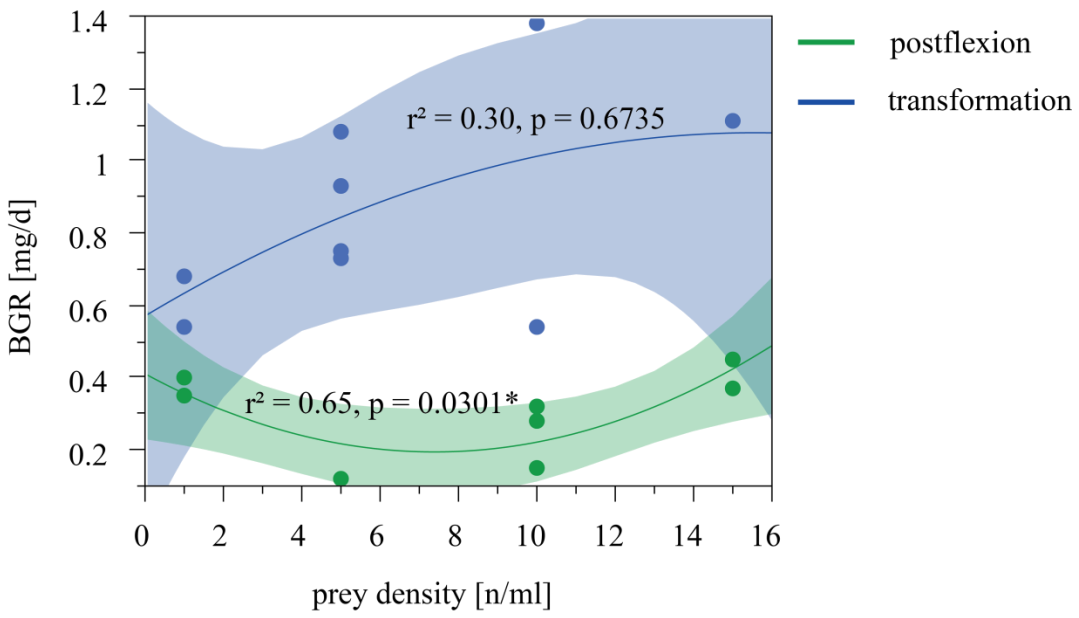

Figure 15: Correlation of BGR [mg d^{-1}] of *Trachurus* spp. and prey density [n ml^{-1}].
The data were grouped regarding size classes: postflexion (8 n), transformation (9 n). The BGR referred to biomass growth rates of each *Trachurus* specimen determined on 8 consecutive days after catch (dpc).

3.1.4 RNA/DNA analysis

Method validation

RNA/DNA methods have not been applied at the ZMT laboratories before. Therefore, it was essential to validate the method before the results were used in this study. One possibility to reassess the RNA/DNA method is to test the relationship between total RNA and DNA content to fish body mass. Both RNA and DNA content increased with elevated GDM [mg]. The method approved that the total RNA content was not only higher, but also slope b of the RNA fitted curve was steeper ($r^2 = 0.89$, $p < 0.0001$*, a = 6.693, b = 5.010) compared to DNA ($r^2 = 0.89$, $p < 0.0001$*, a = 3.482, b = 1.92) (Figure 16). In addition, the method was confirmed by a quality check of the detected fluorescence signals. Only fluorescence values ranging within the boundaries of applied standard cure were utilized. All signals outside of the boundaries would have been rejected. However, all measured fluorescence values met the requirements and hence were used in further analyses.

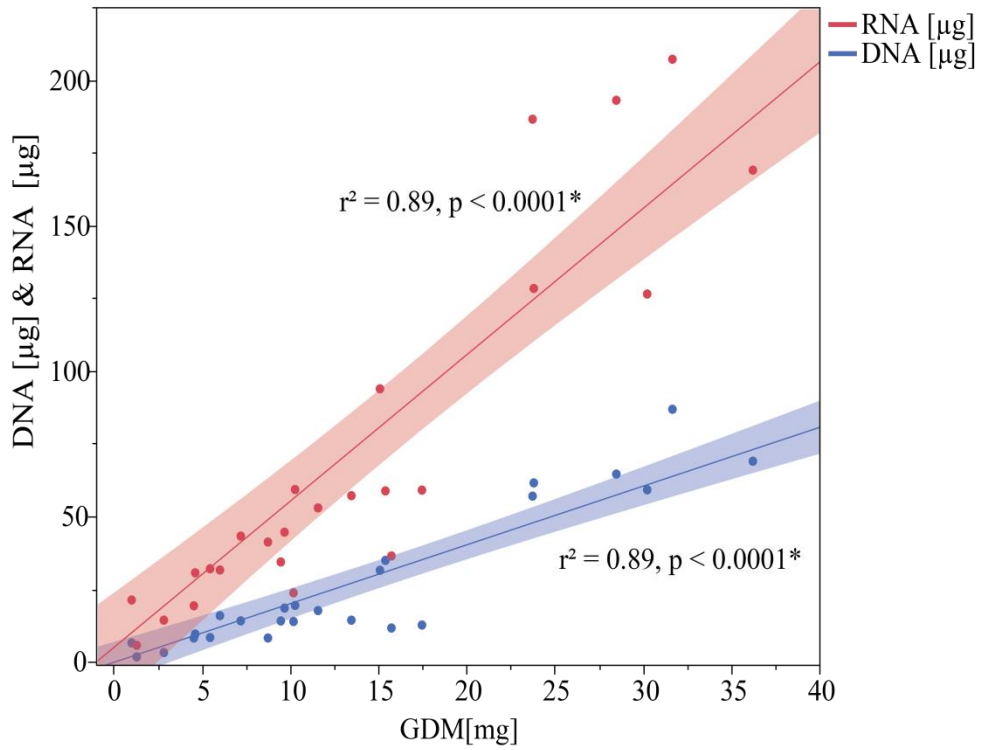

Figure 16: Validation of the RNA/DNA method.
The RNA and DNA content [µg] of 29 fed *Trachurus* individuals increased with weight gain (GDM in mg), whereby RNA is more abundant in fish than DNA (RNA: $r^2 = 0.89$, $p < 0.0001$*, a = 6.693, b = 5.010; DNA: $r^2 = 0.89$, $p < 0.0001$*, a = 3.482, b = 1.92).

Application of the RNA/DNA method

Similar to the growth rate analysis, sample number of juveniles was not sufficient to analyze the generated sRD data. Therefore, only sRD ratios of postflexion and transformation stages were examined (Figure 17). The condition of postflexion larvae did not intercalate with enhanced food density ($r^2 = 0.12$, $p = 0.541$). Postflexion larvae featured the lowest sRD at 1 nauplia ml^{-1} (2.817 ± 0.660), which was similar to transformation larvae. The highest average sRD of postflexion *Trachurus* was determined at 10 nauplii ml^{-1} (3.316 ± 0.783), followed by a decreased ratio of 3.041 ± 0.398 at 15 nauplii ml^{-1}. Transformation larvae exhibited a parabola-shaped pattern in relation to an enhanced prey density. Nevertheless, no significant relationship between sRD of transformation larvae and offered prey quantity was noticeable ($r^2 = 0.3$; $p = 0.1338$). The highest mean sRD ratio of *Trachurus* spp. was determined between 5 nauplii ml^{-1} (3.565 ± 0.892) and 10 nauplii ml^{-1} (3.436 ± 0.123). For both, the lowest and the highest prey densities (1 nauplia ml^{-1} and

15 nauplii ml^{-1}), average sRD were similarly low (1 nauplia ml^{-1}: 2.542 ± 0.709, 15 nauplii ml^{-1}: 2.555 ± 0.700) (Figure 17; appendix, A-Table 3).

Both larval stages were similarly influenced by prey density, offering the best condition between 5 nauplii ml^{-1}and 10 nauplii ml^{-1}(Figure 17). The nonparametric Kruskal-Wallis test confirmed, that the RNA/DNA data did not exhibit a size effect (p = 0.626).

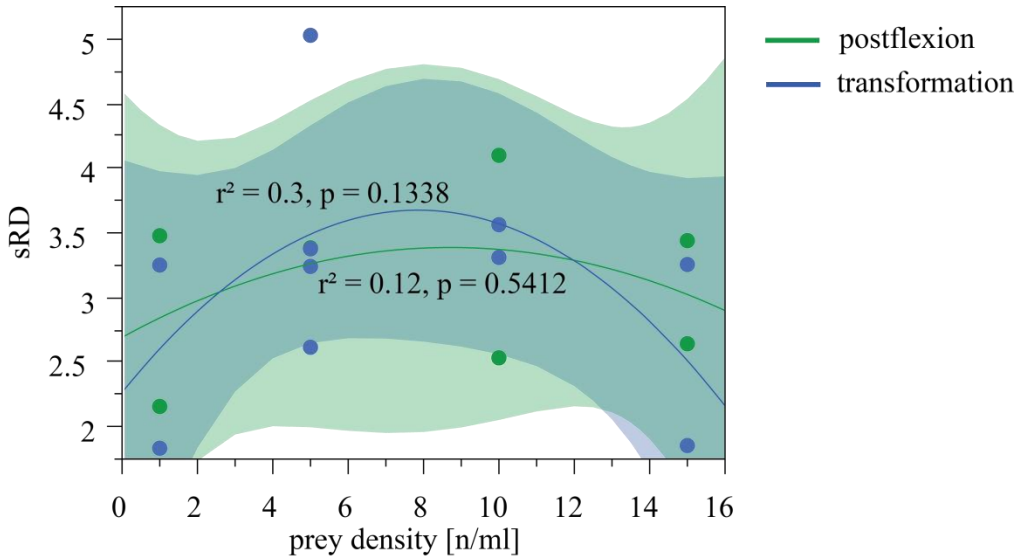

Figure 17: Correlation between sRD of *Trachurus* larvae and prey quantity [n ml^{-1}].
Data were grouped by size classes: postflexion (6 n), transformation (10 n). No significant relationship was observed (Kruskal-Wallis test). The sRD data refer to the last 3 to 4 days of larval life, a mean was calculated for each individual.

3.1.5 Larval condition and growth in relation to food uptake

In order to investigate not only the influence of prey abundance, but also the effect of the actual amount of consumed prey on condition and growth of horse mackerels, relationships between derived parameters (morphological and biochemical) and ingestion rate were examined. All three parameters revealed differences in developmental stages. Neither growth nor condition of postflexion larvae changed considerably with elevated ingestion rate (Figure 18). The CF of transformation larvae increased significantly with enhanced ingestion rate (r^2 = 0.65, p = 0.0046*). Additionally, CF revealed the steepest slope of all examined proxies with regard to ingested prey (b = 0.0004) (Figure 18). The relationship between growth rates and ingestion rates of transformation larvae was not significant, but showed an increasing tendency with enhanced ingestion rate (b = 4.321 * 10^{-5}). sRD values

of transformation stage larvae in relation to food uptake revealed a similar positive correlation (b = 0.0002) than growth rate and consumption rate (Figure 18).

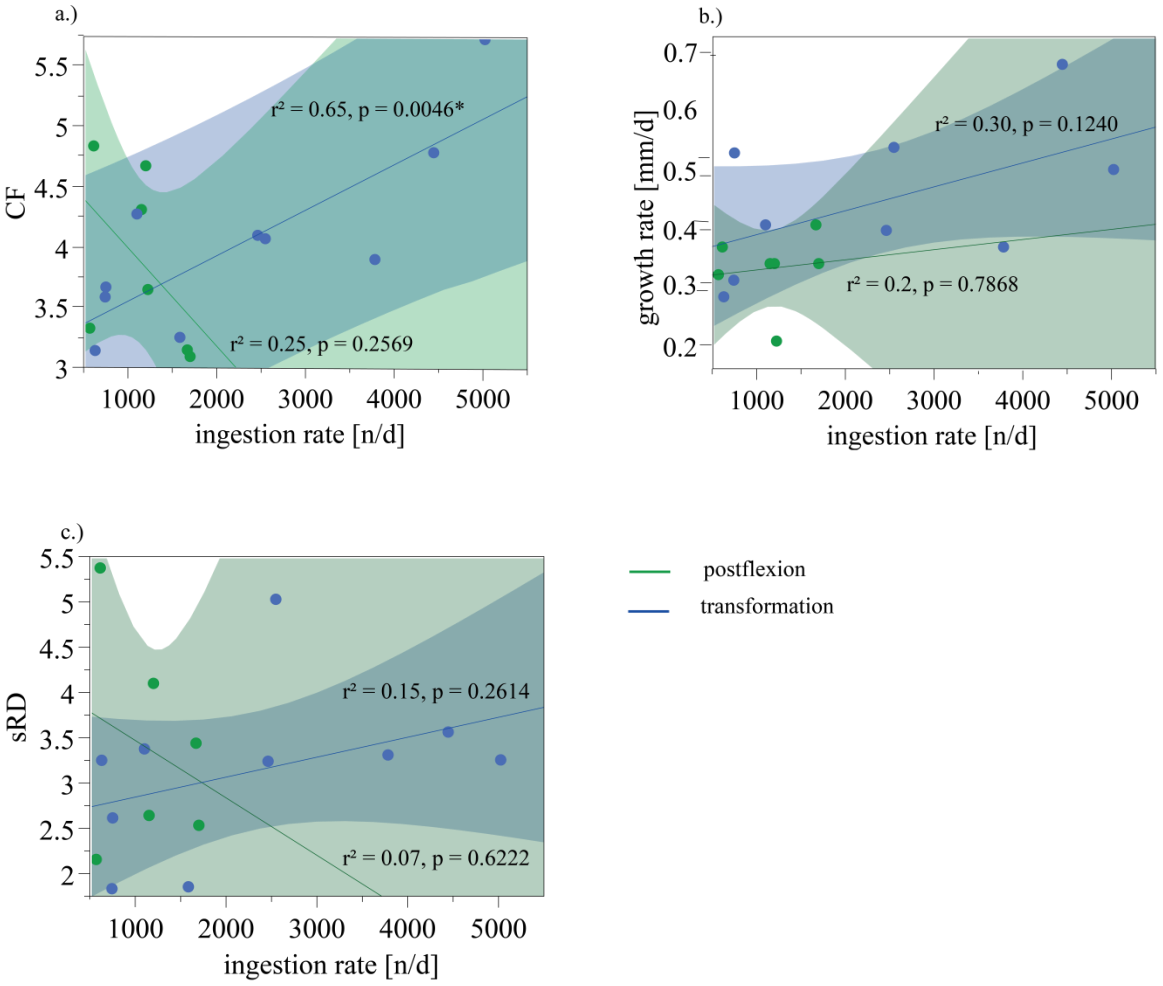

Figure 18: Condition and growth proxies in relation to ingestion rate [n d^{-1}] of *Trachurus* spp.
a) CF b) growth rate [mm d^{-1}] c) sRD. Data were grouped by size classes: postflexion (7 n), transformation (9 n). CF of transformation larvae correlated significantly with ingested food (r^2 = 0.65, p = 0.0046*). No significant influence of consumed prey amount on sRD and growth rate of transformation larvae was observed. Slopes of condition proxies of transformation larvae are subsequently listed: CF: b = 0.0004, growth rate: b = 4.321 * 10^{-5} and sRD: b = 0.0002.

3.2 Starvation experiment of *Trachurus* spp.

The proxies for condition and growth exhibited a high variability, especially between 48 hours and 65 hours. Analyses revealed that the condition is strongly influenced by environmental conditions of *Trachurus'* origin. At several stations (40, 44, 45, 46) only single individuals were caught. In order to guarantee a fundamental comparison, three stations (41, 47, 131) were chosen with which further analysis were conducted. The selection of the stations was based on investigations of environmental conditions and possible time effects. Station 47, located along the Kunene transect (17°S), as well as station 41 at 19°S were sampled during ME 103-1 (January 2014). The third station 131 was situated in the same region (19°S) as station 41, but station 131 was sampled during ME 103-2 (February 2014) (Figure 4). So larvae caught at station 131 and station 41 were exposed to similar thermal conditions although fishing time differed by about 25 days.

3.2.1 Morphometric condition factor

The effect of starvation time on the condition factor of different larval stages was examined. According to a Kruskal-Wallis test the vulnerability to starvation of preflexion and flexion larvae did not differ significantly. Therefore, larvae were grouped by sample origin independent of their larval developmental stage. The morphometric condition factor of *Trachurus* larvae of all three stations (41, 47, 131) declined with an increasing starvation time (Figure 19). At station 41 ($r^2 = 0.44$, $p = 0.0021$*) and 131 ($r^2 = 0.14$, $p = 0.0459$*), a significant effect of starvation stress on larval condition was observed. Good nutritional status of *Trachurus* sampled at station 41 and 47 was prominent (Figure 19). However, these two stations revealed high variabilities within the data compared to station 131. In addition, the calculated CF values from stations 41 and 47 (ME 103-1) were significantly different compared to larval condition at station 131 (ME 103-2) (Kruskal-Wallis test; $p = 0.0308$* - 0.0001*). The CF of larvae from station 131 declined rapidly within the first 24 hours of starvation. However, the CF of 24 and of 65 hours starvation did not change considerably (24 hours: 2.336 ± 0.513; 65 hours: 2.400 ± 0.224) (appendix, A-Table 5). It needs to be noted, that investigations of larvae starved longer than 24 hours were only conducted after 65 hours (Figure 19).

Comparing larval conditions in terms of sampling station, it was striking that larvae sampled at station 41 and 47 had a higher CF than larvae from station 131, despite higher starvation stress at these two station (41, 47) (Figure 19). The lowest CF single value at station 41 (CF = 4.148) after 48 hours of starvation were similar to the highest CF of larvae caught at station 131 (CF = 4.677) after a starvation time of 12 hours. Nevertheless, the CF of larvae sampled at station 131 after 65 starved hours (CF = 2.525) were similar to larval CF of station 41 (CF = 2.402) and 47 (CF = 2.378) after 54 to 55 starved hours, respectively (Figure 19).

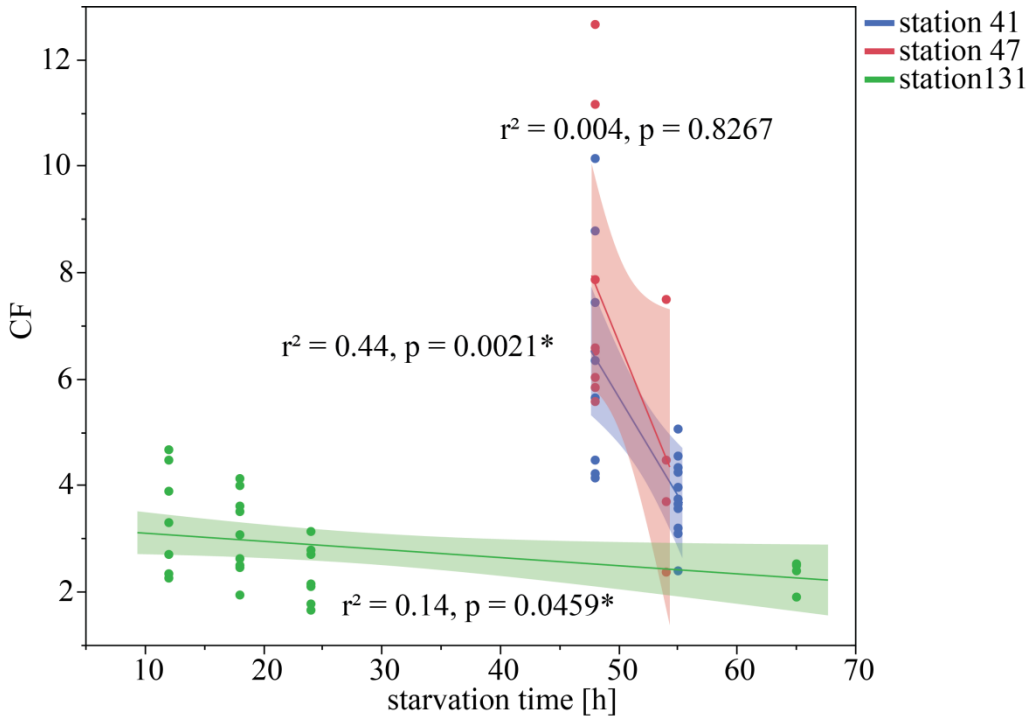

Figure 19: Morphometric condition factor (CF) of *Trachurus* larvae in relation to starvation time [h]. Larvae were grouped by station at which they were caught: 41 (n = 19, b = -0.371), 47 (n = 12, b = -0.5) and 131 (n = 32, b = -0.015).

To complete the analysis of the morphometric condition factor, not only experimental larvae were tested, but also wild larvae, which were not utilized in any experiments. The highest mean CF was observed at station 41 (6.39 ± 2.435) and 131 (6.466 ± 1.9), no significant difference was calculated between these two stations (Kruskal-Wallis test). The mean CF of wild *Trachurus* sampled at station 47 was considerable lower (4.985 ± 3.328) compared to station 41 (Dunn test; p = 0.0197*) and station 131 (Dunn test; p = 0.0111*).

Comparing the CF data of wild and experimental larvae, it was conspicuous that wild *Trachurus* of station 41 featured similar CF value (7.331 ± 1.574) as starved larvae after 48 hours (6.413 ± 2.088). Furthermore, wild larvae caught at station 47 (4.645 ± 3.026) were in an even worse condition than experimental larvae after 48 hours of starvation (7.786 ± 2.499), despite high variance. In contrast, *Trachurus* larvae of station 131 were strongly affected by starvation stress within the first 12 hours. The CF of wild larvae was determined to 7.092 ± 1.597, while CF of starved larvae (12 hours) was halved to 3.838 ± 1.478.

3.2.2 Growth rate determination based on otolith readings

Nonparametric test revealed that also growth rates of preflexion and flexion stages were not differently influenced by starvation stress (Kruskal-Wallis test). Therefore, the grouping of *Trachurus* larvae regarding sample origin was maintained (station 41, 47 and 131). The average growth rate data of *Trachurus* spp. disclosed only a limited distinct pattern concerning starvation stress (Figure 20). Larvae of 19°S latitude (Station 41 and 131) did not offer a significant correlation between growth rate and starvation time (station 41: $r^2 = 0.01$, $p = 0.799$ and station 131: $r^2 = 2.86*10^{-5}$, $p = 0.9798$), whereas growth rate of larvae sampled at 17°S declined significantly with elongated starvation time ($r^2 = 0.43$, $p = 0.0382*$, $b = -0.018$). The larvae caught at station 41 grew independently of starvation stress between 0.228 ± 0.071 mm d^{-1} (at 48 hours of starvation) and 0.252 ± 0.027 mm d^{-1} (at 55 hours of starvation) ($b = -0.001$). Larvae of station 131 were also not negatively affected by starvation stress within the first 24 hours ($b = 1.366*10^{-5}$) (Figure 20). The average growth rate ranged between 0.308 ± 0.039 mm d^{-1} (12 starving hours) and 0.408 ± 0.095 mm d^{-1} (24 starving hours). Even after a starvation time of 65 hours, horse mackerel grew relatively constant with 0.332 ± 0.055 mm d^{-1}. The average growth rate of station 131 after 65 starving hours was similar to growth rates of larvae sampled at station 41 and 47 after 55 hours and 54 hours of starvation, respectively (station 41: 0.252 ± 0.027 mm d^{-1}; station 47: 0.275 ± 0.050 mm d^{-1}) (appendix, A-Table 5).

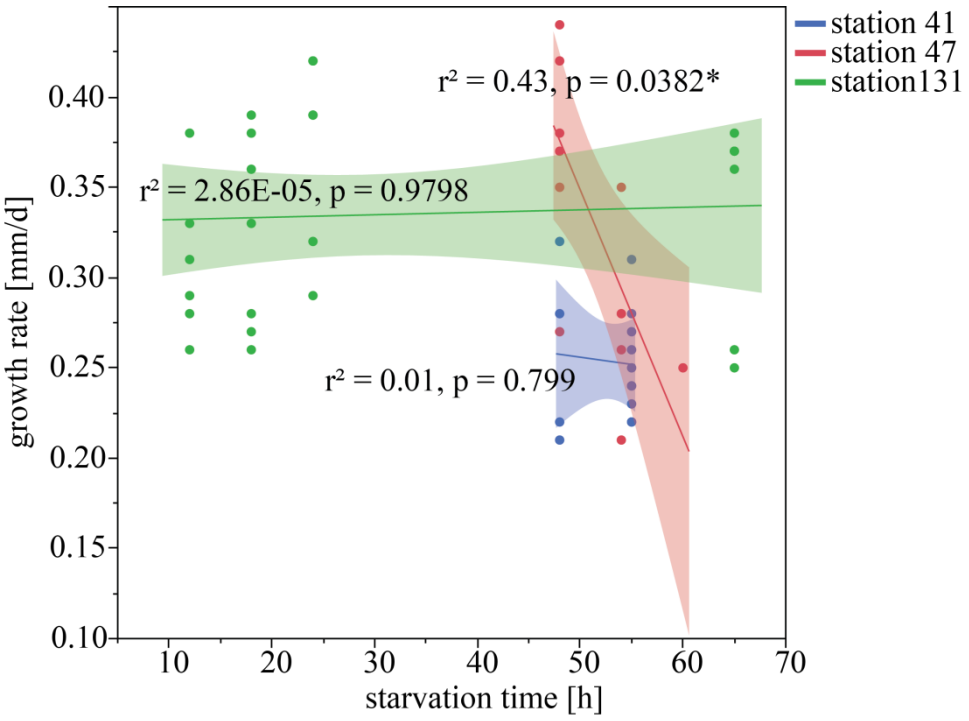

Figure 20: Growth rate [mm d^{-1}] of *Trachurus* spp. related to increasing starvation time [h].
The results were grouped by stations at which *Trachurus* specimens were caught: station 41 (n = 12, b = -0.001), station 47 (n = 11, b = -0.018), station 131 (n = 23, b = $1.366*10^{-5}$). The growth rate referred to mean growth rate of each *Trachurus* specimen determined for 3 consecutive days after catch (dpc).

The back-calculated biomass growth rate [mg d^{-1}] of larvae caught at station 41, 47 and 131 was similarly influenced by starvation stress as growth rate was (Figure 21). BGR of larvae, caught at station 47 decreased with enhanced starvation stress (r^2 = 0.37, p = 0.0632). The larvae gained an average weight of 0.066 ± 0.022 mg d^{-1} at a starvation time of 48 hours, whereas larvae starved for 54 hours exhibited an average BGR of 0.033 ± 0.018 mg d^{-1}. At station 41, BGR-data correlated significantly with increasing starvation time (r^2 = 0.42, p = 0.0095*). However, the BGR rate increased from 0.03 ± 0.013 mg d^{-1} (48 hours starvation) to 0.074 ± 0.031 mg d^{-1} (55 hours starvation) with elongated starvation stress. At station 131, no significant correlation between BGR and starvation time was observed (r^2 = 0.01, p = 0.6915). Despite enhanced starvation stress, horse mackerel constantly gained biomass between 0.072 ± 0.026 mg d^{-1} and 0.139 ± 0.1 mg d^{-1} (Figure 21; appendix, A-Table 5).

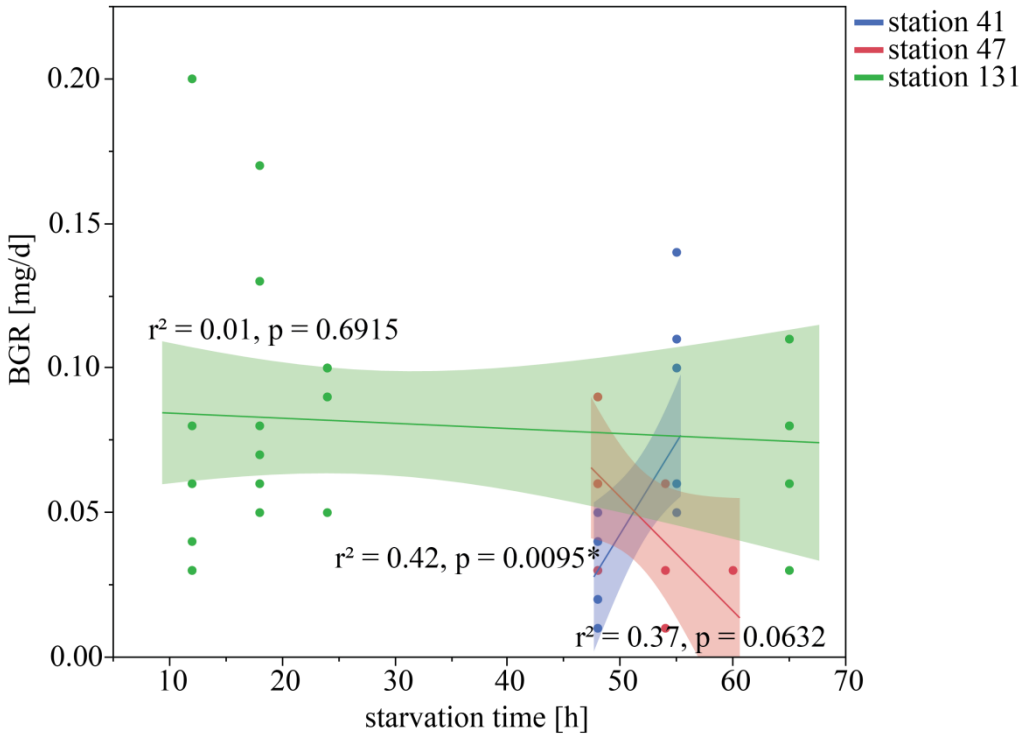

Figure 21: Correlation of BGR [mg d^{-1}] and enhanced starvation time [h].
Trachurus larvae were grouped by stations (station 41 = 9 n, b= 0.006; station 47 = 7 n, b = -0.004; station 131 = 19 n, b = -0.0002) at which larvae were sampled. The BGR referred to biomass increases of each *Trachurus* specimen determined for 3 consecutive days after catch (dpc).

3.2.3 RNA/DNA analysis

In addition to analyses of CF and growth increments of sagittal otoliths, condition and growth potential of *Trachurus* specimens were estimated by nucleic acid data. The condition of both preflexion (r^2 = 0.60, p = 0.0003*) and flexion larvae (r^2 = 0.50, p = 0.0009*) decreased significantly with elongated starvation time. Figure 22 illustrates that the slope b of preflexion larvae (b = -0.023) was steeper than the slope b of flexion larvae (b = -0.019). However, statistical comparison of the slopes and Kruskal-Wallis test (p = 0.5907) revealed that both larvae groups did not significantly differ concerning resistance to starvation stress (Figure 22).

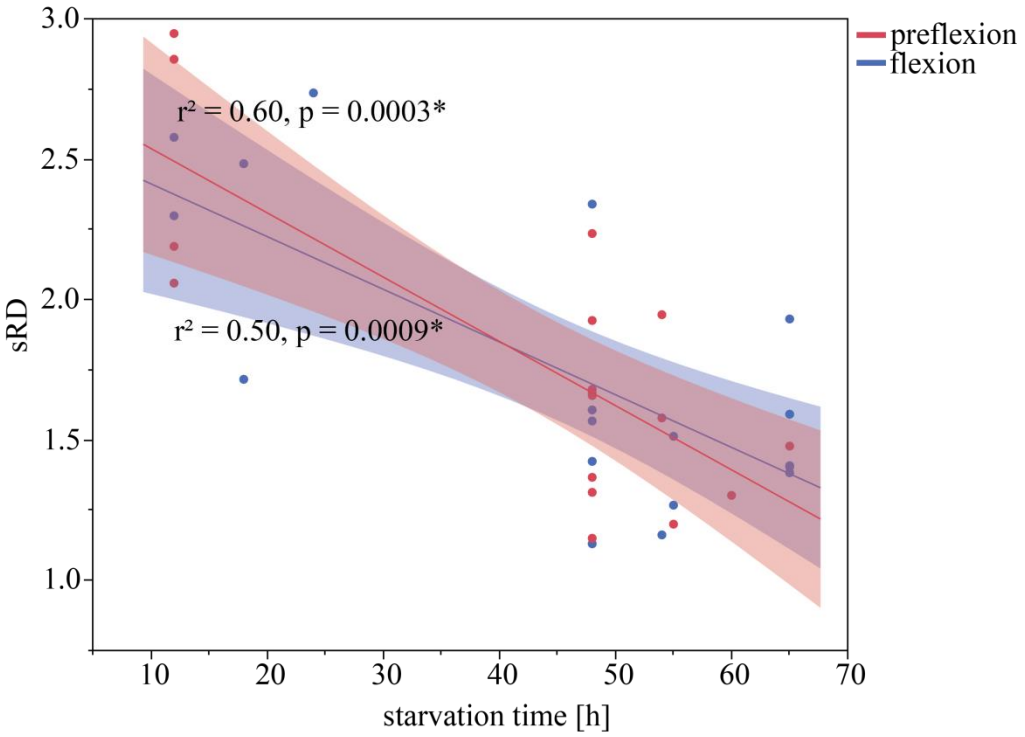

Figure 22: Correlation between sRD values of different developmental stages of *Trachurus* and starvation time [h].
The samples were grouped by size classes: preflexion (n = 28, b = -0.023) and flexion (n = 20, b = -0.019) stage. The sRD data refer to the last 3 to 4 days of larval life, a mean was calculated for each individual.

Therefore, sRD results were again grouped by station (41, 47, 131) at which *Trachurus* larvae were caught. The larval condition of all three stations decreased with elongated starvation time (Figure 23). However, no sRD of larvae sampled at station 41 and 47 correlated significantly with starvation time (Figure 23). Mean sRD of larvae sampled at station 47 declined from 1.663 ± 0.351 to 1.497 ± 0.299 after a starvation time of 48 and 54 hours, respectively. Similar to larvae of station 47, average sRD of larvae caught at station 41 slightly dropped from 1.584 ± 0.358 at 48 starving hours to 1.327 ± 0.135 after 55 hours of starvation. Larval sRD of station 131 decreased significantly with elongated starvation time from 2.488 ± 0.333 after 12 hours of starvation to 1.533 ± 0.191 after 65 hours of starvation (Figure 23). Larval conditions at station 131 after 65 starving hours were similar (1.533 ± 0.191) to the conditions of larvae caught at station 47 (54 hours: 1.562 ± 0.320) and station 41 (55 hours: 1.327 ± 0.135), respectively (appendix, A-Table 5).

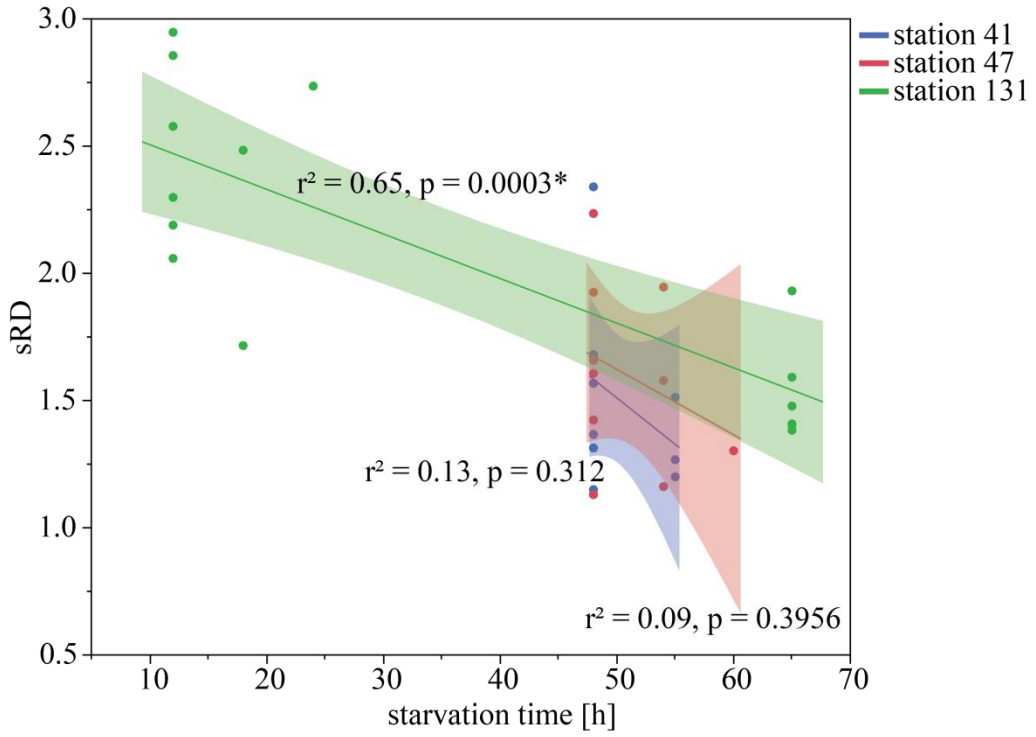

Figure 23: Correlation between sRD of *Trachurus* spp. (grouped by stations) and starvation time [h]. The samples were grouped by station 41 (n = 10, slope b= - 0.031), 47 (n = 9, slope b = - 0.022), 131 (n = 16, slope b = -0.015). sRD data refer to the last 3 to 4 days of larval life, a mean was calculated for each individual.

The threshold level for growth was calculated based on instantaneous growth rates (Gi), using the in situ temperature of the experiment (18 °C). The threshold level for *Trachurus* was determined at a sRD value of 0.84. Despite a starvation time of up to 65 hours, none of the larva fell below this relevant threshold level. Detailed analyses revealed that the 50 % quantile of the data amounted to a sRD value of 1.951. The 25 % quantile of the sRD were retrieved at 1.487, whereas the 10% quantile were estimated at a sRD value of 1.29.

A comparison between sRD data of wild and starved larvae revealed a significant difference between these two groups (Kruskal-Wallis test, p = 0.0002*) (Figure 24). Mean sRD of wild *Trachurus* larvae amounted to 2.616 ± 0.436. The average sRD of the experiment larvae was 1.721 ± 0.472. In conclusion, wild larvae showed a better nutritional condition than experimental *Trachurus* specimens affected by starvation stress. Nevertheless, neither wild nor experimental larvae reached the critical point of 0.84 sRD (Figure 24).

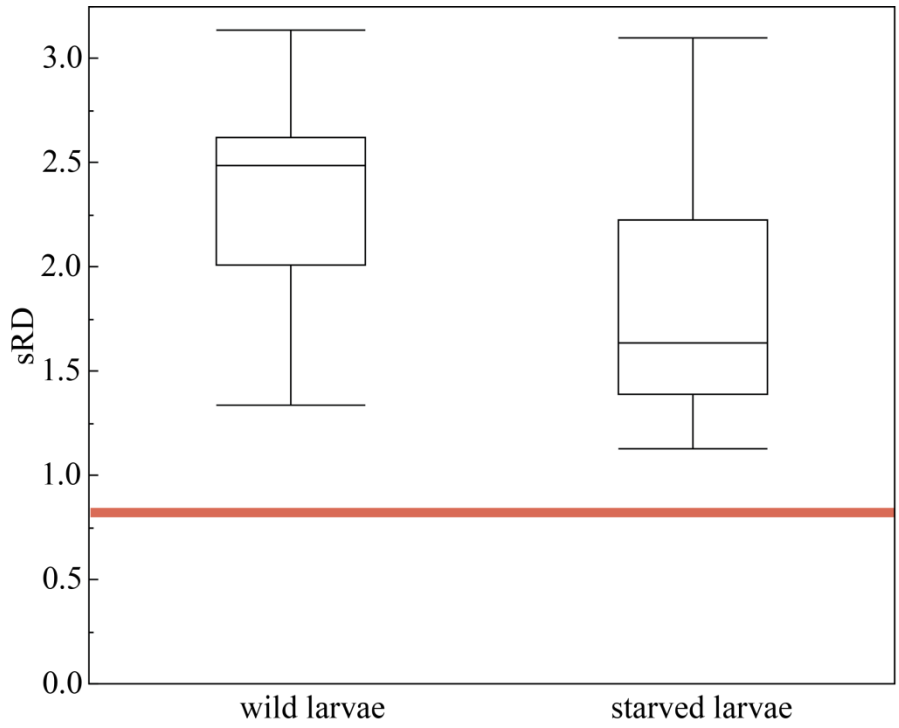

Figure 24: Comparisons of wild and starved *Trachurus* larvae by means of standardized RNA/DNA ratio (sRD).
The wild (n = 77) and starved (n = 82) differed significantly (Kruskal-Wallis test, p = 0.0002*). The red line indicates the calculated threshold level of potential growth (sRD = 0.84) based on a multi-species growth model by Buckley *et al.* (2008).

3.3 Comparison of applied methods

In order to guarantee a scientific and consistent comparison, the analyses focused on *Trachurus* larvae caught at the following stations: 41, 47 (both of ME 103-1) and 131 (ME 103-2). It was ascertained that all methods (growth and sRD) revealed the condition and growth potential of *Trachurus* spp. of the last 3 to 4 days before the specimens were sacrificed.

No significant correlations between the investigated parameters (CF, growth rate, sRD) itself were found. Therefore, residuals of the condition factors with elongated starvation time were compared in order to reveal similar patterns. A decline of *Trachurus* condition proxies (CF and sRD) with enhanced starvation stress was observed in both methods and cruises (s. slope b, Figure 25). Especially condition (CF and sRD) of larvae sampled at ME 103-2 was significantly influenced by starvation. Increment readings of otoliths featured a considerable relation between growth rate and starvation time at station 41 and 47

(b = -0.0282), similar to CF (b = -0.0467) and sRD data (b = -0.0180). However, growth rate (b = 0.0004) of larvae caught at station 131 was not affected by starvation stress (Figure 25). The variability of the generated data was highest in CF, especially within ME 103-1- group, compared to the other two methods (Figure 25).

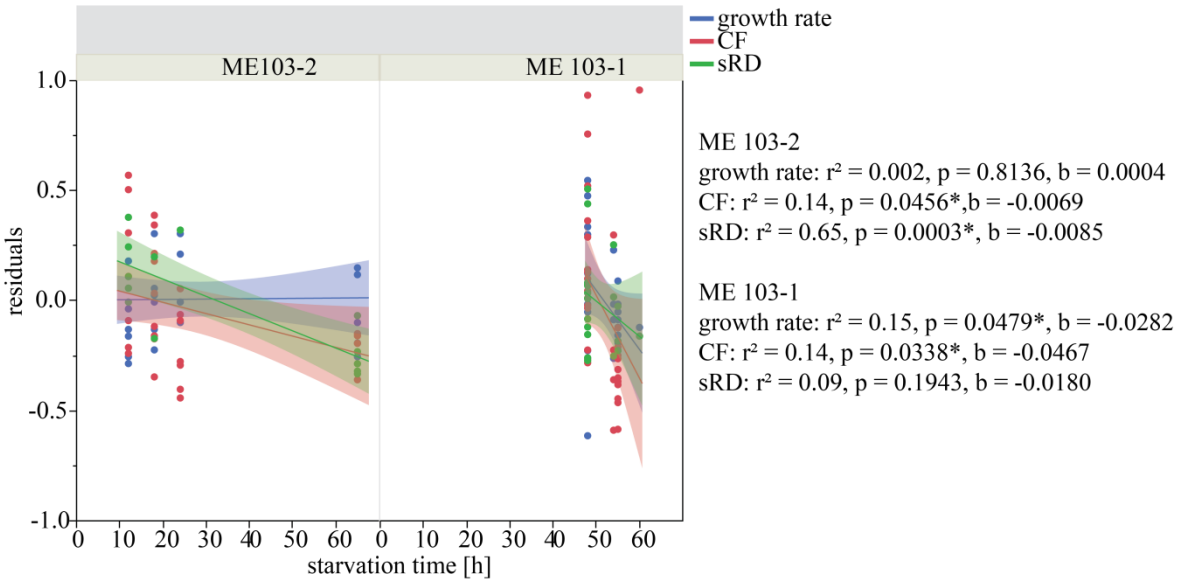

Figure 25: Method comparison: Residuals of CF, sRD and growth rate data of *Trachurus* larvae in relation to starvation stress.
All data (growth and sRD) refer to the last 3 to 4 days of larval life; a mean was calculated for each individual. Slops, r^2 and p-values of condition proxies are listed.

Independent of prevailing environmental condition of larval origin and size classes, the relationship of the two variables and enhanced starvation stress were contrasted (Figure 26). Calculated growth rates based on otolith readings of *Trachurus* did not correlate significantly with starvation time (b = -0.001, r^2 = 0.04, p = 0.2522). Larvae grew daily between 0.243 ± 0.016 mm and 0.453 ± 0.13 mm, independent of starvation. Growth potential (Gi) based on sRD values of larvae declined significantly with elevated starvation stress (b = -0.002, r^2 = 0.47, p < 0.0001*). However, potential growth rate of horse mackerel was roughly less than half of the back-calculated rate using otoliths (appendix, A-Table 6) (Figure 26).

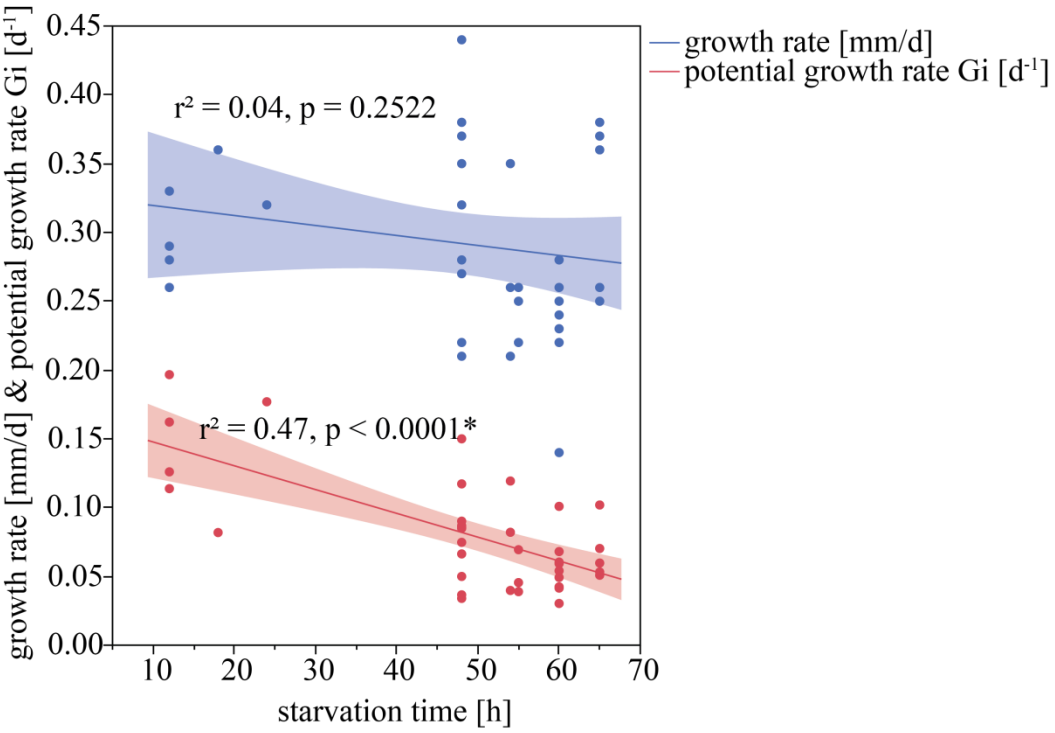

Figure 26: Method comparison between growth rate [mm d^{-1}] and potential growth rate (Gi) [d^{-1}]
Growth rate (b = -0.001) of *Trachurus* was based on otolith reading, whereas Gi (b = -0.002) was calculated by sRD and a multispecies growth model (Buckley *et al.*, 2008). Results of the same *Trachurus* larvae (n = 32) were determined at 3 to 4 consecutive days and of which mean values were calculated.

4 DISCUSSION

Feeding and starvation experiments were conducted under controlled ambient conditions (*e.g.* water temperature, concentration of larvae and prey, *etc.*) to investigate the effect of food quantity on growth and condition of *Trachurus* larvae and juveniles. This study contributes to close the gap in knowledge regarding recruitment success of early life stages of *Trachurus* spp. under changing environmental conditions in the NBCE, which is still existing according to van der Lingen *et al.* (2006), Hutchings *et al.* (2009), Bakun *et al.* (2010) and Ekau *et al.* (2010).

4.1 Assessment of applied methods

In order to evaluate the generated results of *Trachurus*, the restrictions of the applied experimental design and of the analytical methods need to be assessed.

A large sample size and a broad spectrum of developmental stages are essential to thoroughly evaluate the nutritional condition of early life history stages. In contrast to experiments using laboratory-reared larvae, experiments with wild larvae usually deal with a limited amount of samples and a not standardized size spectrum. A successful catch of live fish larvae and early juveniles of a wide size range depends on a high number of sampling stations in their main spawning area, since distribution is patchy and size range at single stations tends to be narrow. Despite restrictions in ship time, sufficient specimens were caught to conduct the scheduled experiments. However, all individuals were sampled during 4 weeks' time; hence juveniles were not from the same cohort as larvae. In addition, the feeding and the starvation experiment could not utilize same size classes. Therefore, no comparisons between these two experiments were possible. Although the number of larvae collected during the cruise limited our interpretation of the results, they give a profound insight into the effect of feeding regime on the condition and growth of larval horse mackerels.

Three methods were applied in order to estimate the nutritional condition of *Trachurus* spp. under changing feeding regimes. The calculation of the morphometric condition factor according to (Heincke, 1908) was part of it. Theilacker (1978) complained about the lack of sensitivity of morphometric measurements to natural variability or more probably the

rapid morphological changes which occur in larval fishes. She further noted that in feeding studies with laboratory reared northern anchovy *Engraulis mordax* larvae, the condition factor was neither constant nor monotonic even when food densities were carefully controlled (Theilacker, 1978). Le Cren (1951) stressed that Fulton's condition factor compares the weight of a specimen or a group of fishes in a length class with that of an ideal fish which is growing without change in form according to the cube law. Neilson *et al.* (1986) and other scientists (Blaxter, 1971; Laurence, 1974) assumed that this index of condition is inappropriate to examine larval condition. Nevertheless, the morphometric condition factor has been constantly used as a rapid and affordable method to evaluate the overall nutritional condition of individual fish larvae during the last decades (*e.g.* in Checkley, 1984; Neilson *et al.,* 1986; Geist *et al.,* 2014).

Increment reading of sagittal otoliths is a useful tool for age and growth determination of fish larvae (ICES, 2004). However, this method faces some restrictions which need to be considered, especially when aging young or slow-growing larvae. Limited resolution of the light microscope, causing several increments to be invisible, is the main reason for the low accuracy found in slow-growing larvae (ICES, 2004). The resolution is affected by both the quality of the equipment and the skills of the operator (Stevenson and Campana, 1992). However, the model organism *Trachurus* spp. is characterized by fast growth (Westhaus-Ekau, 1988) and good readability of otolith increments (Katsuragawa and Ekau, 2003). Furthermore, an extensive training concerning processing and reading of otoliths took place before analyses started. This training and the fact that the otolith readings were controlled by a second person reduced potential bias in this study.

Over the past three decades, RNA/DNA ratios have been widely applied as biochemical index for determining larval condition. It is an ecophysiological index that gives a measure of the synthetic capacity of the cell and correlates with nutritional status (Clemmesen, 1994; Folkvord *et al.,* 1996; Buckley *et al.,* 1999; Olivar *et al.,* 2009). More recently, nucleic acids are used as an estimation tool of weight-specific growth rate (G_i) in fish larvae (Buckley *et al.,* 1984; Caldarone, 2005; Malzahn *et al.,* 2007). Even though some studies recommended caution in the use of RNA/DNA ratios due to a lack of sensitivity of some techniques and the influence of the applied analytical protocol (Caldarone *et al.,* 2006). It was pointed out that the RNA/DNA ratio may be differently influenced by age, size, de-

velopmental stage and temperature (Clemmesen, 1994; Rooker *et al.,* 1997; Satterwhite, 2007; Buckley *et al.,* 2008). Additionally, Olivar *et al.* (2009) investigated systematically various contributions of tissue type to RNA/DNA ratio (*e.g.*, head, eyes, muscle, gut) relative to whole body RNA/DNA and concluded that muscle tissue had consistently higher RNA/DNA values than other tissues. Nonetheless, there are several advantages in using RNA/DNA ratios as a proxy for condition in order to determine critical stages during the early life history of fish (Clemmesen, 1996): 1) The method is reliable and sensitive enough to measure individual larva of a minimum weight of 10 µg dry weight. Consequently, there is no need for pooling larvae, resulting in a high resolution data set. 2) Time from catch to preservation is less critical than in other methods. Clemmesen (1996) proved that 30 minutes between catch and preservation do not change the nucleic composition. 3) The RNA/DNA ratio is not affected by short time stressors resulting from catching. Howbeit RNA/DNA ratios are a measure of physiological stress due to metabolic changes occurring in larvae within the previous 3-4 days (Clemmesen, 1996). In the framework of this study, several precautions were taken in order to minimize the mentioned analytical issues: *Trachurus* larvae were processed according to the protocol developed by Clemmesen *et al.* (2003) and ICES (2004). The results were standardized (Caldarone *et al.,* 2006) and only compared with standardized reference data. Furthermore, results of feeding and starvation experiments were not put in relation, *inter alia,* due to differences concerning developmental stages and analytical procedure (muscle tissue *versus* whole larvae). Thermal differences among the laboratory-reared *Trachurus* larvae and juveniles could be neglected. In conclusion, the applied RNA/DNA method, despite restrictions, responded to changes in food availability within the set time frame of this study. It proved sensitivity to food availability and illustrated the power of this technique for assaying organisms in a changing environment.

Quantitative evaluation of both, growth rate and condition of larvae in relation to environmental conditions at the time of capture, is an essential prerequisite for predictive assessment of survival potential. For the first time, the analyses of growth and condition were combined on the same individual *Trachurus* spp. larvae, presenting the opportunity to directly relate findings from two different growth indices of the same specimen instead of statistical relationships based on analyses of different individuals. ICES (2004) acknowledged the advantages of a combined study, but noted that great care must be taken when

joined studies are conducted. Otolith extraction may lead to a loss of larval tissue and therefore a reduction in nucleic acid content. In this study all precautions of keeping tissue loss as low as possible were taken. Certainly, the generated results of otolith microstructure and nucleic acids of the same *Trachurus* specimens can be used to study long-term and recent growth rates, condition and their relation with environmental variables such as food availability. In the course of method comparisons, growth and condition proxies (CF or sRD) were plotted against each other. No significant correlations were found. This was mainly because the three measurements focused on different organization levels and time scales (Ferron and Leggett, 1994). The condition factor is based on length and weight of fish larvae; hence it is an integrative factor. This might be accompanied with some bias potential. For instance, starvation can lead to water retention in the larval body, thus influencing CF results (Neilson *et al.*, 1986). Increment readings of otoliths refer to carbonate depositions in the larval inner ear, which can be used to gain information about larval long-term growth-rates, but is not very informative about short-term events (Hovenkamp and Witte, 1991). The understanding of the underlying physiology of somatic and otolith growth and development has not been sufficiently advanced. Especially, the decoupling of otolith and somatic growth under some circumstances is recognized but not fully understood (ICES, 2004). Nucleic acid analyses determine the activity and abundance of ribosomes, respectively. Unlike otolith readings, RNA/DNA ratios are commonly used to forecast growth and survival potential of larvae in order to predict recruitment (Clemmesen, 1996). Although the RNA/DNA ratio reflects and is at least partially determined by past feeding success, it is not certain whether the effect of prey density on growth rate is actually mediated or simply accompanied by a change in the RNA/DNA ratio (Buckley, 1979). In conclusion, all three methods revealed information about the condition and growth of *Trachurus* focusing on different time scales. So, it was possible to get insights into short- and possible long-term effects of changing feeding regimes of early life history of *Trachurus* in the Benguela system.

Laboratory-derived functional responses are often consulted to assess the extent to which naturally occurring food regime may influence larval mortality and year-class strength of a fish cohort (Houde, 1978; Anderson, 1988). However, extrapolation from laboratory estimates of food ingestion rates and linked larval condition and growth can bias the interpre-

tation of larval feeding ecology (Anderson, 1988), assuming that laboratory derived data are comparable in form and magnitude to the functional responses of larvae in nature. This assumption may not be valid (MacKenzie *et al.,* 1990). A variety of biotic and abiotic environmental factors have been identified to affect larval growth and biochemical condition. A laboratory experiment can only cover these influences partially. Biotic factors include food availability, ontogenetic stage, parental source, dial periodicity and diseases (Rooker *et al.,* 1997). Abiotic factors are generally associated with temperature, dissolved oxygen, and toxicants (Rooker *et al.,* 1997). Besides, experimental conditions themselves may influence laboratory ingestion and growth rates of larval fish (Houde, 1975). For instance, Buckley *et al.* (1984) and Blaxter (1988) observed that minimal food quantity needed to support growth in the laboratory was higher than those in the field. Based on this assumption, the probability of larger larvae encountering and capturing suitable food items in sufficient quantity for survival increases, whereas the probability of larger faster-growing larvae being eaten by predators decreases (Buckley *et al.,* 1984; Cushing, 1996). Mackenzie *et al.* (1990) pursued this approach and suggested that the rates of encounter might be greater in the wild than in the laboratory due to turbulent water conditions. On the contrary, Geist (2013) observed a lower nutritional condition factor of *Trachurus capensis* when total ichthyoplankton density was high, resulting from a high larval density which lead to food competition and subsequently causes low nutritional condition. In conclusion, the difference between in situ and laboratory estimates of ingestion rates, condition and growth rates as a function of prey density is primarily caused by the inability to adequately represent the real contact rate of larvae and their prey. Most laboratory experimental designs fail to incorporate relevant variables known to influence prey encounter rates and selection, *e.g.* small-scale temporal and spatial patchiness in the distributions of larvae and their prey (MacKenzie *et al.,* 1990). In addition to laboratory conditions, the data collection might be biased as well. The presented study, tried to reduce the personal bias, by standardizing the process of counting living *Artemia* and consistent conduction by the same person. In conclusion, laboratory derived results are essential and should not be underestimated. They make a huge contribution to basic research. Experiments under controlled ambient conditions (*e.g.* water temperature, concentration of larvae and prey, *etc.*), facilitating a reduction of a complex process to essential factors. Therefore, laboratory derived data of this

study can be used as an indication regarding influences of food availability on growth and nutritional condition of *Trachurus* spp. in natural environments.

Food concentration is a crucial determinant to evaluate the nutritional condition and growth potential of fish larvae. The food density was selected based on previous studies (Klumpp and Westernhagen, 1986; Houde, 1972; Garrido *et al.*, 2012) and results of preliminary tests on board of Meteor ME 103-1. However, after analyzing the data there were some indications that the chosen prey densities were well above limiting levels. The consumption rate of *Trachurus* was about 88 % at a prey density of 1 nauplia ml^{-1}, the lowest prey density in feeding experiments, and declined with enhanced prey densities. Estimated gross growth efficiency (K_1), reflecting the part of ingested food incorporated into tissue, also induced such conclusions. K_1 is at maximum at an intermediate ingestion rate and declines when more food is consumed than needed (Klumpp and Westernhagen, 1986). Our feeding experiment with *Trachurus* spp. determined a descending portion of the K_1-ingestion relation, which corresponds to laboratory studies with sea breams (*Acanthopagrus* sp.; Stepien (1976), Houde and Schekter (1980)). It seemed that more food was consumed than the *Trachurus* larvae needed to increase in body size. Consequently, no peak of gross growth efficiency could be determined, although the weight gain and growth rate tended to increase up to a food density of around 10 nauplii ml^{-1}. It seems that the increasing portion of the ingested food not used for growth in size and mass was defecated or metabolized. Growth rate of larval Pacific herring (*Clupea pallasi*) continued to increase but assimilation efficiency declined at high ingestion rates, indicating an increase in the defecated rather than metabolized fraction (Checkley, 1984). He concluded that fish larvae maximize either their rate of growth or gross growth efficiency, but not both simultaneously (Checkley, 1984). The present study indicated that larvae adapt to maximum ingestion and growth rate rather than optimized growth efficiency. This concept is supported by the findings of Laurence (1977) as well as Klumpp and Westernhagen (1986). Such an opportunistic feeding strategy is reasonable for fish specimens forced to respond either to low food concentrations or occasional patches of prey, which are characteristics of larval environment. For future investigations, a broader range of prey densities is recommendable. Especially limiting food levels should be in focus (*e.g.* 0.1 nauplia ml^{-1}).

Not only food density, but also food quality is crucial for larval survival and recruitment success (Cutts *et al.,* 2006). Wild zooplankton was the first choice as food sources for the experimental design. However, the coordination of catching and culturing sufficient amounts of zooplankton and simultaneously sampling fish larvae was not realizable on cruise ME 103. Therefore, this study relied on *Artemia salina* nauplii, which are a well-established food source for fish larvae and juveniles (Flüchter, 1965; Checkley, 1984; Kim *et al.,* 1996). Nonetheless, results of this study indicated that the offered prey *Artemia salina* was not an optimum prey for larger specimens (20-40 mm). Several studies have also questioned the nutritional adequacy of *Artemia* (Dabrowski, 1984; Kraul, 2006). Particularly, highly unsaturated fatty acids (HUFAs), essential for larval development, are available only to a limited amount in brine shrimps (Kraul, 2006). Juvenile *Trachurus* needed to consume high quantities in order to meet their energy demands. Westhaus-Ekau (1988) confirmed a length-dependent change in the prey spectrum of *Trachurus* concerning quantity and quality of food. Takii *et al.* (1994) complimented that nutritional demands change remarkably at various stages, morphological development, growth, and reproduction of fish. The amount of ingested prey by larger larvae decreases when they succeeded to feed on bigger food organisms. In the natural environment, larger larvae of herring may compensate their higher food demands by extending the searching area in order to increase their foraging efficiency (Rosenthal and Hempel, 1970). Despite difficulties in providing adequate food for juveniles, it is assumed that changing quantities of *Artemia salina* as food source for *Trachurus* larvae simulated possible food densities in the marine environment in order to get information about the effect of changing feeding regimes on condition of *Trachurus* early life history stages focused in this study.

The latency of an experiment, determines the duration of environmental parameters necessary to change the condition index. As mentioned above, the applied methods (growth and RNA/DNA ratio) focus on different time scales (long-term *versus* short-term events). The duration of the conducted experiments were supposed to be > 3 days, however this was not realizable due to a limiting sample size. Nonetheless, according to previous studies (*e.g.* Clemmesen, 1994) the time frame of the conducted experiments (feeding experiment: 8 days, starvation experiment: 65 hours) was long enough to detect changes in condition and growth of fish larvae. Clemmesen (1994) reported that fed and starved herring (*Clupea harengus*) larvae (>10 days) could be distinguished after 3 to 4 days. Similarly, Richard *et*

al. (1991) reported that fed and starved larval and juvenile sole (*Solea solea*) could be discriminated within a few days. Theilacker (1978) observed that 3 days-starved jack mackerel (*Trachurus symmetricus*) refused to eat, assumingly because larvae already reached the critical point. The reported feeding capability of jack mackerel, after an initial period of starvation, was similar to other pelagic fish larvae (Blaxter, 1965; Lasker *et al.,* 1970; May, 1974). So it was assumed that the chosen time frame of the experiment was sufficient to detect changes in growth rate and condition of *Trachurus*. Nevertheless, in order to cover a multifaceted effect of starvation stress on the condition and growth of *Trachurus* larvae, further experiments need to be elongated until larvae die. In case the amount of live fish larvae is restricted, the chosen interval of 6 hours can be elongated up to 24 hours in order to cover an expanded starvation period.

4.2 Nutritional effects on early life stages of *Trachurus* spp.

4.2.1 Effect of food quantity on condition and growth of larvae and juveniles

Feeding ecology, influencing the early life history of fish, needs to be investigated in order to understand recruitment success and population dynamics of a fish stock (Cushing, 1975). Temperature and body size are two key factors concerning ingestion rate and thus growth and condition of larvae (McKenzie *et al.,* 1990). Influences of different thermal condition on *Trachurus* could be excluded within the laboratory experiment (18 °C ±1). However, differences between developmental stages were observed. Consequently, the effect of food concentration regarding varying larval stages was separately investigated.

Postflexion larvae consumed the most in relation to their body mass. Interestingly, no distinct response, neither in condition nor in growth of *Trachurus* larvae, to high energy intake was observed. The absence of a correlation between prey density, ingestion rate and condition of larvae was attributed to a gradual development of both, foraging skills and fish digestive tract. The development of the intestine starts at a larval body size of 12 mm (Westhaus-Ekau, 1988). Digestive tract development is important for efficient assimilation of nutrients needed for growth. Westhaus-Ekau (1988) assumed that with increasing length, the digestion of food gets more efficient. The postflexion intestine of *Trachurus* was not fully developed yet, suggesting that the digestion efficiency was low. Hence, lar-

vae needed to consume at high rates in order to gain enough energy to meet metabolic requirements. Therefore, the absence of a response concerning condition proxies (CF, growth rate and sRD) in relation to ingestion rates may be attributed to a low digestion efficiency of small *Trachurus* larvae. Besides varying digestion efficiencies, developmental stages differed concerning the consistency of the generated data. Particularly the consumption rate and the condition (CF) of postflexion larvae exhibited a high variability. It seems that foraging of postflexion larvae was less specific than of transformation larvae and juveniles. Eyesight of horse mackerel is probably the most important sense in finding prey because they are visual predators (Blaxter, 1988). The lack of eye pigmentation at hatching has been found for many teleosts, including *Trachurus*, suggesting that eyes are probably non-functional at this time (Blaxter, 1988). Eyes of *Trachurus* begin to develop pigments in larvae of 2.2 mm in size (Ahlstrom and Bell, 1954). Most larvae from 8 to 12 mm are still short sighted and night-blind, because visual acuity and vision at low light intensity are directly dependent on the diameter of the eye (Miyataki *et al.*, 2000). Thereafter, visual acuity improves, allowing *Trachurus* larvae to detect both prey and predators more easily. Moreover, the ossification of all fins, rays and spines is completed at a *Trachurus* body size of around 15 mm (Haigh, 1972) and leads to a higher swimming capacity enabling a search for prey within an expand water volume. In this study, the incomplete development of eyes and fins of postflexion larvae led to an inefficient foraging and consequently to a high variability in consumption rate and condition of postflexion *Trachurus*. Once physiological and morphological traits were developed (*i.e.* digestion tract, ossification, visual skills), the influence of food density on proxies for condition and growth of *Trachurus* became more prominent.

Transformation larvae and juvenile of *Trachurus* seemed to exhibit a more advanced gastric tract than postflexion larvae, facilitating a more efficient digestion. Transformation larvae ingested prey items at a high rate until a saturation point was reached. This relationship corresponded with the interconnected condition and growth of *Trachurus*. Juveniles' prey consumption increased linearly with prey quantity. However, condition and growth rate data of juveniles were insufficient to provide information about the relation of prey density and the nutritional state of larger *Trachurus*. In conclusion, it is assumed that digestion becomes more efficient with increasing body size during *Trachurus* ontogeny,

which may be an important stage-specific feature representing the end of a critical period in horse mackerel early life history.

In the following, the food uptake and consequently the condition and growth during the transformation stage, due to their positive correlation with enhanced food concentration, are particularly highlighted.

In the present study, transformation larvae ingested prey items at a high rate until a saturation point at around 10 nauplii ml^{-1} was reached. All morphological and biochemical data showed a similar functional response. Laboratory ingestion rate studies involving several species of larval fish also observed such a sharp functional response at low food densities and a saturation of consumption rates at higher prey densities (Ivlev, 1961; Klumpp and Westernhagen, 1986; MacKenzie *et al.*, 1990). McKenzie *et al.* (1990) conducted a meta-study based on consumption rates of eleven marine and estuary fish species (*e.g.* plaice *Pleuronectes platessa*, blenny *Blennius pavo*, herring *Clupea harengus*) during their early life histories. The study revealed almost a 30-fold lower saturation point (185 µg l^{-1}) compared to *Trachurus* larvae of this study (5405µg l^{-1} = 10 nauplii ml^{-1}). The discrepancies between both results can be attributed to several differences within the methodical approaches. MacKenzie *et al.* (1990) determined the saturation point by means of a model. The model, based on ingestion rate of several species of marine and estuarine environment, resulted in a generalization of the data. However, a saturation threshold of food uptake at a much higher food concentration (*Trachurus* spp.) compared to a lower threshold (modeled data) seemed to be more reasonable for fish larvae occurring in a rapidly changing environment and thus forced to utilize food patches most efficiently.

Several scientists (*e.g.* Hjort, 1914; Anderson, 1988; Cushing, 1990) reported a distinct dependency between prey availability, energy intake and consequently the growth and condition of larval fish resulting in a high variability of fish recruitment. In this study, a correlation between food uptake and condition proxies (esp. CF and growth) of *Trachurus* was found. Feeding and growth rates of *Trachurus* spp. increased exponentially with prey density until a saturation level was reached. Johnson and Dropkin (1995) observed a prey-dependent growth rate of American shad larvae (*Alosa sapidissima*) below a prey concentration of 0.5 to 1 *Artemia* nauplia ml^{-1}, whereas feeding success and growth of early Atlantic mackerel larvae (*Scomber scombrus*) increased with density of *Pseudocalanus* sp.

nauplii up to a saturation threshold of 1 µg C l^{-1} (Robert *et al.,* 2009). Despite of unit adjustments, reference values were far below the estimates of horse mackerel (10 nauplii ml^{-1} = 330 µg C l^{-1}). This was mainly attributed to different methodical approaches concerning larval species, prey quantity/quality as well as the geographic area of the investigation. Nevertheless, the saturation point of *Trachurus* larvae seemed to be very high, independent of methodical issues. It is questionable if this can only be explained by a higher food uptake of *Trachurus* larvae or additionally with a higher assimilation efficiency of the species, which was not investigated in the framework of this study. However, similar pattern were also found in the condition (sRD) of transformation *Trachurus*. Despite discrepancies between sRD and ingestion rate, higher food density led to a higher proportion of well-conditioned *Trachurus* larvae until a saturation threshold was reached. Larval *Trachurus* reached a maximum sRD value (3.3-3.4) at around 10 nauplii ml^{-1}, whereas sRD values at food concentrations below and above this threshold were considerably lower (*e.g.* at 1 nauplia ml^{-1}: 2.5-2.8 sRD). Laboratory reared striped brass larvae (*Morone* sp.) already reached a sRD equilibrium at 1 nauplia ml^{-1} (Wright and Martin, 1985). The measured sRD values (2.25-3.0, Wright and Martin, 1985) corresponded with sRD data of *Trachurus* larvae at the lowest food concentration. The high saturation point of *Trachurus* in terms of food uptake may contribute to a good adaptation to natural occurring food patches. Hence, it can be assumed that horse mackerel larvae benefit in terms of inter-specific food competition resulting in a higher nutritional condition compared to other species provided with similar assimilation efficiencies as *Trachurus* larvae.

Trachurus larvae (16-20 mm) consumed up to 71.41 % (4114.27 ± 331.44 n d^{-1} at 10 nauplii ml^{-1}) of their body mass, resulting in a high growth rate (0.535 ± 0.165 mm d^{-1}). High feeding rates and their positive relationship with growth were also reported in larvae of several *Trachurus* species: *T. declivis*, *T. symmetricus*, *T. trachurus* in Tasmania, the California Current region, and the west-central North Sea, respectively (Arthur, 1976; Young and Davis, 1992). Interestingly, the back-calculated growth rate of transformation larvae (0.535 ± 0.165 mm d^{-1} at 18 °C) in this study corresponded with growth rates of *T. lathami* from tropical south-eastern Brazil (15.8 to 25.5 °C) which exhibited a maximum growth rate of 0.4-0.5 mm day^{-1} at a body size of 15 to 53 mm (Katsuragawa and Ekau, 2003), whereas growth rates of *T. capensis* larvae (16-20 mm) caught during 2008 to 2011 in the NBCE was only determined to be 0.296 ± 0.129 mm day^{-1} (median temperature:

18 °C; recalculated data of Geist (2013)). In general, higher temperatures stimulated food consumption by enhancing the larval metabolism, leading to an elevated growth rate (Checkley, 1984). Interestingly, the thermal stimulation of *T. lathami* larval growth (incl. prevailing food concentration) was not higher than the effect of enhanced food concentration on the metabolism of *Trachurus* spp. in a more temperate environment (18 °C laboratory condition). Considering growth rate results of 2008 to 2011 (recalculated data of Geist (2013)) and 2014 (this study) respectively, it seemed that food availability was a limiting factor concerning larval development during 2008 to 2011, reflected in a retarded growth rate of *T. capensis*.

In this study, the condition (CF) of transformation larvae correlated positively with food abundance and ingestion rate. All *Trachurus* larvae were in good condition (CF > 3), whereby a maximum value of 4.335 ± 0.442 at 10 nauplii ml^{-1} was reached. A comparison between the results from feeding experiments and CF data of wild *Trachurus* conveyed huge discrepancies. Transformation larvae, sampled in the Benguela upwelling system in 2008 to 2011, featured only a mean CF of 1.463 ± 0.225 (recalculated data of Geist (2013)). Such a low CF indicates a malnourished status of larvae back then.

The biochemical condition of transformation stage larvae ranged between 2.5 and 3.44 sRD. Comparing these results with wild caught *Trachurus trachurus* larvae of 5.57 mm to 6.25 mm size (3.6 sRD; Díaz *et al.,* 2009), it seemed that sRD values of *Trachurus* of this study were lower than of wild larvae. Many studies estimated a larval RNA/DNA ratio between 3 and 4 (Buckley *et al.,* 1984; Wright and Martin, 1985; Richard *et al.,* 1991; Folkvord *et al.,* 1996; Caldarone, 2005). However, RNA/DNA ratio in reared larvae was generally much lower than in sea-caught larvae, where values of 6 to 8 were common (Buckley *et al.,* 1984). Richard *et al.* (1991) warned of a comparison of wild and laboratory data. Usually, prey offered to reared larvae may be of lower nutritional quality than wild plankton, thus influencing the nucleic acid composition differently (Richard *et al.,* 1991). In addition to prey quality (*Artemia* nauplii *versus* wild zooplankton), differences in larval development (transformation *versus* flexion) may need to be considered. A previous study (Díaz *et al.,* 2009) recommended caution while comparing different developmental stages with regard to prey-dependent condition of fish larvae. Energy storage levels of the earliest larvae remain low, which implies more energy investment in growth

by hyperplasia (increase in the amount of cells due to proliferation) than developmentally advanced larvae. Once larvae develop all essential anatomical characteristics for escape and foraging performances, the energy input in growth declines, while growing by hypertrophy (increase in volume due to the enlargement of its component cells) is enhanced. The decrease in the overall growth rate with age in late larvae and juveniles is reflected in a reduction in RNA/DNA ratios (Chícharo and Chícharo, 2008). Transferring this knowledge to the generated sRD values, the lower sRD value of *Trachurus* spp. during transformation stage may indicate an equally good nutritional condition as *Trachurus trachurus* wild larvae during notochord flexion stage.

An efficient processing of consumed prey as well as an adequate gastric evacuation rate are important to meet the high energetic requirements of the continuous activity of fish larvae (Pillar and Barange, 1998). Knowledge of stomach evacuation rates reveals information about feeding rates and energy budgets of fish (Handeland *et al.*, 2008). Several factors, of both biological and physical nature, influence the evacuation rate in fish, but temperature and food type seemed to have the greatest impact (Pillar and Barange, 1998). Therefore, direct comparisons with values reported in the literature were limited. The highest gut evacuation rate observed for postflexion *Trachurus* spp. (47.35 ± 22.88 minutes, 18 °C) was lower than the rapid evacuation rates of Atlantic mackerels (*Scomber scombrus*; 1-2 hours, at around 15°C) during their flexion stage while feeding on zooplankton (Houde and Schekter, 1980; Peterson and Ausubel, 1984). Gastric evacuation rate for other *Trachurus* species such as larval jack mackerel (*T. japonicus*) in the southern East China Sea were estimated to 2 hours (flexion stage, 21 °C; Sassa and Tsukamoto, 2012) and 4-6 hours of evacuation time for *T. declivis* of eastern Tasmania (postflexion stage, 18 °C; Young and Davis, 1992). The differences in rates can be mainly attributed to variable environmental factors (*e.g.* prey quality, temperature, *etc.*). In addition, this study revealed distinct scaling effects of larval size on stomach evacuation rate. The gastric evacuation rate of postflexion larvae was more extended than the rate of transformation larvae. Differences in developmental stages in terms of digestion rates were also observed in spotted sea trout (*Cynoscion nebulosus;* Wuenschel and Werner, 2004). However, gut evacuation time of sea trouts increased with increasing fish size (Wuenschel and Werner, 2004). In general, the development of fish intestine is accompanied by the formation of gut loops. Westhaus-Ekau (1988) assumed that this development of larval intestine results in an elongation of

digestion and resorption time. However, based on generated results of *Trachurus* spp. an optimization of the digestion efficiency due to a loop-formation was not verified. An increase in digestive enzyme causing higher assimilation efficiency may explain a lower gut evacuation rate coupled with a better nutritional condition of transformation larvae compared to postflexion larvae. Furthermore, the generated *Trachurus* spp. data of gastric evacuation rates demonstrated that all developmental stages were influenced by temperature. For instance, the mean gut evacuation rate of *Trachurus* spp. during transformation stage was determined to 40.72 ± 18.12 minutes at 18 °C, whereas gastric evacuation rate of transformation larvae declined (36.69 ± 0.69 minutes) with enhanced temperature (22 °C). These findings were supported by gut evacuation rates of larvae and early juveniles of spotted sea trouts (Wuenschel and Werner, 2004), the gastric evacuation rate of *Trachurus* decreased with elevated temperatures. The relationship between the instantaneous rate of gastric evacuation and temperature is empirically described by an exponential function, as long as the temperature elevation is within the species-specific thermal window (Pörtner, 2010), which was the case this *Trachurus* experiment. Moreover, a recent study demonstrated that not only developmental stages and thermal conditions influence gastric evacuation rates of *Trachurus*, but also prey quality (Temming and Herrmann, 2001). Adult *T. trachurus* exhibited a decline in gastric evacuation rate with increasing energy content of the prey. Hence, prey of lower energy density (*e.g.* krill compared to brown shrimp) led to a higher gut evacuation rate in *T. trachurus* (Temming and Hermann, 2001). For further investigations, the influence of different wild zooplankton on gastric evacuation rates of *Trachurus* early life history should be considered.

In conclusion, this study found evidence that enhanced food quantity can positively affect the food uptake and its processing, reflected by condition and growth of *Trachurus*. Particularly body size, including species-specific physiological and morphological developmental stages, played a key role in this context. Postflexion larvae were not influenced by food concentration, whereas condition and growth rate of transformation larvae correlated positively until a saturation point was reached. Therefore, both working hypotheses (the existence of a saturation point concerning food uptake and condition of *Trachurus* larvae) were only verified for transformation larvae. Nevertheless, it was proved that a high prey density permits successful feeding, resulting in fast growth associated with a quick development of swimming behaviour which is accompanied by an more effective foraging. All these ac-

quired skills reduce the potential of larval mortality caused by predation or starvation and lead to an increase of recruitment success.

4.2.2 Effect of food deprivation on condition and growth of larvae

Starvation was exposed as one key factor influencing mortality rate in the early life history of *Trachurus* larvae (Hewitt *et al.,* 1985). Houde (1989) hypothesized that larvae from low latitudes have high mortality and growth rates, requiring a high ingestion rate for a short larval stage to ensure survival of cohorts. Indeed, Katsuragawa and Ekau (2003) confirmed that one reason for high mortality rates of cohorts in tropical Brazil was starvation. In this study, the effect of cessation of constant nutrient supply on the condition of *Trachurus* spp. was investigated.

Individuals of ME 103-1 were in an overall better condition (CF) than larvae of ME 103-2. Zooplankton data collected during our cruise (unpublished data of PhD candidate Karolina Bohata (Institut for Hydrobiology and Fisheries Science, Hamburg)), indicated that food availability for larvae was much higher at station 47 (ME103-1) than during ME 103-2 (appendix, A-Table 7). Therefore, it can be assumed that higher prey availability during ME 103-1 resulted in a better nutritional condition of *Trachurus* spp. larvae and consequently in a higher resistance to starvation stress. However, the CF decline of larvae sampled during ME 103-2 slowed down significantly when starvation lasted for 65 hours. This might be an indication for a "metabolic protective mechanism" of *Trachurus* spp. larvae that delayed the crossing of the critical point which is equal to an ecological death. Such a "metabolic protective mechanism" may help *Trachurus* larvae to withstand short-time food deprivation within a variable environment such as the Benguela upwelling system.

Larvae of station 131 and station 41 were caught in the same area (19°S) and exposed to similar environmental conditions, despite different fishing time. Consequently, wild larvae of both mentioned stations exhibited similar CF values. Nevertheless, tremendous differences in starvation resistance between experimental larvae of station 131 and 41 were observed. Therefore, it was assumed that other factors besides nutritional history of larvae influence the vulnerability to starvation. It seemed that varying starvation resistance of *Trachurus* larvae was imparted by maternal effects. Several scientist reported (Hart and Werner, 1987; Clemmesen *et al.,* 2003; Saborido-Rey *et al.,* 2003), that size and quality of

fish eggs determine the quantity and composition of yolk reserves, providing initial protein synthesis machinery (*e.g.* maternal ribosomal RNA) and enabling larvae to withstand deleterious effects of short term food deprivation. Navarro and Sargent (1992) even suspected differences among individuals within a single stock. Therefore, even if utilized *Trachurus* larvae belonged to the same cohort, variations within the resistance to starvation stress would be explained. In conclusion, results of the conducted starvation experiment suggest that mainly environmental conditions (*e.g.* prey availability) of *Trachurus'* origin and maternal effects (for CF and growth) influenced the larval vulnerability to starvation stress.

The proxy for nutritional condition and potential growth rate (sRD) of all *Trachurus* larvae, not affected by sample origin or maternal effect, decreased constantly with increasing starvation stress (similar to Buckley *et al.*, 1984; Wright and Martin, 1985; Clemmesen, 1988). After a starvation time of 65 hours, the condition of *Trachurus* (sRD 1.53 ± 0.19) was higher than sRD values of starved yellowtail kingfish juveniles (*Seriola lalandi*) after 12 days of food deprivation (1.02 sRD). Similar results were also reported for larvae of other marine fish species such as herring (*Clupea harengus*; Clemmesen, 1994; Mathers *et al.*, 1994) and haddock (*Melanogrammus aeglefinus*; Caldarone, 2005). Clemmesen (1996) divided the effect of starvation on larval condition in three phases: phase 1) reduction of ribosomes, phase 2) degradation of ribosomes and loss of RNA and finally phase 3) reaching a plateau, meaning a RNA/DNA value necessary for survival. When the point of no return is passed, larvae can be considered as ecologically dead. The time scale of this process depends on species, larval age and *in situ* temperature (Clemmesen, 1996). Older larvae resist longer starvation stress and thus need longer to reach the plateau-stage (phase 3). Higher temperature leads to faster degradation of ribosomes and a reduced time to reach phase 3 (Buckley *et al.*, 1984; Clemmesen, 1996; Buckley *et al.*, 1999). Clemmesen (1994) assumed that phase 3 starts with an RNA/DNA value of about 1.0 regardless of fish species. In this study, the critical point of *Trachurus* was calculated by means of a growth potential model (Buckley *et al.*, 2008) to 0.84 sRD. This result correlated with a threshold level of whitefish larvae of 0.7 sRD (*Coregonus oxyrhinchus*; Malzahn *et al.*, 2003). Transferring this knowledge to our starvations experiment, it seemed that *Trachurus* larvae were still in phase 2 when the experiment was stopped after a starvation time of up to 65 hours and phase 3 was by far not reached. Further progression of the starvation experiment with *Trachurus* can only be assumed, but based on literature and generated CF results of

Trachurus, there are reasonable indications that RNA content continues to decrease if food is withdrawn for a longer time until a plateau is reached. Small red drum larvae (6-10 mm SL, *Sciaenops ocellatus*) reach their critical point after 6 to 8 days, while larger individuals of red drum (15-20 mm SL) as well as Atlantic herring larvae (*Clupea harengus*) can survive up to 17 days without food (Checkley, 1984; Rooker *et al.,* 1997). Only salmon (*Coregonus oxyrhinchus*) surpassed the starvation duration of up to 20 days until larvae died (Malzahn *et al.,* 2003). In conclusion, *Trachurus* larvae were stressed after a starvation time of 65 hours, but not in a considerably life-threatening way. There were indications that *Trachurus* may withstand longer starvation periods than 65 hours. A high starvation resistance of larval *Trachurus* would facilitate the adaptation to a rapidly changing environment such as the Benguela upwelling system, characterized by alternate food availability.

Growth of *Trachurus* based on sagittal otoliths was only marginally influenced by starvation. Interestingly, growth rates of larvae sampled at station 47 decreased with further food deprivation, while larvae of station 41 and 131 grew almost constantly despite increasing starvation stress and decreasing larval condition. An uncoupled relationship between growth and starvation stress within the first 3 days of food deprivation was also observed by several scientists (Marshall and Parker, 1982; Maillet and Checkley, 1989; Johnson and Dropkin, 1995). Johnson and Dropkin (1995) found that food deprivation for as little as 2 days had significant effects on survival of American shad larvae (*Alosa sapidissima*), but growth effects were not detectable until 4 days of starvation. In contrast, other studies, investigating formation of otoliths, found that periods of starvation immediately affected the rate of increment formation (Townsend and Graham, 1981; McGurk, 1984; Shoji *et al.,* 2002; Shoji and Tanaka, 2006). Shoji *et al.* (2002) reported that the growth of post-first-feeding Japanese Spanish mackerel (*Scomberomorus niphonius*) larvae was significantly depressed after 1- or 2-day(s) of starvation. However, *Trachurus'* coupled and uncoupled relationship between growth and food deprivation within a single species has not been observed yet. It is questionable if these results can be traced back to different nutritional histories of *Trachurus* larvae or intra-specific differences concerning maternal effects or a combination of both.

Several scientists examined the relationship between nucleic acid ratios and growth rate based on otolith readings in terms of starvation (Raae *et al.*, 1988; Clemmesen and Doan, 1996). Nucleic acids have been shown to decrease after 1 day of food deprivation and correlate well with reduced or stunted growth rate over periods up to about 1 week (Clemmesen, 1994; Buckley *et al.*, 1999; Caldarone, 2005). In this study sRD values and growth potential (Gi) of *Trachurus* were sensitive to starvation stress for 18 to 65 hours, whereas growth based on sagittal otoliths was only limitedly influenced by starvation. Furthermore, both condition proxies (CF and sRD) revealed a similar overall trend concerning starvation stress (Figure 25), however nucleic acids content seemed not to be influenced by environmental factors or maternal effects compared to CF. It was assumed that these influences were masked by the sensitivity of the method to short-term changes in the environment such as food deprivation.

The comparison between wild and experimental larvae with regard to their condition proxies (CF and sRD) resulted in some discrepancies. Wild larvae of ME 103-1 (station 41 and 47) were shaped similarly or even worse than experimental larvae after a starvation time of 48 hours. Only wild larvae of station 131 offered a better condition than the experimental ones. These findings might be attributed to the selectivity of the catching procedure. Only better shaped *Trachurus* larvae survived the sampling procedure, whereas weaker larvae died during sampling, assumingly due to less stress resistance and were used as reference larvae ("wild" larvae). Therefore, "wild" larvae might not be representative for a "better" condition since only the stronger larvae survived sampling procedure and the subsequent starvation stress. Interestingly, biochemical analysis revealed that not even in "wild" larvae a sRD value below the critical threshold was detected (sRD > 0.84). It was assumed that weak or moribund larvae were eliminated by predation.

In the conducted starvation experiment, no differences between the developmental stages of *Trachurus* were observed. It seemed that preflexion and flexion larvae were similarly vulnerable to starvation stress. In contrast, (Overton *et al.*, 2010) demonstrated a high potential of first-feeding cod yolk-sac larvae (*Gadus morhua*) to withstand periods of prey deprivation presumably due to remaining yolk-sac energy reserves. However, yolk-sac reserves of *Trachurus* are usually used up at larval body size of around 3 mm (MacGregor,

1966). The size of utilized *Trachurus* larvae ranged between 3-7 mm. Therefore, it was assumed that neither preflexion larvae nor flexion *Trachurus* larvae benefited from yolk-sac reserves. Consequently, larval starvation resistance owed to environmental conditions and maternal effects could be examined without any scaling effects regarding body size. However, in future studies using a broader range of size spectrum it needs to be considered that larvae pass through multiple "critical periods" (*e.g.* first feeding, metamorphosis) where starvation resistance and growth capacity are linked (Meyer *et al.,* 2012). Johnson and Dropkin (1995) complained that most food deprivation studies have been done with early yolk-sac fish larvae, probably because smaller larvae are considered to be more susceptible to predation than larger ones (Miller *et al.,* 1988). However, short-term food deprivation for as little as 2 days can significantly reduce growth potential and hence survival in older larvae (Johnson and Dropkin, 1995). *Trachurus* larvae prey on a wide spectrum due to their wide mouth gap resulting in a fast growth rate. Therefore, it can be assumed that first-feeding larvae find optimal prey items quickly, gain in body size and overcome the critical larval stage. The early development of visual and swimming skills lead to an increase in foraging efficiency which may help to pass through multiple "critical periods" concerning food shortage during early life history of *Trachurus* larvae and may explain, *inter alia*, the high abundance of *Trachurus* in the NBCE.

Coming back to our study objective, starvation stress (12 to 65 hours) negatively affected the nutritional condition of *Trachurus*. However, the hypothesis of stagnation and later decrease in the condition parameters was supported only to a certain extent. Growth rates of larvae caught at station 41 and 131 seemed not to be influenced by starvation stress, whereas larvae sampled at station 47 showed retarded growth. Both condition proxies (CF and sRD) revealed a decline in larval condition once the starvation period started. The CF parameter suggests that *Trachurus* reached a plateau after 65 hours of starvation, while biochemical analyses revealed that the degradation of the ribosomes remained constant. Influences of environmental conditions and maternal effects on larval vulnerability to starvation were only detected by means of CF and otolith readings. A prolongation of the starvation period would presumably indicate a more distinct relationship between growth/condition of *Trachurus* and starvation. Nevertheless, it can be assumed that early

life stages of *Trachurus* spp. are well adapted to short-term food deprivation in order to survive in a rapidly changing environment such as the Benguela upwelling system.

5 CONCLUSION AND FUTURE PERSPECTIVES

In this study, the effects of prey density on food consumption, condition and growth rates of *Trachurus* spp. larvae and juveniles were experimentally investigated. The results revealed a correlation between food quantity, growth and condition. Especially transformation larvae tend to increase their prey consumption rate at elevated food density and consequently achieve higher growth rates and a better condition. The positive correlation only lasted until a saturation point has not been passed (at around 10 nauplii ml^{-1}). Beyond this saturation point, condition and growth are not affected by prevailing feeding regimes. The observed variability between developmental stages is likely caused by differences in digestion efficiencies and foraging skills. Furthermore, the presented study revealed that food scarcity negatively affects the condition of *Trachurus* larvae. Growth was only marginally influenced by starvation. The differences in larval response, especially in CF and growth rate data, were mainly attributed to maternal effects and environmental conditions experienced by the larvae before sampling. Despite a starvation period of up to 65 hours, *Trachurus* larvae were stressed, but not life-threateningly influenced.

The Benguela upwelling system, in which *Trachurus* spp. occurs, is characterized by a changing environment, requiring good adaptation skills in order to survive. Based on this study it can be assumed that early life stages of *Trachurus* benefit due to their high saturation point in terms of food consumption and a simultaneous high starvation resistance (at least up to 65 hours), resulting in a good position concerning inter-specific food competition. Larvae quickly acquire swimming and visual skills needed to avoid suboptimal feeding regimes and predation, permitting a high survival rate and a successful recruitment under prevailing hydro- and trophodynamic conditions of the northern Benguela upwelling system. In case upwelling intensity changes due to global warming it can be assumed that early life stages of *Trachurus* are equipped with high growth rates and quickly acquire foraging/escaping skills in order to adapt to changing environmental conditions (*e.g.* zooplankton community).

Future investigations should be conducted with a higher amount of samples, which covers the whole size range of *Trachurus* early life stages. In addition, an elongation of the starvation experiment is recommendable in order to verify the above mentioned assumption. Besides, further investigations should not only focus on effects of prey quantity, but also

stress the importance of prey quality. Wild zooplankton is assumed to be a more adequate energy source than *Artemia salina*. Moreover, survival and recruitment are not only influenced by food availability, but also by hydrographic conditions (temperature, O_2) and oceanographic processes (*e.g.* larval transport). Incorporation of biotic and abiotic environmental factors increases our knowledge about the contact rates of fish larvae with their prey and consequently about recruitment success of early life stages of *Trachurus* spp. under changing environmental conditions in the NBCE. By providing a great deal of information about *Trachurus'* food consumption, growth and condition, this study might help to parameterize feeding and starvation behaviour of larval *Trachurus* in individual-based models (IBMs), which is a fundamental tool for estimating recruitment dynamics. Based on these models predictions management rules can be established in order to regulate fisheries in a reasonable manner.

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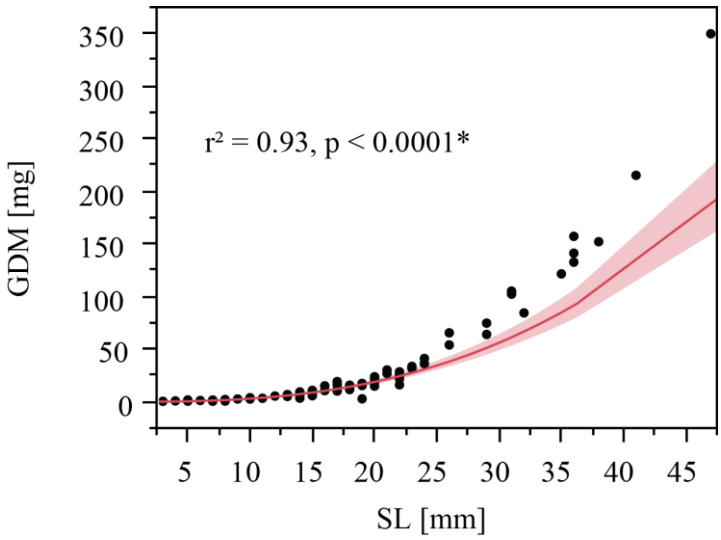
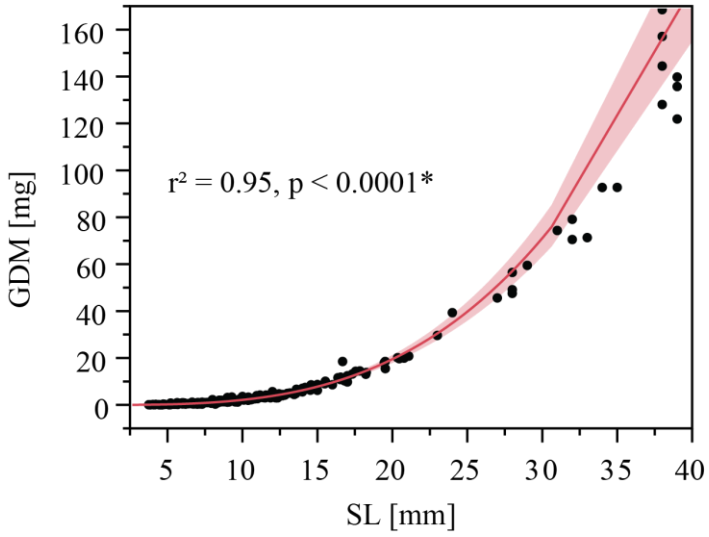
7 APPENDIX

7.1 Figures

Weight-Length relationship of *Trachurus* spp. (Abbreviation: GDM = gutted dry mass [mg], SL = standard length [mm])

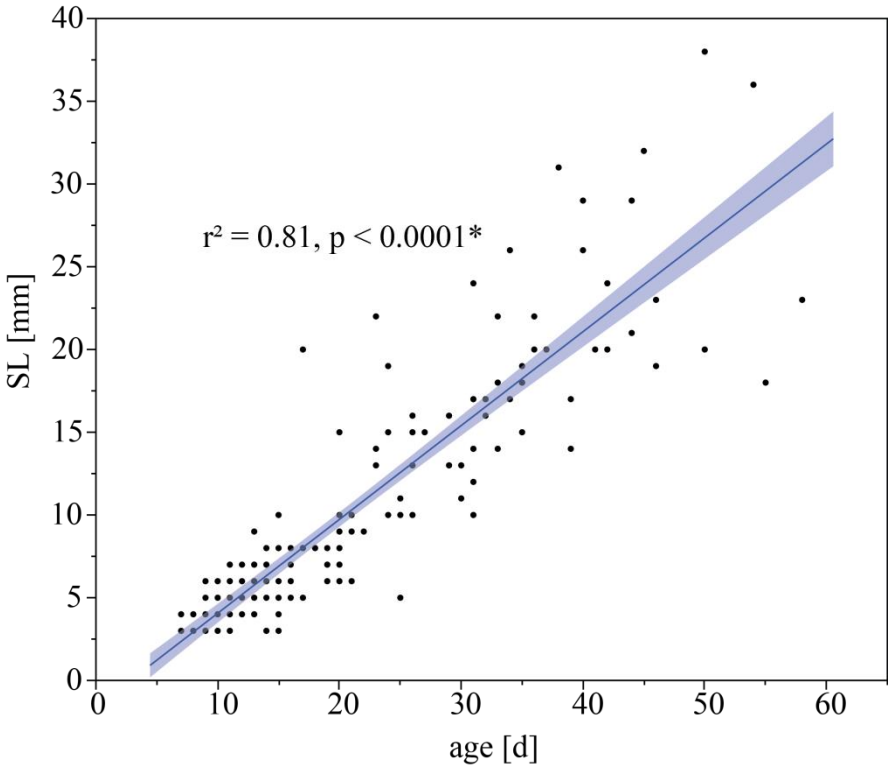


A-Figure 1: Length-weight relationship of early life history stages of *Trachurus* spp. (ME 103).
Specimens (n = 265) were sampled in the northern Benguela upwelling system.
Fitted function: Ln (GDM [mg]) = -4.926711 + 2.8406413*Ln(SL [mm]) with r^2 = 0.933, p <0.0001*.



A-Figure 2: Length-weight relationship of early life history stages of *Trachurus* spp. (MSM 07, Afr 258, D 356, MSM 17-3, MSM 19-1b, ME 100, ME 103).
Specimens (n = 265) were in the Benguela upwelling system. Fitted function: GDM [mg] = -5.85617 + 2.9308041 * Ln (SL) with r^2 = 0.95, p < 0.0001*.

Length-age relationship of *Trachurus* spp.



A-Figure 3: Length-age relationship of early life history stages of *Trachurus* spp. (ME103).
Specimens (n = 265) were sampled in the northern Benguela upwelling system.
Fitted function: SL [mm]: -1.61069 + 0.567088 * increments [n] with r^2= 0.81, p< 0.0001*.

7.2 Table

A-Table 1: Ichthyoplankton net casts during ME 103-1 (st. 2281-061) and ME 103-2 (st. 079-146).
Abbreviations: SST = sea surface temperature, MNo = Multinet oblique, RT = Ring Trawl, TT = Tucker Trawl.

Ship station	Date	Latitude [°S]	Time at depth [UTC]	Water depth [m]	SST [°C]	MNo Haul No.	RT Haul No.	TT Haul No.	Living *Trachurus* spp.
2281	28.12.13	24°00’	9:35	115	16.7	-	1	-	-
2282	28.12.13	24°38’	16:25	146	-	-	-	1	-
2284	29.12.13	25°08’	2:58	90	13.8	1	-	-	-
2286	29.12.13	25°16’	12:23	192	15.5	2	-	-	-
2287	29.12.13	25°21’	18:36	250	15.2	3	-	-	-
2289	30.12.13	25°28’	2:14	800	16.2	4	-	-	-
2290	30.12.13	25°31’	10:23	996	16.7	5	-	-	-
002	1.1.14	28°36’	14:08	113.5	15.6	6	-	-	-
006	2.1.14	28°36’	7:23	157	19.6	7	-	-	-
007	2.1.14	28°36’	14:22	365	20.0	8	-	-	-
008	2.1.14	28°36’	23:02	732	19.7	9	-	-	-
011	5.1.14	23°00’	23:21	895	20.0	10	-	-	-
014	6.1.14	23°00’	22:16	455	20.2	11	-	-	-
018	7.1.14	23°00’	9:18	350	18.7	12	-	-	-
022	7.1.14	23°00’	22:09	144	18.6	13	-	-	-
030	8.1.14	23°00’	17:12	128	18.5	14	-	-	-
035	9.1.14	22°00’	10:28/12:54	118	20.1	15	-	2	-
036	9.1.14	21°00’	20:26	295	21.1	16	2	-	-
038	10.1.14	20°00’	7:40	150	19.0	17	3	-	-
039	10.1.14	19°30’	13:41	231	21.2	18	4	-	x
040	10.1.14	19°00’	18:36	123	19.5	19	5	-	x
041	10.1.14	19°00’	21:34	204	20.0	20	6	-	x
044	11.1.14	17°14’	15:57	133	19.7	21	7	-	x
045	11.1.14	17°14’	22:40	217	19.9	22	8	-	x
046	12.1.14	17°14’	5:12	502	20.1	23	9	-	x
047	12.1.14	17°14’	16:35	1041	-	24	10	-	x
053	14.1.14	20°00’	19:50	408	-	-	11	-	-
057	15.1.14	20°00’	5:16	195	-	-	12	-	-
061	15.1.14	20°00’	15:22	151	19.5	-	13	-	-
079	25.1.14	20°00’	19:55	47.5	18.2	25	-	3	-
080	26.1.14	20°02’	00:31	93	18.7	26	-	4	-

Continuation A-Table 1: Ichthyoplankton net casts during ME 103-1 (st. 2281-061) and ME 103-2 (st. 079-146).

Abbreviations: SST = sea surface temperature, MNo = Multinet oblique, RT = Ring Trawl, TT = Tucker Trawl.

Ship station	Date	Latitude [°S]	Time at depth [UTC]	Water depth [m]	SST [°C]	MNo Haul No.	RT Haul No.	TT Haul No.	Living *Trachurus* spp.
081	26.1.14	20°05’	05:39	123	19.2	27	14	-	-
083	26.1.14	20°12’	15: 41	250	20.9	28	15	-	-
085	27.1.14	20°20’	1:42	500	21.2	29	16	-	-
086	27.1.14	20°23’	8:49	843	20.9	30	17	-	-
088	27.1.14	20°31’	19:56	1200	21.2	31	18	-	-
089	28.1.14	20°39’	09:02	1750	22.1	32	19	-	-
104	29.1.14	19°40’	18:35	45	17.4	33	20	-	x
105	30.1.14	19°46’	00:38	90	19	34	21	-	x
107	30.1.14	19°00’	8:21	130	19.8	35	22	-	x
110	30.1.14	19°57’	9:18	350	18.7	36	23	-	-
114	31.1.14	20°07’	13:53	500	21.6	37	24	-	-
116	31.1.14	20°10’	22:15	860	18.5	38	25	-	-
118	1.2.14	20°14’	13:18	1260	22.1	39	26	-	-
119	1.2.14	20°21’	21:38	1470	22.9	40	27	-	-
120	2.2.14	20°00’	7:41	1400	22.5	41	28	-	x
121	2.2.14	19°51’	19:48	1200	21.8	42	29	-	-
123	2.2.14	19°47’	8:48	840	22.0	43	30	-	-
125	3.2.14	19°41’	16:35	500	21.0	44	31	-	-
131	3.2.14	19°32’	20:46	350	20.8	45	32	-	x
133	5.2.14	19°30‘	5:45	250	-	-	33	-	-
135	5.2.14	19°25’	14:49	132	19.5	46	34	-	x
137	5.2.14	19°21’	21:06	80	18.6	47	35	-	-
138	6.2.14	19°20’	1:42	50	17.2	48	36	-	-
142	7.2.14	20°32’	00:51	500	21.1	49	37	-	-
144	7.2.14	20°07’	13:21	500	22.5	50	38	-	-
145	7.2.14	19°54’	21:19	520	22.4	51	39	-	-
146	8.2.14	19°24‘	09:51	550	21.0	52	40	-	x

A-Table 2: Fitted function of food uptake, growth, condition proxies to prey density/ starvation time of *Trachurus* spp. (ME 103).
Trachurus spp. are either groups by stage development (preflexion = 3-4 mm, flexion = 5-7 mm, postflexion = 8-15 mm, transformation = 16-20 mm, juvenile = 21-40 mm) or stations at which the specimens were caught (st 41, 47, 131).

y-axis	x-axis	grouped by	Function (y = a + bx or y = a * xb)	r^2	p-value
ingestion rate [n/d]	prey density [m/ml]	post	ingestion rate [n/day] = 815.19382 + 62.395037*prey density [n/ml] - 6.3245069*(prey density [n/ml]-7.84416)^2	0.79	<0.0001*
		trans	ingestion rate [n/day] = 1840.1809 + 151.06007*prey density [n/ml] - 37.472267*(prey density [n/ml]-7.84416)^2	0.59	<0.0001*
		juv	ingestion rate [n/day] = 1153.2325 + 288.2875*prey density [n/ml] + 0*(prey density [n/ml]-7.84416)^2	0.93	<0.0001*
ingestion rate [n/mg GDM fish]	prey density [m/ml]	post	ingestion rate [n/d/mg GDM of fish larvae] = 0.1761348 + 0.1811366*prey density [n/ml]	0.71	<0.0001*
		trans	ingestion rate [n/d/mg GDM of fish larvae] = -0.084642 + 0.091689*prey density [n/ml]	0.84	<0.0001*
		juv	ingestion rate [n/d/mg GDM of fish larvae] = 0.0128608 + 0.0305295*prey density [n/ml]	0.91	<0.0001*
consumption rate [%]	prey density [m/ml]	all	Sqrt(consumption rate [%]) = 11.065745 - 1.8963763*Sqrt(prey density [n/ml])	0.86	<0.0001*
Gross growth efficiency (K_1)	ingestion rate	all	Sqrt(Gross growth efficiency) = 0.027826 - 0.0002642*Sqrt(average ingestion rate [n/d])	0.72	<0.0001*
CF	prey density [m/ml]	post	CF = 3.8417322 - 0.0179201*prey density [n/ml] + 0.009192*(prey density [n/ml]-8.54167)^2	0.14	0.4465
		trans	CF = 4.3599458 - 0.017789*prey density [n/ml] - 0.0187732*(prey density [n/ml]-8.54167)^2	0.62	0.0067*
		juv	N/A		

Continuation of A-Table 2: Fitted function of food uptake, growth, condition proxies to prey density/ starvation time of *Trachurus* spp. (ME 103).
Trachurus spp. are either groups by stage development (preflexion = 3-4 mm, flexion = 5-7 mm, postflexion = 8-15 mm, transformation = 16-20 mm, juvenile = 21-40 mm) or stations at which the specimens were caught (st 41, 47, 131).

y-axis	x-axis	grouped by	function	r^2	p-value
growth rate [mm/d]	prey density [m/ml]	post	growth rate = 0.3082186 - 0.000547*prey density [n/ml] + 0.0011714*(prey density [n/ml]-7.45)^2	0.20	0.3185
		trans	growth rate = 0.3906872 + 0.017954*prey density [n/ml] - 0.0026939*(prey density [n/ml]-7.29412)^2	0.47	0.2098
		juv	N/A		
BGR [mg/d]	prey density [m/ml]	post	BGR= 0.1996278 - 0.0007311*prey density [n/ml] + 0.0039604*(prey density [n/ml]-7.29412)^2	0.65	0.0301*
		trans	BGR = 0.6811647 + 0.03461*prey density [n/ml] - 0.002084*(prey density [n/ml]-7.29412)^2	0.30	0.6735
		juv	N/A		
sRD	prey density [m/ml]	post	sRD = 3.1696749 + 0.0272337*prey density [n/ml] - 0.009173*(prey density [n/ml]-7.22222)^2	0.12	0.5412
		trans	sRD = 3.4567797 + 0.0290131*prey density [n/ml] - 0.0228171*(prey density [n/ml]-7.22222)^2	0.30	0.1338
		juv	N/A		
CF	ingestion rate [n/ml]	post	CF = 4.805267 - 0.0008152*average ingestion rate [n/d]	0.25	0.2569
		trans	CF = 3.1691161 + 0.0003804*average ingestion rate [n/d]	0.65	0.0046*
growth rate [mm/d]	ingestion rate [n/ml]	post	growth rate = 0.310124 + 1.8349e-5*average ingestion rate [n/d]	0.02	0.7868
		trans	growth rate = 0.3490638 + 4.3213e-5*average ingestion rate [n/d]	0.30	0.124
sRD	ingestion rate [n/ml]	post	sRD = 4.1031202 - 0.0006336*average ingestion rate [n/d]	0.07	0.6222
		trans	sRD = 2.6247826 + 0.0002201*average ingestion rate [n/d]	0.15	0.2614

Continuation of A-Table 2: Fitted function of food uptake, growth, condition proxies to prey density/ starvation time of *Trachurus* spp. (ME 103).
Trachurus spp. are either groups by stage development (preflexion = 3-4 mm, flexion = 5-7 mm, postflexion = 8-15 mm, transformation = 16-20 mm, juvenile = 21-40 mm) or stations at which the specimens were caught (st 41, 47, 131).

y-axis	x-axis	grouped by	function	r^2	p-value
DNA content [µg]	starvation time [h]	all	Total DNA [µg] = 3.4818782 + 1.9197095*GDM [mg]	0.89	<0.0001*
RNA content [µg]	starvation time [h]	all	Total RNA [µg] = 6.6931011 + 5.01008*GDM [mg]	0.89	<0.0001*
CF	starvation time [h]	st 41	CF = 24.220766 - 0.371152*starvation time [h]	0.44	0.0021*
		st 47	CF = 31.782038 - 0.4999072*starvation time [h]	0.00	0.8267
		st 131	CF = 3.261815 - 0.0152408*starvation time [h]	0.14	0.0459*
growth rate [mm/d]	starvation time [h]	st 41	growth rate = 0.2952143 - 0.0007857*starvation time [h]	0.01	0.7999
		st 47	growth rate = 1.2461905 - 0.0180159*starvation time [h]	0.43	0.0382*
		st 131	growth rate = 0.3371966 + 1.3666e-5*starvation time [h]	0.00	0.9798
BGR [mg/d]	starvation time [h]	st 41	BGR = -0.274762 + 0.0063492*starvation time [h]	0.42	0.0095*
		st 47	BGR = 0.2522727 - 0.0039394*starvation time [h]	0.37	0.0632
		st 131	BGR = 0.0861982 - 0.000178*starvation time [h]	0.01	0.6915
sRD	starvation time [h]	st 41	sRD = 2.8102755 - 0.0308237*starvation time [h]	0.13	0.312
		st 47	sRD = 2.4413074 - 0.0215586*starvation time [h]	0.09	0.3956
		st 131	sRD = 2.253167 - 0.0147475*starvation time [h]	0.65	0.0003*
		flex	sRD = 2.6002621 - 0.018774*starvation time [h]	0.50	0.0009*
		pref	sRD = 2.7673823 - 0.0229046*starvation time [h]	0.60	0.0003*
growth rate [mm/d]	starvation time [h]	all stations, sizes	growth rate = 0.3268461 - 0.0007273*starvation time [h]	0.04	0.2522

Continuation of A-Table 2: Fitted function of food uptake, growth, condition proxies to prey density/ starvation time of *Trachurus* spp. (ME 103).
Trachurus spp. are either groups by stage development (preflexion = 3-4 mm, flexion = 5-7 mm, postflexion = 8-15 mm, transformation = 16-20 mm, juvenile = 21-40 mm) or stations at which the specimens were caught (st 41, 47, 131).

y-axis	x-axis	grouped by	function	r^2	p-value
Gi	starvation time [h]	All stations, sizes	Gi = 0.165016 - 0.0017314*starvation time [h]	0.47	<0.0001*
residuals of growth rate	starvation time [h]	st 131, pref, flex	residuals of growth rate = -0.01254 + 0.0004443*starvation time [h]	0.00	0.8136
residuals of growth rate	starvation time [h]	st 41,47, pref, flex	residuals of growth rate = 1.4686381 - 0.0282833*starvation time [h]	0.15	0.0479*
residuals of sRD	starvation time [h]	st 131, pref, flex	residuals of SD of sRD = 0.2949566 - 0.0084758*starvation time [h]	0.65	0.0003*
residuals of sRD	starvation time [h]	st 41,47, pref, flex	residuals of SD of sRD = 0.9114496 - 0.0180307*starvation time [h]	0.09	0.1943
residuals of CF	starvation time [h]	st 131, pref, flex	residuals of CF = 0.1877335 - 0.006902*starvation time [h]	0.14	0.0456*
residuals of CF	starvation time [h]	st 41,47, pref, flex	residuals of CF = 2.4048385 - 0.0466676*starvation time [h]	0.14	0.0338*

A-Table 3: Mean values (± SD) of condition and growth proxies in relation to offered prey densities (1, 5, 10, 15 *Artemia* naulpii ml^{-1}) at 18 °C.
Used *Trachurus* spp. were grouped regarding their developmental stage: preflexion = 3-4 mm, flexion = 5-7 mm, postflexion = 8-15 mm, transformation = 16-20 mm, juvenile = 21-40 mm.

size class	prey density [n/ml]	n (reduced n for sRD)	average ingestion rate [n/d]	average ingestion rate [n/d/mg GDM of fish]	average CF	average growth [mm/d]	average BGR [mg/d]	average sRD
postf	1	3 (2)	591.5 ± 22.00	0.14 ± 0.03	3.36 ± 1.2	0.35 ± 0.03	0.38 ± 0.03	2.82 ± 0.66
postf	5	1	N/A	N/A	3.46 ± 0.00	0.37 ± 0.00	0.12 ± 0.00	3.38 ± 0.00
postf	10	3	1374.83 ± 230.14	2.36 ± 0.49	3.80 ± 0.65	0.29 ± 0.07	0.25 ± 0.07	3.32 ± 0.78
postf	15	2	1410.04 ± 258.47	2.43 ± 0.84	3.92 ± 0.55	0.38 ± 0.04	0.41 ± 0.04	3.04 ± 0.40
trans	1	2	686.21 ± 56.46	0.08 ± 0.01	3.36 ± 0.22	0.30 ± 0.02	0.61 ± 0.07	2.54 ± 0.71
trans	5	4	1715.12 ±799.84	0.37 ± 0.09	3.95 ± 0.25	0.48 ± 0.07	0.87 ± 0.14	3.56 ± 0.89
trans	10	2	4114.27 ± 331.44	0.7 ± 0.28	4.33 ± 0.44	0.54 ± 0.17	0.96 ± 0.42	3.44 ± 0.13
trans	15	2 (1)	3304.09 ±1719.59	1.01 ± 0.48	3.25 ± 0.00	0.51 ± 0.00	1.11 ± 0.00	2.55 ± 0.70
juv	5	2	2462.73 ± 131.94	0.27 ± 0.10	2.90 ± 2.39	0.52 ± 0.15	0.96 ± 0.02	3.32 ± 0.99
juv	15	1	5931.42 ± 0.00	0.41 ±0.00	4.35 ± 0.00	0.59 ± 0.00	1.82 ± 0.00	2.67 ± 0.00

A-Table 4: Consumption rate [% ± SD] of all size classes of *Trachurus* spp. in regard to offered prey density (1, 5, 10, 15 *Artemia* nauplii ml^{-1}) at 18 °C.

size class	amount of *Trachurus* spp. [n]	prey density [n/ml]	consumption rate [%]
all	5	1	87.59 ± 8.94
all	6	5	42.89 ± 10.36
all	5	10	28.79 ± 10.73
all	3	15	14.10 ± 0.76

A-Table 5: Mean values (± SD) of condition and growth proxies of *Trachurus* larvae in relation to starvation stress at 18 °C.
Used *Trachurus* spp. were grouped regarding the station, where the larvae were caught: station 41, 47, 131. The amount of larvae (n) utilized is listed in brackets after the results.

Station	starvation time [h]	average CF	average growth rate [mm/d]	average BGR [mg/d]	average sRD
41	48	6.413 ± 2.088 (8)	0.23 ± 0.07 (5)	0.03 ± 0.01 (6)	1.58 ± 0.36 (7)
41	55	3.807 ± 0.712 (11)	0.25 ± 0.03 (10)	0.07 ± 0.03 (9)	1.33 ± 0.13 (3)
47	48	7.786 ± 2.499 (8)	0.38 ± 0.06 (7)	0.07 ± 0.02 (5)	1.66 ± 0.35 (6)
47	54	4.516 ± 1.880 (4)	0.28 ± 0.05 (4)	0.03 ± 0.02 (4)	1.5 ± 0.3 (3)
47	60	11.303 ± 0.00 (1)	0.25 ± 0.00 (1)	0.03 ± 0.00 (1)	1.30 ± 0.00 (1)
131	12	3.838 ± 1.478 (8)	0.31 ± 0.04 (6)	0.07 ± 0.06 (6)	2.49 ± 0.33 (6)
131	18	3.100 ± 0.718 (9)	0.33 ± 0.05 (8)	0.09 ± 0.04 (7)	2.1 ± 0.38 (8)
131	24	2.336 ± 0.513 (7)	0.41 ± 0.09 (6)	0.14 ± 0.1 (6)	2.41 ± 0.25 (6)
131	65	2.400 ± 0.224 (6)	0.33 ± 0.05 (6)	0.07 ± 0.03 (5)	1.53 ± 0.19 (6)

A-Table 6: Growth rate [mm/d] (± SD) and growth potential Gi [mm/d] (± SD) based on sRD values of *Trachurus* with enhanced starvation time (18 °C).
Used *Trachurus* spp. (n = 32) were summarized and not grouped by size class or station where they caught.

starvation time [h]	growth rate [mm/d]	Gi [mm/d]
12	0.29 ± 0.03	0.05 ± 0.04
18	0.36 ± 0.00	0.08 ± 0.00
24	0.45 ± 0.13	0.15 ± 0.02
48	0.32 ± 0.07	0.08 ± 0.04
54	0.27 ± 0.06	0.08 ± 0.03
55	0.24 ± 0.02	0.05 ± 0.01
60	0.23 ± 0.04	0.06 ± 0.02
65	0.33 ± 0.05	0.07 ± 0.02

A-Table 7: Zooplankton composition of the first 20 m of the water column at stations (or nearby) where *Trachurus* spp. larvae were caught (ME 103). Zooplankton is grouped in class, order, genus and/or species. Amount of zooplankton is indicated in individual m^{-3}. Data were provided by Karolina Bohata (Institut für Hydrobiologie und Fischereiwissenschaft, Hamburg).

		Cruise	**M103**						
		Station	**47**	**104**	**107**	**110**	**114**	**125**	**138**
		Depth interval [m]	0-20	0-20	0-20	0-20	0-20	0-20	0-20
Copepoda	Cyclopoida	**Oithona sp.**	220.00	100.00	860.00	75.00	25.00	12.50	0.00
		Oncaea sp.	700.00	2660.00	6620.00	275.00	25.00	106.25	450.00
	Harpacticoida	**Microsetella sp.**	80.00	60.00	360.00	1300.00	1100.00	125.00	200.00
	Calanoida		280.00	60.00	200.00	50.00	50.00	12.50	25.00
	nauplii larvae		6580.00	980.00	12340.00	8025.00	3350.00	475.00	2925.00
		Sum	7860.00	3860.00	20380.00	9725.00	4550.00	731.25	3600.00
Tinntinida		**Codonellopsis sp.**	940.00	120.00	0.00	0.00	22475.00	137.50	300.00
		Codonella galea	0.00	0.00	20.00	1075.00	100.00	0.00	0.00
		Cymatocyclis vanhoffeni	2480.00	2580.00	0.00	25.00	75.00	0.00	0.00
		Cyttarocalis cassis	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Dictyocysta elegans	20.00	0.00	0.00	200.00	300.00	6.25	0.00
		Epiplocylis acuminata	240.00	0.00	0.00	0.00	50.00	0.00	0.00
		Eutintinnus sp.	40.00	20.00	0.00	75.00	175.00	12.50	0.00
		Rhabdonella spiralis	0.00	0.00	20.00	50.00	0.00	50.00	0.00
		Salpingella acuminata	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Petalotricha ampulla	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Undella sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Xystonella treforti	20.00	0.00	0.00	50.00	0.00	0.00	50.00
		Sum	3740.00	2720.00	40.00	1475.00	23175.00	206.25	350.00
Mixotrophe Dinoflagellata		**Ceratium sp.**	3640.00	1580.00	4160.00	3675.00	700.00	175.00	1050.00
Heterotrophe Dinoflagellata	Protoperidinae		8880.00	1140.00	980.00	1625.00	650.00	37.50	275.00
		Noctiluca scintilans	16820.00	2540.00	240.00	0.00	0.00	18.75	1725.00
		Sum	29340.00	5260.00	5380.00	5300.00	1350.00	231.25	3050.00
		Total sum	**40940.00**	**11840.00**	**25800.00**	**16500.00**	**29075.00**	**1168.75**	**7000.00**