Early life history traits
of
coastal pelagic fishes
in the
northern
Benguela Current
ecosystem
off Namibia

Simon Joscha Geist

Early life history traits of coastal pelagic fishes in the northern Benguela Current ecosystem off Namibia

Simon Joscha Geist

Dissertation zur Erlangung des akademischen Grades eines Doktors der Naturwissenschaften (Dr. rer. nat.)

im

Fachbereich Biologie/Chemie

Universität Bremen

August 2013

In partial fulfillment of the requirements for the degree of

Doctor of Natural Sciences (Dr. rer. nat.)

First Examiner: Prof. Dr. Ulrich Saint-Paul

University of Bremen, Bremen, Germany

Mangrove Ecology, workgroup leader at Leibniz Center for Tropical Marine Ecology, Bremen

Second Examiner: Dr. Werner Ekau

Fisheries Biology, workgroup leader at Leibniz Center for Tropical Marine Ecology, Bremen

Thesis committee examiners

Additional Examiner I: Prof. Dr. Wilhelm Hagen

University of Bremen, Bremen, Germany

Marine Zoology, head of department at University of Bremen

Additional Examiner II: Prof. Dr. Thomas Brey

University of Bremen, Bremen, Germany

Functional Ecology, section head at Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven

»Und dann standen wir auf einmal am Meer und schauten ganz benommen in die Ferne …
›Das ist der Horizont‹, erklärte mein Vater. – ›Und was kommt hinter dem Horizont?‹ fragte
ich.«

Elisabeth Mann Borgese

Thesis supervisors: Drs Werner Ekau and Andreas Kunzmann

Leibniz Center for Tropical Marine Ecology, Bremen

External advisor: Dr. Hans Verheye

Oceans and Coasts Research, Department of Environmental Affairs, and Marine Research
Institute, University of Cape Town, Cape Town, South Africa

This work has been accomplished at the Leibniz Center for Tropical Marine Ecology in
Bremen between May 2009 and August 2013

Cover by Simon Geist; Backcover drawing by Alexander Gürten

Table of content

Abstract

Coastal pelagic fish species, such as sardine, anchovy and horse mackerel, are globally important fisheries resources and are used for human consumption and the production of fish meal and oil. Their population dynamics are characterised by variability and instability expressed by strong fluctuations in stock size. Environmental influences are widely assumed to be responsible, acting particularly on eggs, larvae and juveniles, the so called "early life history" (ELH) stages.

The Benguela Upwelling system in the south-east Atlantic is one of the most productive marine ecosystems worldwide and its northern subsystem off Namibia once harboured large populations of coastal pelagics. However, in the northern Benguela Current ecosystem (NBCE), sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) stocks collapsed during the 1970s and 1980s and have not recovered, leaving Cape horse mackerel (*Trachurus capensis*) the only remaining species of economic importance at present. Changes in upwelling activity, affecting water temperatures, dissolved oxygen concentrations and species composition in the zooplankton have been proposed as underlying factors responsible for the present stock situations. However, possible mechanisms are greatly understudied, particularly during ELH stages.

To fill this gap, a set of ELH traits, with the potential to influence the survival of fish larvae and via recruitment success to adult stock size, were investigated in this thesis for the three above mentioned fish species and additionally for the invasive species *Sardinella aurita.* The study is based on samples from four consecutive research cruises conducted in the NBCE region at different times of the year during March 2008, December 2009, September 2010 and February 2011. I analysed spatio-temporal distribution patterns of larvae and investigated their trophic ecology, nutritional condition and daily growth rates, focussing on interspecific differences and the influence of upwelling activity-associated environmental conditions (water temperature, oxygen concentration, plankton composition). Furthermore, I measured metabolic rates to estimate minimal energy requirements and the response of respiration rates to low oxygen concentrations to determine hypoxia tolerance of larval and juvenile *T. capensis.*

The summarised key findings of my thesis are:

Larvae of all four species showed maximum densities during the cruises in February and March. They were mainly caught over the continental shelf and in well-oxygenated water within the upper 50 m of the water column. Larvae of all four species were daytime feeders, occupied a similar trophic level and fed mainly on different groups of planktonic crustaceans.

Diatoms constituted an important base of the food web in larvae of all four species as inferred from fatty acid trophic markers.

T. capensis larvae showed the most equal densities of the four species with regard to spatial and temporal distribution patterns. Their occurrence over a wide temperature range classified them as eurythermal species. Both larvae and juveniles tolerated the exposure to hypoxic conditions and did not show a response in respiration rates until oxygen concentrations below 2 mL O_2 L^{-1}. *T. capensis* larvae were characterised as voracious feeders with a high feeding success, preying on a wide range of copepod taxonomic groups, including the small *Oithona* sp. and *Oncaea* sp.. *T. capensis* larvae showed the highest daily biomass growth rates of the studied species and good nutritional condition.

In contrast to *T. capensis*, larvae of the three clupeoid species (*S. sagax*, *S. aurita* and *E. encrasicolus*) were almost exclusively caught during the two cruises in February and March and occurred in very high densities in the Walvis Bay region in 02/2011. *S. sagax* larvae appeared stenothermal with a limited distribution towards the upper end of the temperature range, whereas *E. encrasicolus* and *S. aurita* larvae should be considered eurythermal. In the prey spectrum of early *S. sagax* and *E. encrasicolus* larvae, copepod nauplii were more important than *Oithona* sp. and *Oncaea* sp. Feeding success of clupeoid larvae appeared to be lower compared with *T. capensis*, also reflected by a lower nutritional condition of *E. encrasicolus* larvae as inferred from total fatty acid concentrations. The nutritional condition of clupeoid larvae was significantly lower during 02/2011 compared to 03/2008 probably caused by limited food supply at high larval densities.

In conclusion, the revealed interspecific differences in ELH traits suggest a good adaptation of *T. capensis* larvae to the present environmental conditions in the NBCE, which are characterised by frequent periods of quiescent upwelling and intrusions of warm water, shoaling of the oxygen minimum zone and a shift in the species composition of copepods towards *Oithona* sp.. The differences in ELH traits may provide an advantage for *T. capensis* over the clupeoid species and in particular over *S. sagax,* allowing for prolonged retention times in coastal regions with good food supply and a higher capacity to overcome periods of food scarcity. The latter two mechanisms can enhance larval survival and by this the recruitment success to the adult stock.

Zusammenfassung

Kleine pelagische Fischarten, wie Sardine, Sardelle oder Stöcker, sind weltweit wichtige Fischereiressourcen und werden sowohl für den direkten menschlichen Verzehr als zur Herstellung von Fischmehl und –öl genutzt.

Die Populationsdynamik dieser Arten ist durch eine hohe Variabilität und Instabilität gekennzeichnet und spiegelt sich in großen Schwankungen ihrer Bestände wider. Veränderungen in den Umweltbedingungen, die sich besonders auf die frühen Lebensstadien wie Eier, Larven und Juvenile auswirken, werden als Hauptursache dieser Schwankungen angesehen.

Das Benguela Auftriebsgebiet, im süd-östlichen Atlantik gelegen, ist eines der produktivsten Meeresökosyteme der Welt. Das nördliche Benguela Auftriebsgebiet (NBCE) vor Namibia beherbergte bis in die 1970er Jahre große Populationen kleiner pelagischer Fischarten. Allerdings brachen dort sowohl die Bestände der Sardine (*Sardinops sagax*) als auch der Sardelle (*Engraulis encrasicolus*) während der 1970 und 1980er Jahre ein und haben sich bis heute nicht erholt. Dadurch ist die Kap-Bastardmakrele (*Trachurus capensis*) die einzig verbleibende Art von wirtschaftlicher Relevanz für den Fischereisektor. Als Ursache für diese Bestandssituation wird vor allem eine Veränderung der Auftriebsaktivität angenommen, die sich auf die Temperatur und den Sauerstoffgehalt des Wassers auswirkt. Außerdem beeinflusst sie auch die Artenzusammensetzung des Zooplanktons, welches wiederum die Hauptnahrungsquelle der besagten Fischarten ausmacht. Die zugrundeliegenden Wirkmechanismen sind bis jetzt nur zum Teil untersucht und verstanden. Insbesondere Prozesse, die während der frühen Lebenstadien der Fischarten eine Rolle spielen, sind unzureichend erforscht.

In der vorliegenden Arbeit wurden Eigenschaften früher Lebensstadien der drei erwähnten Fischarten untersucht, die das Potential besitzen, die Überlebensrate und damit den Fortplanzungserfolg zu beeinflussen. Zusätzlich wurde mit *Sardinella aurita* eine weitere Art untersucht, die von Norden her in das Gebiet einwandert. Diese Studie basiert auf Proben, die während unterschiedlicher Jahreszeiten im März 2008, im Dezember 2009, im September 2010 und im Februar 2011 auf vier aufeinanderfolgenden Expeditionen mit Forschungsschiffen genommen wurden. Es wurde die räumliche und zeitliche Verteilung der Fischlarven analysiert und die trophische Ökologie, der Ernährungszustand und die täglichen Wachstumsraten an Larven der vier unterschiedlichen Fischarten untersucht. Der Fokus lag dabei auf zwischenartlichen Unterschieden und auf dem Einfluss von Umweltfaktoren wie Wassertemperatur, Sauerstoffgehalt und Planktonzusammensetzung, welche durch die Stärke der Auftriebsaktivität beeinflusst werden. Außerdem wurden die metabolischen Raten von

Larven und Juvenilen von *T. capensis* bestimmt um ihren Energiebedarf abzuschätzen. Zusätzlich wurde die Entwicklung der Atmungsrate bei erniedrigten Sauerstoffkonzentrationen untersucht um etwaige Anpassungen an hypoxische Umweltbedingungen aufzudecken.

Aus den Untersuchungen gingen die folgenden zentralen Ergebnisse hervor:

Die Larven aller vier Fischarten wurden überwiegend in Regionen über dem Kontinentalschelf gefangen und erreichten die höchsten Individuendichten während der Fahrten im Februar 2011 und März 2008. Die Fischlarven wurden hauptsächlich in sauerstoffreichen Wasserschichten in den oberen 50 m der Wassersäule angetroffen. Die Nahrungsaufnahme fand bei allen vier Fischarten tagsüber statt. Die Larven der untersuchten Arten besetzten die gleiche trophische Ebene und ihre Nahrung bestand zum Großteil aus unterschiedlichen Gruppen planktonischer Krebstiere (Crustaceen). Abgeleitet aus dem relativen Anteil der entsprechenden trophischen Markerfettsäuren, war die Diatomeen basierte Nahrungskette von großer Wichtigkeit für die Larven.

Die Individuendichte der Larven von *T. capensis* war im Vergleich der vier Arten am gleichmäßigsten verteilt, sowohl in räumlicher Hinsicht als auch in Bezug auf die unterschiedlichen Zeiten des Jahres. Durch das Vorkommen dieser Art über einen weiten Temperaturbereich ließ sich eine eurytherme Verteilung ableiten. Zudem tolerierten sowohl Larven- als auch Jugendstadien von *T. capensis* hypoxische Bedingungen und zeigten erst bei Sauerstoffkonzentrationen unter 2 mL O_2 L^{-1} eine Veränderung ihrer Respirationsraten. In Bezug auf ihre Nahrungsökologie zeichneten sich *T. capensis* Larven durch ihre Gefräßigkeit und einen hohen Fraßerfolg aus. Ihre Nahrung bestand zum Großteil aus verschiedenen taxonomischen Gruppen von Ruderfußkrebsen (Copepoda), insbesondere auch der kleinen Arten der Gattungen *Oithona* und *Oncaea*. Die Larven von *T. capensis* zeigten die höchsten täglichen Wachstumsraten bezogen auf die Biomasse und zeichneten sich durch einen gleichbleibend guten Ernährungszustand aus.

Im Gegensatz zu *T. capensis* wurden die Larven der drei clupeoiden Arten (*S. sagax*, *S. aurita* and *E. encrasicolus*) fast ausschließlich während der zwei Ausfahrten im Februar und März gefangen. Sie erreichten besonders hohe Individuendichten in der Region um Walvis Bay im Februar 2011. Im Gegensatz zu den eurythermalen Larven von *E. encrasicolus* und *S. Aurita* zeigten *S. sagax* Larven eine auf niedrigere Temperaturen begrenzte Verteilung und ließen sich somit als stenothermal charakterisieren. Im Nahrungsspektrum junger *S. sagax* und *E. encrasicolus* Larven nahmen die Larvalstadien von Copepoden (Nauplien) eine zentrale Rolle ein, während *Oithona* sp. und *Oncaea* sp. keine große Bedeutung zukam. Der Fraßerfolg der clupeoiden Larven war niedriger als jener von *T. capensis*. Dies spiegelte sich in einem vergleichsweise schlechteren Ernährungszustand der *E. encrasicolus* Larven wieder, abgeleitet

von einem zwischenartlichen Vergleich der Fettsäurekonzentrationen. Zur gleichen Jahreszeit war der Ernährungszustand clupeoider Larven bei extrem hoher Individuendichte (Februar 2011) signifikant schlechter als bei geringerer Individuendichte (März 2008).

Zusammenfassend deuten die gefundenen, zwischenartlichen Unterschiede auf eine vergleichsweise bessere Anpassung von *T. capensis* an die zur Zeit im nördlichen Benguela Auftriebsgebiet vorherrschenden Umweltbedingungen hin. Diese zeichnen sich durch häufige Perioden mit geringer Auftriebsaktivität und dem Eindringen von wärmeren Wassermassen, eine Ausbreitung der Sauerstoffminimumzone sowie eine Verschiebung der Artenzusammensetzung der Ruderfußkrebse zugunsten von *Oithona* sp. aus. Die in dieser Arbeit identifizierten, artspezifischen Merkmale der jungen Lebensstadien von *T. capensis* könnten ihnen sowohl eine längere Verweildauer in küstennahen Regionen mit guter Nahrungsverfügbarkeit als auch ein besseres Überleben in Perioden mit verminderter Nahrungsverfügbarkeit erlauben. Diese zwei Mechanismen können die Überlebenswahrscheinlichkeit der Larven und dadurch den Fortpflanzungserfolg der adulten Population erhöhen.

Scientific background

General Introduction

Around the world, a great number of economically important fish stocks have declined or collapsed during the last decades due to the impact of overfishing and environmental changes (Mullon *et al.* 2005; Murawski, 2010; Perry *et al.*, 2010; Planque *et al.*, 2010). Among the latter, rising water temperatures (IPCC, 2007) and expanding hypoxic zones (Diaz and Rosenberg, 2008; Diaz and Breitburg, 2009) influence the spatial distribution (Perry *et al.*, 2005; Cheung *et al.*, 2009; Stramma *et al.*, 2012) and body size of fishes (Cheung *et al.*, 2013a) and affect thereby fisheries catches (Sumaila *et al.*, 2011; Cheung *et al.*, 2013b).

The four major eastern boundary upwelling ecosystems (EBUE) are highly productive shelf seas and comprise the most valuable fishing grounds of the world including small and medium pelagic fish as important economic resources (Blaxter and Hunter, 1982; Crawford, 1987; Fréon *et al.*, 2005; Chavez and Messié, 2009; Fréon *et al.*, 2009b; Pikitch *et al.*, 2012). The Humboldt, California, Canary and Benguela Currents are characterised by constant, periodical or poly-pulsed upwelling events, driven by trade winds. Offshore Ekman transport brings cold, nutrient-rich water from deeper layers to the surface, allowing for high primary production and very productive pelagic food webs with low species diversity (Chavez and Messié, 2009; Fréon *et al.*, 2009a, and b; Messié *et al.*, 2009). Two groups of small pelagic Clupeiformes usually dominate the fish community in EBUE in terms of abundance and biomass: sardine (genera: *Sardinops*, *Sardina*) and anchovy (genus: *Engraulis*) species (Schwartzlose *et al.*, 1999). Through their high numbers, small pelagics usually are key species in the food web, where they occupy central positions in "wasp-waist systems" (Cury *et al.*, 2000; Cury and Shannon, 2004). They build up high biomass, making them important resources for human consumption and the basis of fishmeal and -oil production (Alder *et al.*, 2008; Pikitch *et al.*, 2012). In addition to small pelagics, medium pelagic fish like horse mackerel (genus: *Trachurus*) and chub mackerel (genus: *Scomber*) are important members of EBUE and both groups together are combined under the term coastal pelagic fish (Fréon *et al.*, 2005). EBUE's fisheries resources are intensively harvested and account for an average annual catch of 16.8 million tons during 2004-2007 (Fréon *et al.*, 2009b), representing ca. 20% of the world's marine fisheries catch (FAO data). Small pelagic fish (Clupeiformes: herrings, sardines and anchovy) are the main target species in all four EBUE (11.5 million tons yr^{-1} = 68% of total catch), followed by medium pelagics (e.g. horse and jack mackerels, chub mackerels), contributing 15% (2.5 million tons yr^{-1}) to total landings during 2004-2007 (Fréon *et al.*, 2009b). The Peruvian anchovy (*Engraulis ringens*) from the Humboldt Current supports the largest fishery in the world (FAO, 2010). Together with the valuable demersal hakes (genus:

Merluccius), coastal pelagic fish provide a substantial income source for many EBUE neighbouring countries and contribute substantially to food security in many of these regions (Fréon *et al.*, 2005).

Coastal pelagics population dynamics and climate change in upwelling systems

Drastic multi-decadal fluctuations of small pelagics' stock sizes have been frequently observed and are considered a naturally occurring phenomenon resulting in regime shifts between states in which either sardine or anchovy dominate the ecosystem (Schwartzlose *et al.*, 1999; Alheit and Niquen, 2004; Cury and Shannon, 2004; Fréon *et al.*, 2005). In addition, intense fishing pressure may enhance the susceptibility to, and thus the frequency of fluctuations (Anderson *et al.*, 2008). Climatic effects, such as changes in upwelling intensity, water temperature and oxygen concentration, accompanied by associated changes in the food web, have been suggested as drivers for fluctuations in size, biomass and distribution of fish populations (Steele, 2004; Litzow *et al.*, 2006; van der Lingen *et al.*, 2006a; Alheit, 2009; Bertrand *et al.*, 2011). Since EBUE are driven by large-scale atmospheric patterns (Jury, 2006; Alheit and Bakun, 2010; Bakun *et al.*, 2010b; Collins *et al.*, 2010), a wide range of ecological processes may be significantly affected by climate variability, e.g. water chemistry, water temperature and currents that influence species dispersal and recruitment (Iles *et al.*, 2012).

One major effect expected to influence EBUE is a change in wind patterns (Lutjeharms *et al.*, 2001; Fréon *et al.*, 2009b), affecting upwelling intensity and thereby water temperature, oxygen concentration, advective processes and plankton composition (quantity and quality). Consequently, it may affect small pelagic fishes on all levels of organization and throughout life history stages (Checkley *et al.*, 2009; Fréon *et al.*, 2009c; Rijnsdorp *et al.*, 2009). However, the direction of changes in upwelling intensity is debated. Upwelling activities may weaken, intensify or become more variable. Stronger trade winds and an increased temperature difference between land and sea may lead to intensified upwelling (Bakun, 1990), causing higher phytoplankton production of large algae (diatoms), but also increased advective transport to the open ocean (Bakun and Weeks, 2008). In contrast, weakened upwelling activity would lead to higher stratification of the water column, resulting in warmer surface waters and possibly decreased primary production due to reduced nutrient supply (van der Lingen *et al.*, 2006a). Chavez *et al.* (2003) emphasised water temperature as a simple proxy for different regime states in the Humboldt Current. They related the "sardine (*S. sagax*) regime" to periods of relatively warm conditions compared to the "anchovy (*E. ringens*) regime" during relatively cold periods. A reason could be the interaction of physical forcing and tropho-dynamics as proposed by van der Lingen *et al.* (2006a). Ocean warming and a higher stratification can lead to a shift of the phytoplankton community from diatoms to flagellates

(Mitchell-Innes and Pitcher, 1992; Legendre and Rivkin, 2002; Sommer *et al.*, 2002; Leterme *et al.*, 2005; Hauss *et al.*, 2012). This could favour smaller-sized zooplankton and subsequently sardine (*S. sagax*) which is adapted to smaller prey organisms than anchovy (*E. encrasicolus*), which in turn is supposed to be trophodynamically advantaged under "cold conditions" (van der Lingen *et al.*, 2006a). A propagation of changes in the phytoplankton community to higher trophic levels in the food web has been proposed by several authors, e.g. van der Lingen *et al.*, 2006a; Rykaczewski and Checkley, 2008; Alheit, 2009; Fréon *et al.*, 2009c. However, evidence is still scarce (Alheit and Bakun, 2010).

Hypoxia, i.e. a decrease in dissolved oxygen concentration, is another important factor structuring coastal marine ecosystems. This phenomenon is of increasing importance and affecting benthic and pelagic marine ecosystems worldwide (Stramma *et al.*, 2008; Breitburg *et al.*, 2009; Levin *et al.* 2009, Paulmier and Ruiz-Pino, 2009; Ekau *et al.* 2010; Zhang *et al.*, 2010; Gilly *et al.*, 2013). For example, extensive oxygen minimum zones (OMZ) exist in the northern Humboldt and northern Benguela Current, with the oxygenated surface water layer reduced to a few tens of meters or less (Fréon *et al.*, 2009b). The expansion of hypoxic zones can be the result of in- or decreasing upwelling activities due to climate induced changes. Increased activity can cause the upwelling of low-oxygenated waters (Mohrholz *et al.*, 2008; Bakun *et al.* 2010b), whereas decreased activity enhances stratification and oxygen depletion through decay processes in the upper productive water layer (Bakun *et al.*, 2010b). Based on the observation that increased upwelling activity results in a shoaling of the OMZ, Bertrand *et al.* (2011) proposed two mechanisms for a structuring effect of hypoxia leading to regime shifts in the Humboldt Current. Firstly, they suggested that sardines (*S. sagax*) are physiologically more affected by hypoxia than anchovies (*E. ringens*), due to their larger body size-related oxygen demand. Secondly, a shallow oxycline may lead to an accumulation of hypoxia-intolerant zooplankton in surface waters, favouring particle-feeding anchovy bio-energetically; whereas a deeper oxycline may favour sardines allowing them to effectively use its energetically preferred filter-feeding mode (Bertrand *et al.*, 2011).

Traditional fisheries management follows the stock-recruitment relationship (Ricker, 1954; Beverton and Holt, 1957) and modern management is still widely based on the paradigm that a long-term yield of fish stocks depends on a stable stock size (Beddington *et al.*, 2007; Vert-pre *et al.*, 2013). During the last 50 years, however, fisheries management has often failed to prevent the collapse of fish stocks (Mullon *et al.*, 2005) and the stock-recruitment relationship model poorly reflected reality for small pelagics (Zheng, 1996). Indeed, stock production was correlated to environmental regimes instead of population abundance alone for the majority of 230 fish stocks analysed recently (Vert-pre *et al.*, 2013). Hilborn (2010) showed that the recovery potential of decimated stocks is mostly determined by the intensity of recruitment

compensation. Cury *et al.* (2008) promote the "ecosystem oceanography" concept, which integrates environmental conditions into fish stock management models as approach to tackle future climate related changes. Thus, the need to investigate and understand the underlying processes of such environment-stock-recruitment relationships is evident. Interestingly enough, the concepts of small pelagics population dynamics, as outlined above, focus on adult fish and ignore the importance of processes during early life stages for recruitment success and population size during the early life stages, which is further impeded by the lack of data at present.

The role of recruitment for the size of fish stocks and environmental influences

Understanding the factors that determine the size of fish stocks has been the central research question for fisheries biologists since the beginning of the discipline in the 2nd half of the 19th century (Lehodey *et al.*, 2006; Houde, 2008), when fluctuations of the Norwegian cod, European herring and sardine populations were puzzling researchers (Bohuslän periods). First, fluctuations in stock size were believed to be a consequence of changes in patterns of fish migration or fishing effort (see Houde, 2008). Soon after the foundation of the International Council for the Exploration of the Sea (ICES) in 1902, the importance of recruitment for stock development, as regulated by processes during the early life stages, was acknowledged. Today, recruitment variability is commonly understood as driven by complex interactions between tropho- and hydrodynamic processes, acting throughout pre-recruit life from the egg to the juvenile phase (Houde, 1987; Lehodey *et al.*, 2006; Houde, 2008).

The central idea behind this theory is that survival and mortality rate during the early life phases determine recruitment strength, thereby affecting the size of the adult population. Consequently, environmental conditions and life-history characteristics are thought to be important criteria for stock recovery after population collapses (Hutchings, 2000; Hutchings and Reynolds, 2004; Hammer *et al.*, 2010). Generally, "stage duration" is accepted to be critical for the survival of early life stages. High growth rate allows for passing larval stages faster, which reduces the risk of mortality by starvation and predation through an increase in size as well as more effective foraging and escape potentials with the development of swimming capacity (Houde, 1987; Takasuka *et al.*, 2003; Fuiman *et al.*, 2005; Houde, 2008).

Environmental factors act on physiological processes in fish larva (Brett and Groves, 1979; Houde, 1987; Neill *et al.*, 1994). In his "physiological classification of the environment", Fry (1947, 1971) divided the environmental factors by their effect on metabolism in five groups: controlling, limiting, masking, directive and lethal factors. The major abiotic factor is temperature, influencing the metabolic performance of an organism as outlined in the conceptual model of oxygen- and capacity-limited thermal tolerance (Pörtner, 2010). The

resulting "thermal window of performance" can differ between and within species, across life-stages or between populations. Synergistic stressors, e.g. hypoxia or elevated CO_2 concentrations, can narrow the thermal window (Pörtner and Farell, 2008). Temperature acts at different organizational levels (cellular, individual, population, community and ecosystem) and affects various processes related to recruitment (e.g. time of spawning, larval feeding rates and success, growth, distribution, natural mortality, swimming activity; for details see: Neill *et al.*, 1994; Ottersen *et al.*, 2010). Survival rate of individuals and recruitment success of populations is influenced by physiological performance, which can ultimately result in ecosystem regime shifts (Pörtner and Peck, 2010).

Most of the existing recruitment theories concentrate on bottom-up factors (e.g. hydrological and trophic conditions) and vary in their focus on abiotic/climatic or biotic factors (reviewed by Houde, 2008; Bakun, 2010; Drinkwater *et al.*, 2010; Ottersen *et al.*, 2010). Adults can also influence the potential for successful recruitment via quantity and quality of their offspring (Rose *et al.*, 2001; Houde, 2008; Grote *et al.*, 2011). Furthermore, top-down regulation via predation and fishing can also play a direct or indirect role on recruitment (reviewed in: Bakun, 2010; Perry *et al.*, 2010). For example, size-selective fishing can result in a lower offspring quality, leading to a higher instability of recruitment patterns (Anderson *et al.*, 2008; Perry *et al.*, 2010).

The role of oceanography in recruitment – bottom up

Oceanographic features can influence larval survival both directly, e.g. by advection, and indirectly, e.g. by determining prey availability. The "Aberrant Drift Hypothesis" (Hjort, 1914) emphasizes the negative role of currents that disperse early life stages into regions with unfavourable prey densities. The "Stable Ocean Hypothesis" (Lasker, 1978, 1981) concentrates on the importance of temporarily stable conditions in the water column, allowing for the formation of fine-scale patches of dense aggregations of larvae and prey in stratification boundaries/fronts. This hypothesis was developed with focus on small pelagic fish stocks in highly dynamic upwelling systems. As an extension, the "Optimal Environmental Window Hypothesis" (Cury and Roy, 1989) proposes a dome-shaped relation of wind speed and recruitment. Intermediate wind speeds are considered optimal, being strong enough to allow for sufficient upwelling intensities for supporting sufficient prey production and weak enough for preventing losses by advection away from coastal feeding grounds. Finally, the "Ocean Triad Hypothesis" (Bakun, 1996) unites all previous mentioned theories by stating that three major groups of physical processes define a favourable recruitment habitat: (i) enrichment (upwelling, mixing, etc.), (ii) concentration (convergence, fronts, water column stability) and (iii) retention mechanisms preventing offshore transport.

The role of trophic processes in recruitment – bottom up and top down

In this context, trophic processes are considered very important for survival and growth of fish larvae. The fundamental "Critical Period Hypothesis" (Hjort, 1914, 1926) proposes that a failure in finding sufficient food quantities during the first feeding phase of fish larvae greatly affects mortality rates. Today, this general idea is still accepted, but the focus on first-feeding larvae is considered to be too narrow (Cushing, 1996; Houde, 2008). The "Match-Mismatch Hypothesis" (Cushing, 1974, and 1990) focuses on the importance of the fact that the spawning period of fish has to overlap with periods of high prey abundance. In a situation of limited food resources, the competition for prey can negatively influence growth rates and change recruitment success according to the "Stage Duration Hypothesis" (Houde, 1987, and 2008). However, density-effects have been rarely described by studies of larval stages (Houde, 2008).

In addition to the above-mentioned bottom-up processes, top-down regulation can influence recruitment strength through predation. The "Predator-Pit" hypothesis (Bakun, 2006) proposes a density-dependent predation on larvae. Concentration processes are leading to favourable feeding conditions on the one hand, but also attract predators on the other hand, causing a situation of "feeding heaven and predation hell".

Study region - the northern Benguela Current Ecosystem (NBCE)

The Benguela Current (BC) extends from the Cape of Good Hope (35°S) to the Angola-Benguela Front (ABF, around 17°N; Fig. 1) and is the only EBUE bordered by tropical waters at both ends: the warm Agulhas Current from the Indian Ocean in the South and the warm Angola Current (AC) water in the North (Shelton *et al.*, 1985). The BC has a northward flowing main stream, fed primarily by cold polar waters of the South Atlantic Current (SAC) and warm water of the Agulhas Current (Peterson and Stramma, 1991). Five major upwelling cells exist in the BC (Fig. 1) with the perennial Lüderitz cell (27°S) being the strongest worldwide. It divides the BC into a southern (SBCE) and a northern ecosystem with distinct hydrographical and biological features (Duncombe Rae, 2005).

The bathymetry of the northern BC area is characterised by a broad shelf around Walvis Bay (23-21°S), the Walvis Ridge (20°S), and a narrow shelf and a steep slope at the Kunene River Mouth (17.5°S). Upwelling is wind-driven and occurs year-round, with maximum intensities in winter and early spring, and quiescent periods during summer (Shannon, 1985; Bartholomae and van der Plas, 2007). The influence of cold equator-wards and warm pole-wards currents varies seasonally (Barange and Pillar, 1992). During the warm season (austral summer, January-April), the ABF is situated further south than during the cold season (austral winter, June-October; Shannon *et al.*, 1987). The extent of the southward intrusion of warm water also varies between years and an increasing frequency of deeper southward penetrations was observed during the last decades (Bartholomae and van der Plas, 2007). In some years, these near shore intrusions of warm and saline AC waters are extraordinarily

Fig. 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. Bathymetric lines show 200, 1000 and 3000 m. Abbreviations: SAC = South Atlantic Current, ABF = Angola Benguela Front (from Ekau *et al.*, 2010, Fig. 8)

strong, lasting from summer to winter and termed "Benguela Niño" (Boyd *et al.*, 1987; Gammelsrød *et al.*, 1998). Time-series analysis of wind anomalies at Lüderitz showed lower wind speeds between 1960 and 1975, stronger winds during 1975-1987, and a subsequent decrease of wind speeds reaching very low levels during 2000-2006 (Bailey *et al.*, 2009; Hutchings *et al.*, 2009). Similarly, development of sea surface temperature (*SST*) anomalies indicates a warming of the system (Hutchings *et al.*, 2009). Thus, both wind and *SST* data indicate an increase of quiescent upwelling periods in the NBC during the last two decades.

The ratio of new vs. total (new and regenerated) primary production is low in the NBCE compared to other EBUE, suggesting that only a small proportion of the total production is readily available to supply the food-web (Lutjeharms *et al.*, 2001). This makes it vulnerable to reduced nutrient supply during periods of quiescent upwelling (Lutjeharms *et al.*, 2001). However, total phytoplankton production in the NBCE is estimated to be higher than its consumption, with a surplus of ca. 25% of the carbon flux deposited in organic-rich sediments on the shelf floor (reviewed by Lutjeharms *et al.* 2001; Inthorn *et al.*, 2006) and the collapse of small pelagics may have increased these sedimentation processes (Bakun *et al.*, 2010b). In these mud-belts, decay processes create extensive hypoxic zones (Bartholomae and van der Plas, 2007). Together with the upwelling of oxygen-depleted water originating from the Angola Current, these conditions cause coastal hypoxia (Monteiro *et al.*, 2006; Mohrholz *et al.*, 2008). A trend of the shoaling of the 2.5 mL O_2 L^{-1} iso-surface has been shown over the last 50 years (Ekau *et al.*, 2010).

The zooplankton community of the BC is distinct from the tropical Angolan waters north of the ABF, and between the NBCE and SBCE most populations are separated (Shannon *et al.*, 1988; Gammelsrød *et al.*, 1998; John *et al.*, 2004; Lett *et al.*, 2007; von Bodungen *et al.*, 2008). The dominant mesozooplankton group in terms of abundance and biomass are copepods (Timonin *et al.*, 1992) followed by euphausiids (Olivar and Barange, 1990). The copepod orders Cyclopoida, Poecilostomatoida and Harpacticoida only contain few and/or small species (Gibbons, 1999), whereas the order Calanoida is richer in species and more diverse in terms of body size and ecological characteristics of species (Richardson *et al.*, 2001; Loick *et al.*, 2005; Schukat, 2012). During the last two decades the small cyclopoids showed positive anomalies in their densities, parallel to a warming of the system (Verheye and Kreiner, 2013).

Coastal pelagic fish in the NBCE - biology, population dynamics and fisheries

Sardine was the dominant pelagic fish species in the NBCE over long periods during the last 3000 years and, in contrast to other EBUE, horse mackerel instead of anchovy was the 2nd most important species (Shackleton, 1987; Finney *et al.*, 2010). Spawning grounds are located in the vicinity of Walvis Bay (21-24°S) and in the north of the NBCE (17-19°S; Hutchings *et al.*, 2002, Axelsen *et al.*, 2004). The main spawning area of *S. sagax* moved from the northern to the southern region from the 1980s to the 2000s (Tjizoo, 2008; Kreiner *et al.*, 2011), whereas the centre of *T. capensis* spawning lies in the north (Kirchner, 2012).

With the cease of whaling after World War II, pelagic fish became the main target of industrial fisheries (Griffiths *et al.*, 2004). Sardine (*Sardinops sagax*) dominated catches until the mid-1970s, but after the second abrupt decline during 1976-78, their biomass and landings never recovered, with actual catches being less than 7% of the historical maximum (Fig. 2; van der

Lingen *et al.*, 2006b; Kirchner *et al.*, 2009; Roux *et al.*, 2013). Anchovy (*Engraulis encrasicolus*) landings were relevant only during the 1980s (Fig. 2). From the beginning of the 1990s, Cape horse mackerel (*Trachurus capensis*) has been the only important pelagic fisheries resource in the NBCE (Fig. 2), with its estimated biomass remaining relatively stable until present (Boyer and Hampton, 2001; van der Lingen *et al.*, 2006b; Kirchner *et al.*, 2010). Still, the estimated level of stock depletion since the inception of fisheries is about 40-50% for *T. capensis,* with the size at 50% maturity reduced
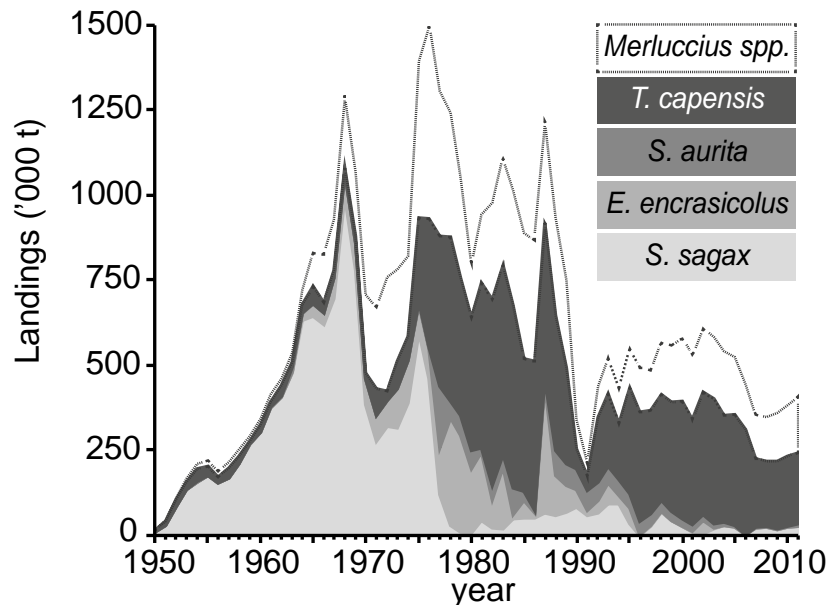
Fig. 2: Historical development of annual fisheries landings in the NBCE from 1950-2011. Data sources: 1950-1994: www.seaaroundus.org, 1994-1999: FAO data, 2000-2011: Kirchner, 2012

from 26 to 19 cm (Kirchner, 2011, and 2012). The fishing sector, with *T. capensis* and the valuable hakes (*Merluccius capensis* and *M. paradoxus*) as main targets, contributed >6% to the Namibian GDP and some 20% of Namibia's exports in 2005 (Sherbourne, 2007).

In summary, the NBCE turned from an area with the 3rd highest ever recorded maximum fish catch and fisheries productivity (Cury *et al.*, 1998) to a degraded upwelling ecosystem during the last decades due to the long absence of both sardine and anchovy (Bakun *et al.*, 2010a). Horse mackerel, hakes (*Merluccius capensis* and *M. paradoxus*) and the pelagic goby *Sufflogobius bibarbatus* are the central fish species in the food web of the new ecosystem state, and it is likely that jellyfish are gaining influence (Cury and Shannon, 2004; van der Lingen *et al.*, 2006b; Flynn *et al.*, 2011; Roux *et al.*, 2013). Triggers of this regime shift were the combined effect of high fishing pressure and environmental changes (Cury and Shannon, 2004). Environmental factors linked to climate change effects (e.g. increased temperature, shoaling of hypoxic zones), together with self-enhancing mechanisms (e.g. feedback loops in the food web as potential food competition with jellyfish and their predation on fish larvae), were proposed to be mainly responsible for the persistent trapping of the ecosystem in the new state (e.g. Boyer *et al.*, 2001; Bakun and Weeks, 2006; van der Lingen *et al.*, 2006b; Bakun *et*

al., 2010a&b). To date, both the recovery failure of clupeoid stocks and the mechanisms leading to the persistence and stability of the new ecosystem state in the NBCE are not fully understood. Processes during the early life history (ELH) stages (egg, larva, and juvenile) were proposed to be major regulative mechanisms for recruitment success (van der Lingen *et al.*, 2006a; Ekau *et al.*, 2010).

Objectives and outline

As outlined above, ELH traits are important for the recruitment success of a species and they are of particular interest to understand fish species' dominance patterns. ELH stages are very sensitive to environmental changes due to their limited movement potential and their fragile morphology, both associated with their planktonic lifestyle. Feeding success can be affected by inter- and intraspecific competition and depends on prey composition and availability. Prey quantity and quality determine nutritional condition and growth rate, which are both important for surviving the vulnerable larval phase. High mortality during this phase makes it a potential bottleneck for stock development.

However, detailed studies on the physiological and ecological traits of ELH stages of sardine, anchovy and Cape horse mackerel in the Benguela Current are still missing. Existing knowledge on temperature preferences and critical dissolved oxygen concentrations for ELH stages of coastal pelagic fishes stems from the relation of egg and larval abundance to environmental parameters. In regard to temperature preferences, different studies yield contradictory results and were mainly based on *SST*-data (Le Clus, 1991; Daskalov *et al.*, 2003; Twatwa *et al.*, 2005; Tjizoo, 2008). Comparative studies on ecological and eco-physiological ELH traits of pelagic fish species beyond these observations are missing and the few existing data (e.g. Cram, 1977; Thomas, 1986) were collected in the 1970s and 1980s (e.g. Cram, 1977; Thomas, 1986), which are periods distinctly different from today's hydrographical and biological conditions (Fréon *et al.*, 2005; van der Lingen *et al.*, 2006b). In addition, acclimation or adaptation of ELH traits to changing environmental conditions (increased periods of warm water temperatures, shoaling of hypoxic zones) over the last decades is conceivable.

Consequently, the importance of determining ELH traits of coastal pelagic fish in order to understand the underlying mechanisms of the current ecosystem state in the NBCE has been addressed several times in recent years (e.g. van der Lingen *et al.*, 2006b; Boyer and Hampton, 2007; van der Lingen *et al.*, 2009; Hutchings *et al.*, 2009).

This doctoral thesis is part of the larger interdisciplinary research project GENUS (**G**eochemistry and **E**cology of the **N**amibian **U**pwelling **S**ystem, http://genus.zmaw.de/), which uses the NBCE as a natural laboratory to study the interacting effects of climate change factors, namely global warming and shoaling of hypoxic zones, on ecosystem processes in upwelling systems. Within GENUS, the working groups Fisheries Biology and Ecophysiology at the Leibniz Center for Tropical Marine Ecology/Bremen investigate trophic ecology, growth, condition and physiological adaptations of key fish species (sardines, anchovy, horse mackerel, goby, flatfish) to environmental factors (temperature, oxygen, zooplankton

11

composition). As the core of this research, my doctoral thesis focuses on ELH traits of the four main small and medium pelagic fish species in the NBCE, sardine (*S. sagax*), anchovy (*E. encrasicolus*), Round sardinella (*Sardinella aurita*) and Cape horse mackerel (*T. capensis*). It aims to contribute to a better understanding of bottom-up processes relevant for their recruitment success by addressing the following questions:

1. Which mechanisms hinder sardine and anchovy from recovery of their populations under the present environmental conditions in the NBCE?

2. Why could the invading sub-tropical Round sardinella not substitute the two species during the last 20-30 years?

3. Which characteristics allow Cape horse mackerel to maintain a fairly stable population, even under changing environmental conditions?

4. Can competitive advantages during the larval and early juvenile phase of *T. capensis* explain their different success in comparison to clupeoid species in the NBCE?

For this, the following specific research questions are addressed in three separate chapters of my thesis:

In chapter I, an experimental approach at the organism level was chosen to investigate energy demand and hypoxia tolerance of *T. capensis* larvae and juveniles. In chapter II and III, a multi-methodological approach was used to investigate early life history traits of the three clupeoid species (chapter II) and *T. capensis* (chapter III) during different times of the year, focussing on: (i) spatio-temporal distribution, (ii) feeding ecology, (iii) nutritional condition and (iv) daily growth rates in relation to ambient environmental conditions (temperature, oxygen concentration, plankton abundance and composition).

Chapter I

"**Energy demand of larval and juvenile Cape horse mackerels, *Trachurus capensis*, and indications for hypoxia tolerance as an advantage in a changing environment**"

Geist, S. J., Ekau, W., Kunzmann, A. (accepted) Marine Biology

Contribution of the authors: Werner Ekau and Andreas Kunzmann wrote the respective part of the GENUS project proposal (applies also to Chapter II and III). All three authors designed the study. Simon Geist and Andreas Kunzmann adopted methodology to larval fish and conducted experiments. Simon Geist analysed data and wrote the manuscript. Werner Ekau and Andreas Kunzmann advised on data analysis and commented on the manuscript.

Chapter I focuses on eco-physiological traits of Cape horse mackerel to answer the following specific questions:

- What is the energy demand of larval and juvenile *Trachurus capensis*?

- How much is it converted in prey equivalents?

- How does metabolic activity relate to body size?

- Does this relationship change during the larval and juvenile phase?

- To what extent are larval and juvenile *Trachurus capensis* adapted to hypoxic conditions?

- At which oxygen saturation levels do they show a reaction in their metabolic rates?

Chapter II

"**Larval feeding ecology of clupeoid fish in the degraded northern Benguela Current upwelling system and its implications for stock recruitment processes**"

Geist, S. J., Kunzmann, A., Verheye, H. M., Ekau, W. (in review)

Contribution of the authors: Simon Geist, Werner Ekau and Andreas Kunzmann designed the study. All authors took part in field sampling. Simon Geist analysed samples and data, and wrote the manuscript. Werner Ekau guided data analyses and commented on the manuscript together with Andreas Kunzmann and Hans Verheye.

Chapter II compares the three species of Clupeiformes and addresses the following questions:

- Are there different preferences in regard to water temperatures between *S. sagax*, *E. encrasicolus* and *S. aurita*?

- Are larvae of the three species different in regard to their trophic ecology?

- How does the environment affect nutritional condition and growth rates?

Chapter III

"**Early life history traits determine the success of Cape horse mackerel, *Trachurus capensis* Castelnau, 1861, in the degraded northern Benguela upwelling ecosystem off Namibia**"

Geist, S. J., Kunzmann, A., Verheye, H. M., Ekau, W. (in review)

Contribution of the authors: Simon Geist, Werner Ekau and Andreas Kunzmann designed the study. All authors took part in field sampling. Simon Geist analysed samples and data and wrote the manuscript. Werner Ekau advised on data analyses and commented on the manuscript together with Andreas Kunzmann and Hans Verheye.

Chapter III concentrates on *T. capensis*, the new dominant pelagic species. It is compared to Clupeiformes (Chapter II) in the discussion in order to clarify the questions:

- Does the relation of larval distribution to in-situ temperature and dissolved oxygen provide a hint for a preference of warmer conditions?

- Can larval trophic ecology uncover the reasons for successful recruitment?

- What are the potential advantages of horse mackerels in comparison to clupeoids during their early life history?

Methodological approach

Field work

Fish larvae and data of prevailing environmental conditions were collected in the NBCE (~16°S to ~27°S) during four research cruises at different times of the year (Table 1; Annex I) at 118 sampling stations (Fig. 3). Quantitative ichthyoplankton collections in the upper 200 m were conducted at 94 stations using a MultiNet type Midi (Hydrobios™, mouth area: 0.25 m^2, mesh size: 500 µm) equipped with five nets and hauled obliquely at 1 m s^{-1} from 200 m to the surface (Plate I/1-9).

Table 1: Sampling campaigns analysed for the thesis

Cruise	time period	Research Vessel	quantitative and qualitative hauls	qualitative hauls only	*Trachurus capensis*	*Sardinops sagax*	*Engraulis encrasicolus*	*Sardinella aurita*
			NBCE stations (16-27°S)		No. of larvae in quantitative hauls			
MSM7	9.3.-17.4.2008	Maria S. Merian	32	9	596	3	147	71
Afr258	1.-17.12.2009	Africana	17	2	115	7	2	12
D356	10.9.-13.10.2010	Discovery	10	6	134	0	0	0
MSM17	30.1.-7.3.2011	Maria S. Merian	38	4	750	1 665	484	221
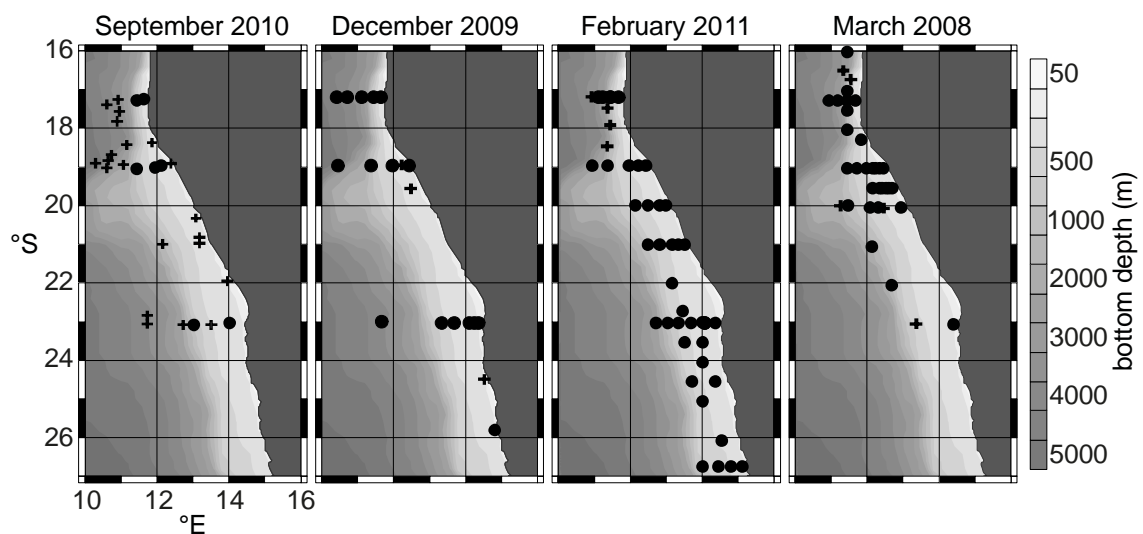
Fig. 3: Station grid during the four research cruises. Crosses indicate stations were only qualitative hauls were made

15

At each station, the nets were sampled in depth strata according to water column structure in terms of temperature and dissolved oxygen identified from preceding CTD-casts (Mohrholz, 2012a-c and pers. comm.). The two uppermost nets were equipped with net-inlays (Plate I/10; mouth diameter: 10 cm, mesh size: 55 µm) for simultaneous sampling of microzooplankton in these depth strata, except during 03/2008. In order to augment the number of fish larvae used for stomach content, growth and biochemical analyses, additional hauls were made with a trawled or drifting ring net (Plate I/11; mouth area: 2 m^2, mesh size: 1000 µm), a Tucker trawl (Plate I/12; mouth area: 1 m^2, mesh size: 1000 µm) and a MOCNESS (mouth area: 1 m^2, mesh size: 2000 µm). Incoming hauls were immediately checked for live larvae, which were carefully transferred to beakers with filtered seawater for subsequent respiration experiments (Plate I/24-26; details in Chapter I). From the remaining larvae subsamples were sorted out on board and deep-frozen at -80°C immediately after catch for further laboratory analyses at the ZMT Bremen. Finally, the remaining samples of MultiNets and net inlays were preserved in a 4% buffered formalin-seawater-solution for community composition analyses of ichthyo-, zoo- and microzooplankton. Fish larvae were identified according to Olivar and Fortuno (1991).

Distribution: spatial and in relation to in-situ temperature and oxygen concentration

Larval densities per station were calculated from the MultiNet catches for each single net (ind. 100 m^{-3}), and standardised per unit area (ind. 10 m^{-2}). For a combined analysis of the spatial distribution of the larvae and the thermal regime between stations, the temperature at 20 m (T_{20m}) was chosen, based on the observed depth distribution of the larvae. It is also a simple indicator of upwelling intensity (Boyd, 1983). Larval depth distributions of the four species were related to temperature and oxygen saturation, with the values from the closing (when both oxygen and temperature were analysed) or the median (when only temperature was analysed) depth of the respective net was used, to reflect *in-situ* conditions.

Respiration experiments

Oxygen consumption rates under fully oxygen-saturated conditions and under lowered oxygen concentration were measured in 52 experiments of larval and juvenile *T. capensis*. Respirometry of larvae was done in a closed setup, and post-larvae and juveniles were measured in an intermittent-flow setup (Plate I/28). Experiments were mostly conducted on-board in a cooling container modified to hold a constant temperature during MSM-17 (Plate I/27-28). Some juveniles were sent to the ZMT after the cruise and experiments were continued there (PlateI/29). Larger juveniles were caught around Cape Town, South Africa and measured at the Seapoint Laboratory, Cape Town.

Analytical lab work

For each of the following analyses subsamples of larvae were used to allow for inter- and intraspecific comparisons between seasons and between geographic areas to cover conditions of different upwelling activities.

Basic measurements

Body length of larvae was measured as standard length (*SL*; notochord length in early larvae). *Trachurus* larvae were staged according to distinctive morphological developments (Plates II-VI; Chapter III). For a better comparison of ontogenetic stages of the morphologically different clupeoid and *T. capensis* larvae the ontogenetic index was calculated additionally for the synopsis as $O_L = \log L / \log L_{juv}$ with L = larval length and L_{juv} = length at which species completes metamorphosis (Fuiman, 1994, and 2002). L_{juv} was estimated at 22 mm *SL* for *T. capensis* and at 35 mm for *S. sagax* and *E. encrasicolus*, based on a literature review for species of the respective genus (Annex III). Body mass was determined as wet (*WM*) and dry mass (*DM*) using a high-precision balance after freeze-drying the larvae, which had their intestinal tract carefully removed. Relationships of *WM* to *DM*, and *DM* to *SL* are given in Annex IV.

Trophic ecology

We used an integrated approach combining three different methods to study the trophic ecology of coastal pelagics larvae, providing information at different time scales and at different taxonomic resolutions. Gut content analysis (intestinal tract) provides information about the ingested food items at the time of catch and allows for the highest taxonomic resolution, but can be biased towards hard-structured, undigested items that are more easily identifiable. $\delta^{15}N$-SI-ratios of larval muscle tissue and potential food organisms (phyto- and zooplankton) were analysed to obtain an intermediate to long-term record of metabolised food and trophic position (Vander Zanden and Rasmussen, 2001). Fatty acid trophic markers (*FATM)* were used as a medium- to long-term record of metabolised food (Dalsgaard *et al.*, 2003) to reveal the relative importance of carnivory and of diatom- and dinoflagellate-based prey in the larval food.

Nutritional condition

The morphometric condition factor (Heincke, 1908) was adjusted for a species-specific length-body mass relation and calculated separately for each species as: $k = GDM\ SL^{-b}\ 10^{-5}$, where *GDM* is gutted dry mass (mg), *SL* is standard length (mm) and *b* is derived from species-specific potential length-weight regressions. It was used for intra-specific comparisons between cruises and sites. To allow for interspecific comparison, total fatty acid (*TFA*) content (% *DM*) was measured as biochemical indicator of nutritional condition (Osako *et al.*, 2003).

Growth rates

Fish larvae invest surplus energy mainly in somatic growth (Houde, 1987), which makes daily growth rates (*DGR*) an indirect indicator of nutritional condition. *DGR* during the first month of life were estimated using back-calculations from growth increment readings of sagittal otoliths. The daily formation of increments has been validated earlier for larvae of *Trachurus* (Jordan, 1994; Waldron and Kerstan, 2001; Xie *et al.,* 2005), *S. sagax* and *E. encrasicolus* (Thomas, 1986). Otoliths from the smallest larvae (ca. 3-5 mm) were placed on a cavity slide with a drop of in Immersion Oil (Zeiss), to increase contrast. Otoliths from larvae >5 mm were mounted with epoxy resin and polished and grounded respectively with silicon carbide paper of 2400 and 4000 granulation to reveal all the growth increments. The back-calculation followed the procedure described by Grote *et al.* (2012) using the model of Folkvord and Mosegaard (2002).

Synopsis

Response to environmental key factors – synoptic results and discussion

Spatiotemporal distribution of larvae in relation to water temperature

Fish larvae of all four species were mainly caught over the shelf at water depths < 500 m (Fig. 4) and occurred in highest numbers during the two cruises in February 2011 and March 2008 (MSM 7 and 17). This indicates spawning peaks during late summer and is in accordance to spawning data of anchovy and horse mackerel from 1983/1984 and sardine from 1999-2005 (Boyd *et al.*, 1985; Kreiner *et al.* 2011). Only *T. capensis* larvae were also caught in significant numbers during the two cruises in September 2010 and December 2009 (D356 and Afr 258). In addition, they showed the most equal density distribution of larvae of all four species and were found at relatively more stations throughout the NBCE (Fig. 4). The highest larval densities were encountered in the Walvis Bay region (~23°S) during February 2011, mainly due to the high abundance of clupeoid larvae. By comparison, *E. encrasicolus* and *S. aurita* larvae showed a wider latitudinal distribution compared to *S. sagax* larvae, being also present at northern stations up to the Kunene River mouth. *S. sagax* larvae were caught in significant numbers around Walvis Bay, only (Fig. 4).

Table 2: Water temperature (°C) at net closing depths with positive larval catches separately for the four coastal pelagic fish species. All positive nets from MultiNet hauls included. Temperature data taken from CTD casts (Mohrholz, 2012 a, b, c, and unpub. data)

	N (nets)	Min.	25%	median	75%	Max
S. sagax	37	12.3	14.8	17.6	19..2	21.0
E. encrasicolus	60	12.1	17.7	19.0	20.1	23.5
S. aurita	28	13.8	17.2	18.2	19.3	21.6
T. capensis	113	12.8	16.0	18.0	20.0	25.7

During the two summer cruises, the water temperature increased towards the north (Fig. 4), indicating periods of quiescent upwelling and/or intrusions of warm tropical waters from Angola. The comparison of water temperatures at catching depths suggested that *S. sagax* larvae are more stenothermal in contrast to the more eurythermal larvae of *E. encrasicolus* and *T. capensis* (Table 2; Kruskal Wallis Test, $\chi^2_{(3,\,235)} = 11.67$, p = 0.0086; see also Chapter II and III). Based on their spatial distribution patterns, these results suggest a higher water temperature tolerance of *T. capensis*, *E. encrasicolus* and *S. aurita* larvae compared to *S. sagax* larvae. These findings contrast two previous studies (Le Clus, 1991; Tjizoo, 2008), which regarded both *S. sagax* and *E. encrasicolus* as eurythermal with similar temperature preferences. Both studies covered a longer time span and larger data sets, but correlated larval

abundances to sea surface temperatures (*SST*). *SST*, instead of T_{20m} or *in-situ* temperatures, is probably not suitable to distinguish fine scale temperature preferences of different species. Further support for the results of the present investigation is given by the modelling study of Daskalov *et al.*, 2003, who found a relation between a better recruitment success of sardines and lower water temperatures in the NBCE.

In the Japanese Sea (Takasuka *et al.*, 2008) and in the north-east Atlantic (Ibaibarriaga *et al.*, 2007), anchovy larvae (*Engraulis japonicus* and *E. encrasicolus*, respectively) occured over a wider temperature range and also at higher temperatures compared to sardine larvae (*Sardinops melanostictus* and *Sardina pilchardus*, respectively), paralleling the pattern I revealed for the NBCE. Contrasting pattern was found in the Eastern Pacific, where anchovy larvae (*E. mordax* and *E. ringens*) preferred lower spawning temperatures than sardine (*S. sagax*), for the California (Lluch-Belda *et al.*, 1991) and Humboldt Current (Schwartzlose *et al.*, 1999), respectively. Moreover, in the southern Benguela Current, egg and larval surveys suggested *S. sagax* to be eurythermal with a preference for higher temperatures compared to *E. encrasicolus* (Twatwa *et al.*, 2005). Thus, assuming that my data adequately reflect the actual physiological thermal windows of clupeoids in the NBCE, larval temperature preferences appear to be species- and, with regard to the Benguela Current species, even population specific.

In contrast to clupeoid species, *Trachurus* populations were regularly observed to thrive under "warm conditions", e.g. in the Humboldt Current (Alheit and Niquen 2004), the North Sea (Alheit *et al.* 2005) and the NBCE (Boyd, *et al.*, 1985; van der Lingen *et al.* 2006b; Hutchings *et al.*, 2009). This is reflected by the "mean temperature of the catch" which was higher for *T. capensis* than for *S. sagax* and *E. encrasicolus* (Cheung *et al.*, 2013b). Here, I showed that a wide thermal window is already apparent in early life stages in *T. capensis* (Chapter III). This enables *T. capensis* larvae to cope with "warm water events" that develop during periods of quiescent upwelling and a southward extension of the ABF. These conditions were frequently observed during the last decade, especially in the peak spawning period of pelagic fish larvae during summer/autumn (Bartholomae and van der Plas, 2007; Hutchings *et al.*, 2009). The tolerance of a wider range and higher water temperatures is one likely reason allowing for the observed wider spatial distribution of *T. capensis*, *E. encrasicolus* and *S. aurita* larvae. Such a scattered distribution can decrease the risk of larval mortality through locally confined deleterious environmental conditions and be an advantage for the three species over stenothermal *S. sagax* larvae. However, the *E. encrasicolus* stock size has been low for the last twenty years, suggesting that other factors than temperature, e.g. trophic interactions, are responsible for the poor recruitment of the species.

A different strategy may explain the higher maximum larval densities recorded for *S. sagax* compared to *T. capensis* and also *E. encrasicolus*. Higher larval densities can allow for stronger recruitment in contrast to *T. capensis*, provided that larval mortality is similar. This could be one reason why the *T. capensis* stock never reached a biomass similar to historic *S. sagax* levels. Although the Walvis Bay area is the most suitable spawning ground in the NBCE according to Bakun's (1996) "Ocean Triad" hypothesis, a broad continental shelf assures high enrichment, concentration and retention of plankton (Bakun and Weeks, 2006; Kreiner *et al.*, 2011), there is an inherent elevated risk of recruitment failure. Various predators of fish larvae such as jellyfish and the amphipod *Themisto gaudichaudii*, concentrate in the Walvis Bay area during summer (Auel and Ekau, 2009; Flynn *et al.*, 2011), which likely increases larval losses. Based on *S. sagax* larvae catches during the three GENUS cruises during March 2008, December 2009 and September 2010, and reported data from previous years (Kreiner *et al.*, 2011), high larval densities seem to be an exceptional phenomenon and an overall low abundance the rule, being one reason for the usually poor recruitment of sardines in the NBCE during the last years.

S. aurita, a subtropical species, is invading the NBCE from the north. The occurrence of its larvae in the Walvis Bay region during February 2011 demonstrated suitable environmental conditions for spawning during summer months. Nevertheless, low larval numbers of this species found during the four cruises suggest that spawning in this region is not significant.

Spatiotemporal distribution of larvae in relation to dissolved oxygen concentrations and metabolic adaptation

The shoaling of hypoxic water to shallow depths, as observed during the two summer cruises in 03/2008 and 02/2011 (Fig. 5), is not an exceptional phenomenon. Over the last 50 years a trend to a shallower 2.5 mL O_2 L^{-1} isopleth has been observed at Walvis Bay (Ekau *et al.*, 2010). Therefore, tolerance to hypoxic conditions is likely an advantageous trait for fish larvae in the NBCE. The majority of fish larvae was caught at stations characterised by a 2.5 mL O_2 L^{-1} isopleth of 50-100 m depth (Fig. 5). Larvae of all four species occurred most frequently in well-oxygenated water bodies in the upper 50 m of the water column; but *T. capensis* was also found in deeper water layers with low oxygen concentrations (Chapter II and III).
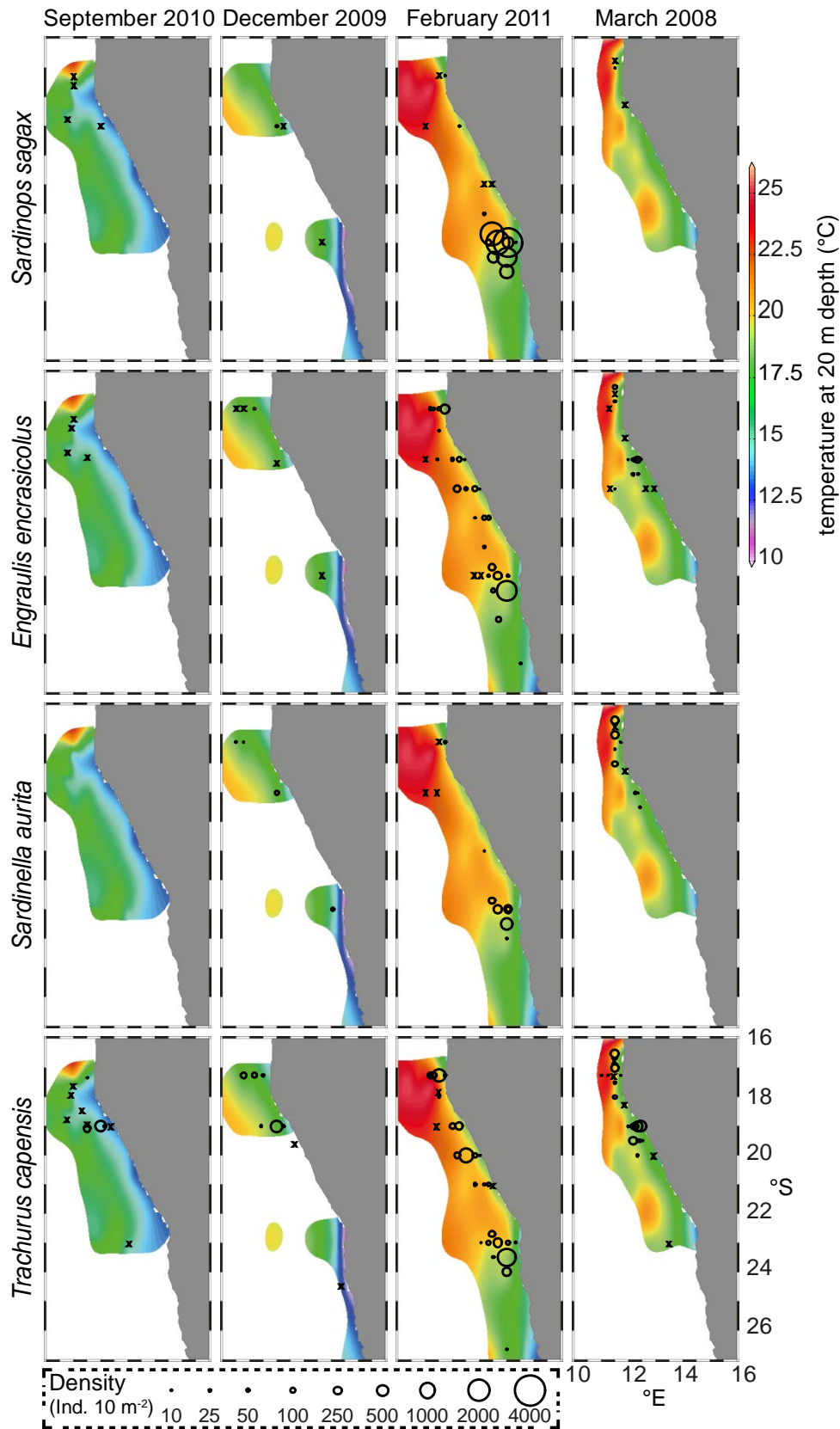
Fig. 4: Larval densities of pelagic fish species (Ind. 10 m^{-2}) in MultiNet hauls superimposed on water temperatures at 20 m depth (°C, colour bar index) during the four GENUS-cruises ordered by season. Crosses indicate the presence of larvae in qualitative catches when no parallel positive catch was made in quantitative hauls. Temperature data taken from CTD casts (Mohrholz, 2012 a,b,c, unpublished data) extrapolated with 30‰-DIVA-gridding (ODV version 4.5)
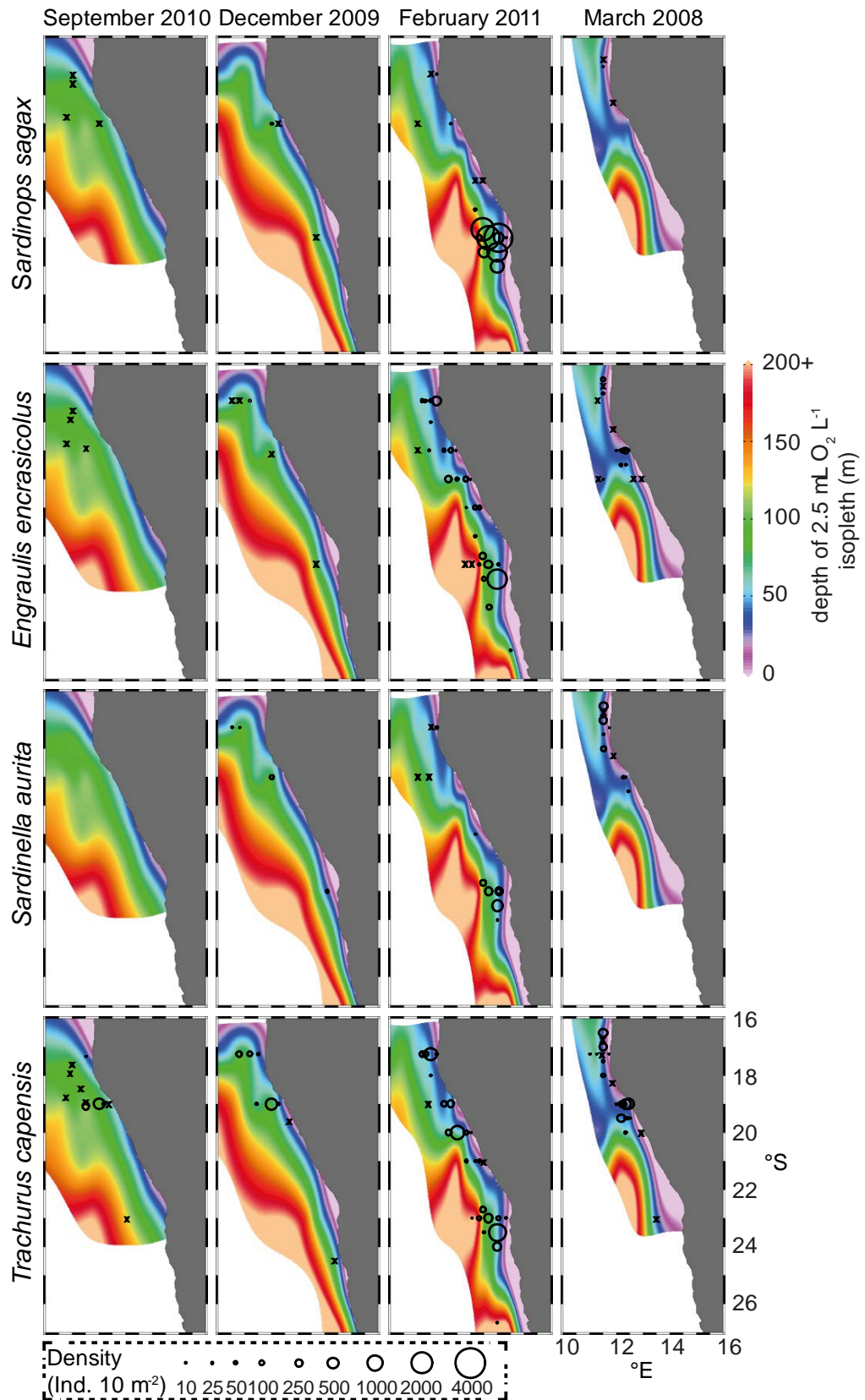
Fig. 5: Larval densities of pelagic fish species (Ind. 10 m^{-2}) in MultiNet hauls superimposed on the depth of the 2.5 mL O$_2$ L^{-1} oxypleth (m, colourbar index) during the four GENUS-cruises ordered by season. Crosses indicate the presence of larvae in qualitative catches when no parallel positive catch was made in quantitative hauls. Oxygen data taken from CTD casts (Mohrholz, 2012 a,b,c, unpublished data) extrapolated with 40‰-DIVA-gridding (ODV version 4.5)

Dissolved oxygen concentrations are an important abiotic factor for the physiological performance and survival of larvae (e.g. Rombough, 1988; Ekau *et al.*, 2010; Pörtner, 2010). Furthermore shoaling of hypoxic water may affect the larval retention mechanisms described by Stenevik *et al.* (2003, and 2007), and could thereby influence larval survival. The authors proposed that fish larvae in the NBCE actively increase retention times in coastal waters by temporal vertical migrations from subsurface water layers, characterised by high prey densities and strong Ekman transport offshore, into water depths with onshore flow below the Ekman layer. Low oxygen concentration**s** in water depths with onshore flow could prevent hypoxia intolerant larvae to enter this layer and result in increased advective losses.

A preference for well-oxygenated water was apparent for larvae of all four study species (Table 3) and is in accordance to earlier studies (Ekau and Verheye, 2005; Kreiner *et al.*, 2009). Short-term hypoxia tolerance experiments (Chapter I) showed that respiration rates of *T. capensis* larvae are not affected until oxygen concentrations reach about 1.7 mL $O_2\,L^{-1}$. In addition, the comparison of anaerobic metabolic enzyme activity (lactate dehydrogenase, pyruvate kinase) showed a higher activity in *T. capensis* compared to *S. sagax* and *E. encrasicolus* larvae (Michalek, 2012). Higher concentrations of these enzymes allow for a faster recovery from a physiological oxygen debt and are therefore regarded as proxies for hypoxia tolerance (Almeida Val *et al.*, 1995; Hochachka et al, 1996; Ton *et al.*, 2003). Furthermore, juvenile *T. capensis* were shown to tolerate short- to medium exposure (up to 24 hours) to severe hypoxia (at 20°C: $P_{crit} < 20\%$ O_2 sat., Chapter I), which may enable them to exploit food sources in the oxygen minimum zone.

Table 3: Dissolved oxygen concentrations (mL O_2 L^{-1}) at the closing depths of nets with positive larval catches, separately for the four coastal pelagic fish species (all positive nets from MultiNet hauls included). Oxygen data taken from CTD casts (Mohrholz, 2012 a, b, c, unpublished data)

	N (nets)	Min.	25%	median	75%	Max
S. sagax	27	0.16	2.54	4.66	5.68	6.20
E. encrasicolus	57	0.57	2.92	4.67	5.58	6.35
S. aurita	24	0.98	2.30	3.88	5.41	6.10
T. capensis	107	0.13	2.23	4.28	5.20	6.35

Thus, physiological and biochemical traits suggest a good adaptation of *T. capensis* ELH stages to short-term hypoxic exposure, and assumingly higher than in *S. sagax* and *E. encrasicolus*. This species-specific difference is another likely advantage for *T. capensis*, supporting its more successful recruitment under present NBCE environmental conditions.

Response to environmental key factors –perspectives

A next step in this line of research would be the investigation of coupled effects of temperature and oxygen concentration in different life stages of the four study species to define their physiological "thermal windows" (sensu Pörtner, 2010). In addition to the determined standard and routine metabolic rates in this study, the response of (a) active metabolic rates measured at maximum sustained swimming speed, (b) the maximum metabolic rate measured after exposure to stress, and (c) specific dynamic actions of fed larvae exposed to low oxygen levels, should be investigated.

Access to live clupeoid larvae involves hatching them from eggs, since they are almost impossible to catch and maintain alive in captivity (pers. obs.). Therefore, indirect approaches, such as interspecific comparisons at the molecular (e.g. hypoxia inducing factors, HIF; heat shock complex, see also: Richards, 2009) and the biochemical level, extending the work of Michalek (2012) (e.g. adaptation mechanisms of metabolic suppression: anaerobic enzymes, metabolic end products), could provide a better understanding of the mechanisms involved. Further, hypoxia exposure experiments, the subsequent determination of growth rates and the molecular and biochemical response could reveal insights into the acclimatisation potential of larvae at different time scales (hours to weeks). Finally, since the ontogenetic development of gill structures and haemoglobin production positively affect hypoxia tolerance (Rombough, 1988), the onset of these processes could differ among the four species and favour species with an earlier development.

Trophic ecology, nutritional condition and growth - synoptic results and discussion

Trophic ecology

Daytime feeding was shown for larvae of three investigated species (except *S. aurita,* whose larvae had empty guts throughout, Chapters II and III). This behaviour has been described for members of the investigated genera in a number of studies (Arthur, 1976; Young and Davis, 1992; Morote *et al.*, 2008 and 2010; Sassa and Tsukamoto, 2012). *T. capensis* showed a much higher feeding success in comparison to clupeoid larvae in terms of the relative amount of filled guts (Chapter II and III). To a certain extent, this result was likely biased by regurgitation in clupeoid larvae during the catching process, which are facilitated by their straight gut in contrast to the looped gut of *T. capensis.*

T. capensis larvae were found to ingest larger prey items than clupeoid larvae (Fig. 6). This difference was less pronounced between *T. capensis* and *S. sagax*, when prey width was related to the ontogenetic index (O_L) instead of body size at $O_L > 0.72$ (Fig. 6). Access to a
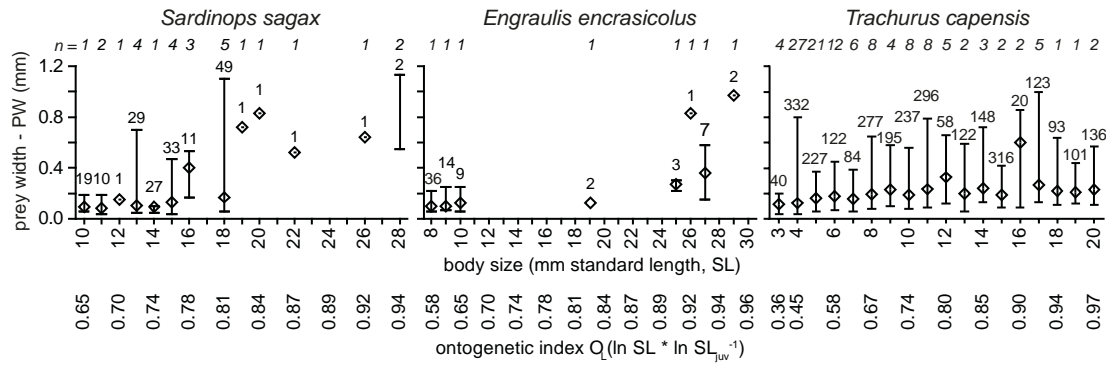
Fig. 6: Ontogenetic development of prey size spectra, represented by prey width, in *S. sagax*, *E. encrasicolus* and *T. capensis* larvae. The x-axes give both the actual body size and the ontogenetic index (Fuiman, 1994, and 2002) to account for differences in larval morphology. Data are shown as means and range. Italic numbers on top of each graph refer to analysed guts and numbers above the whiskers represent the respective prey item counts. The range of the x-axes is not equal for the three species

wider prey size spectrum earlier in life could cause the relatively higher gut fullness of *T. capensis* larvae and is a hint that they are more successful feeders than clupeoid larvae.

Gut content composition of *S. sagax*, *E. encrasicolus* and *T. capensis* larvae was dominated by different groups and life stages of copepods (Fig. 7). In all three species, a shift from smaller (eggs, nauplii, Harpacticoida) to larger (Calanoida, Euphausiacea larvae) prey items with increasing body size was observed (Fig. 7). Of notable difference was the significant proportion of small copepods of the genera *Oithona* and *Oncaea* in the guts of *T. capensis*, which were almost absent in the guts of the two clupeoid species (Fig. 7). By comparison, copepod nauplii are typical first-food of clupeoid larvae (Blaxter and Hunter, 1982) and were important in the diet of small *S. sagax* and *E. encrasicolus* larvae (Fig. 7). Since clupeoids show a higher dependence on copepod nauplii as first food than *T. capensis*, the match-mismatch risk for clupeoid larvae is higher, and the wider prey spectrum of small *T. capensis* makes them less vulnerable to starvation.

Off Walvis Bay, the copepod community was subject to changes during the last decades: copepod abundance increased from the 1970-1980s to 2000-2007, whereas average copepod size decreased due to a shift to the cyclopoid genus *Oithona* as dominant copepod group (Verheye and Kreiner, 2009). Since 2000, absolute numbers of *Oithona* sp. increased, whereas most calanoid species showed negative anomalies since the mid-2000s (Verheye and Kreiner, 2013). The low number of clupeoid larvae with full stomachs impedes robust conclusions, but if clupeoid species relied on copepod nauplii and were not able to prey on smaller copepodit stages (e.g. *Oithona* sp.), it would disadvantage them, in comparison to *T. capensis* under current NBCE conditions. Differences in the development speed of the jaws, with a much earlier ossification in *Trachurus* (*T. capensis,* 3-5 mm *SL*, Haigh, 1972) in comparison to *Sardinops* (*S. melanostictus*, 10-20 mm, Matsuoka, 1997), and a typically larger mouth width
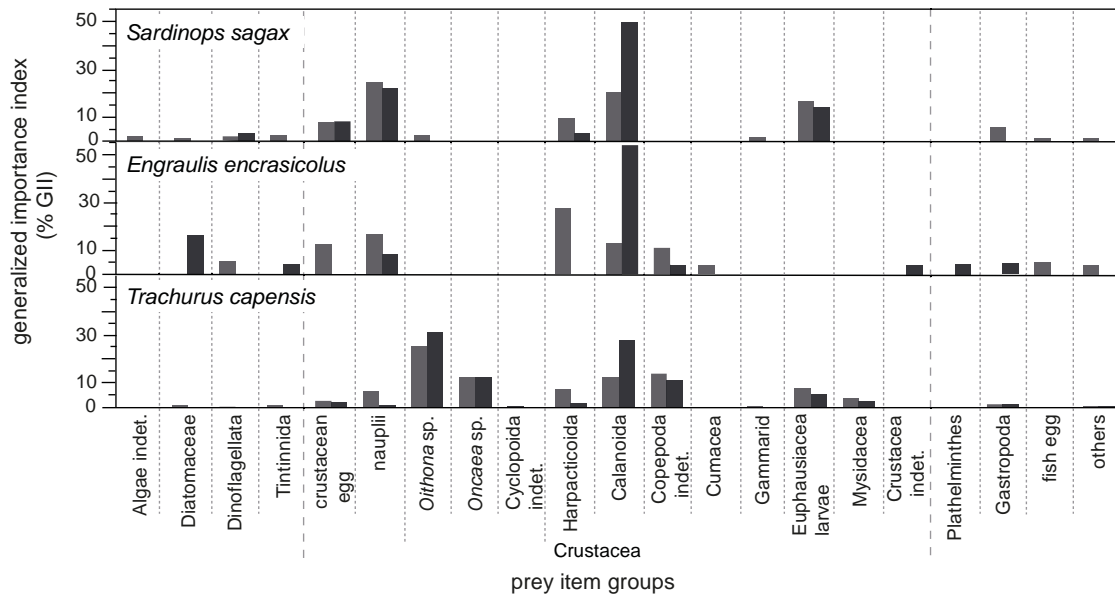
Fig. 7: Gut content composition of *S. sagax*, *E. encrasicolus* and *T. capensis* larvae and juveniles as generalised importance index (%GII, Assis 1996) based on relative abundance, relative biovolume and frequency of occurrence. Each species is split into a smaller (light grey bars) and larger (dark grey bars) size group to show ontogenetic changes. *S. sagax*: 10-16 mm, *n* = 16 and 18-28 mm, *n* = 9; *E. encrasicolus*: 8-10 mm, *n* = 3 and 19-38 mm, *n* = 6; *T. capensis*: 3-9 mm, n = 65 and 10-38 m, n = 48

of *Trachurus* (Arthur, 1976; Hunter 1980), support this hypothesis. This functional advantage allows *T. capensis* larvae to feed on more agile, larger and more nutritious prey (copepodits vs. nauplii) earlier in life.

For all four species, similar δ^{15}N-signatures were measured when caught during the same season or at the same station (Fig. 8; Chapter II and III). This indicates similar prey spectra of the larvae at the third trophic level supporting the results from gut content analyses. For *T. capensis*, sample number from three cruises allowed for a high resolution of continuous size classes. In all three years, an increase of δ^{15}N-signatures with body size was observed (Fig. 8), which indicates a continuous diet shift towards a higher trophic level with size. These results support the positive correlation between increasing body size from larval to juvenile stages and a) the size of ingested calanoid copepods as well as b) the proportions of fatty acid trophic markers for carnivory/calanoid copepods (Chapter III). Furthermore, feeding on larger, more nutritious prey items is needed to meet the increasing energy demand at larger body size (Chapter I). For *S. sagax* and *E. encrasicolus,* sample size and size distribution did not allow for a similar resolution of the size classes. The lower δ^{15}N-signatures measured during the spring cruise in 2010 were probably caused by a baseline shift, since a trend to lower δ^{15}N-signatures in phytoplankton at colder temperatures indicative of recent upwelling was observed (Chapter II).
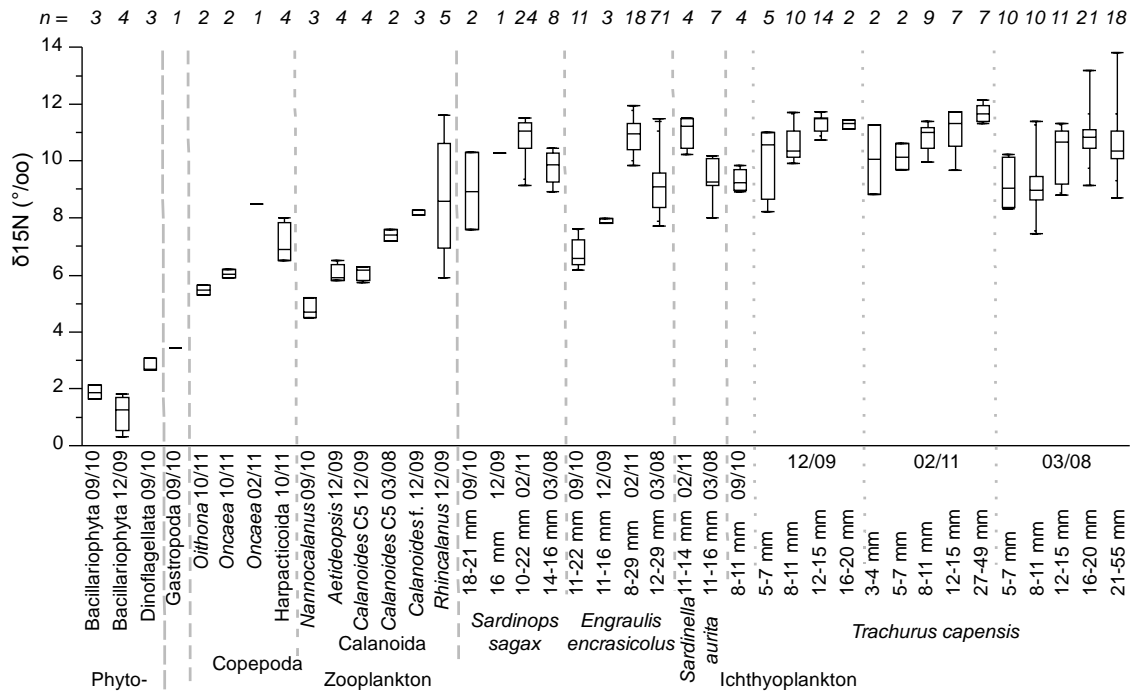
Fig. 8: δ^{15}N-signatures of larvae and juveniles of *S. sagax*, *E. encrasicolus* and *T. capensis* (divided into size classes) and potential prey items. Each group calculated separately for cruises and ordered in sequence of season from austral winter to summer. Phytoplankton samples were mixed samples dominated by *Coscinodiscus wallesii* ("Bacillariophyta", diatoms) or *Noctiluca* sp. ("Dinoflagellata"). "Gastropoda" is *Limacina* sp. and "Harpacticoida" is *Microsetella* sp. Mid-line, box and whiskers represent median, 1st and 3rd quartile and range. Labels on the x-axis show taxonomic groups

Significant proportions of fatty acid trophic markers (*FATM*) for diatoms were regularly measured in larvae all four species suggesting that the diatom-based food web is equally important for all of them (Chapter II and III). Clupeoid larvae showed a similar fatty acid composition, indicating potential food competition in the case of limited resources (Chapter II). *T. capensis* larvae showed significantly lower proportions of diatom and dinoflagellate trophic markers and higher proportions of heterotrophy markers and stearic acid (Table 4), which is an additional indication of a dinoflagellate-based diet (Dalsgaard *et al.*, 2003). The higher amount of *FATM* related to a dinoflagellate-based diet in *T. capensis* larvae is probably reflecting its distribution pattern. They occurred in warmer water indicative of quiescent upwelling. Under these conditions, dinoflagellate blooms and smaller copepods (e.g. *Oithona* sp., *Oncaea* sp.) are favoured, with the latter making up a significant amount in the guts of *T. capensis* larvae (Fig. 7).

Table 4: Comparison of fatty acid trophic marker (*FATM*) and stearic acid (18:0) proportions (% of total fatty acids, as mean ± standard deviation) in muscle tissue of *S. sagax*, *E. encrasicolus* and *T. capensis* larvae. Results of interspecific comparisons using Welch-ANOVAs accounting for inhomogeneity of variances are given

	S. sagax	*E. encrasicolus*	*T. capensis*	*F-value*	*p-value*
n	18	41	121		
Diatom *FATM*	6.4 ± 0.3	6.4 ± 0.2	4.9 ± 0.1	21.89	<0.0001
Dinoflagellate *FATM*	1.4 ± 0.5	1.5 ± 0.5	0.9 ± 0.5	25.36	<0.0001
Heterotrophy *FATM*	5.7 ± 2.6	6.3 ± 1.4	7.2 ± 2.5	5.56	0.0071
Stearic acid (18:0)	6.0 ± 2.3	5.1 ± 1.1	8.5 ± 1.5	122.14	<0.0001

Nutritional condition and daily growth rates

Total fatty acid (*TFA*) -content in muscle tissue of fish larvae was low, probably due to a limited storage of lipids above the basic amount of structural lipids (Osako *et al.*, 2003) caused by priority investment of surplus energy into growth during the larval phase. *T. capensis* larvae had a significantly higher *TFA*-content in their muscle tissue compared to *E. encrasicolus* larvae in 3 of 4 cruises, but not in comparison with *S. sagax* larvae (Table 5). This indicates perennially better feeding- and hence nutritional conditions in *T. capensis* compared to *E. encrasicolus* and may be another reason, why *T. capensis* is the more successful of the two species with a wide-spread distribution. The average *TFA*-content of *E. encrasicolus* was also lower than in larvae of the same species from the Mediterranean (4.2 ± 0.8 % *DM*, Costalago *et al.*, 2011), which suggests that nutritional condition and not species-specific differences were the cause for its lower *TFA*-content in comparison to *T. capensis*.

Table 5: Total fatty acid (*TFA*)-content (% *DM*, as mean ± standard deviation) in muscle tissue of *S. sagax* (<20 mm *SL*), *E. encrasicolus* (<22 mm *SL*) and *T. capensis* (<20 mm *SL*) larvae during the four cruises. Interspecific comparisons for each cruise and intraspecific comparisons between cruises were analysed using ANOVA or t-test, respectively. Welch ANOVA was applied in case of inhomogeneity of variance. Respective sample size denoted in brackets

mm/yyyy	*S. sagax*	*E. encrasicolus*	*T. capensis*	F-/t-value	p-value
09/2010	3.85 ± 0.32 (6)	3.11 ± 0.47 (11)	3.77 ± 0.38 (15)	8.71	0.0032
12/2009		2.90 ± 0.34 (5)	3.97 ± 0.67 (11)	3.79	0.0008
02/2011	3.14 ± 0.40 (9)	3.32 ± 0.75 (4)	3.62 ± 0.81 (35)	2.91	0.11
03/2008		3.00 ± 0.24 (7)	3.58 ± 0.65 (27)	4.22	0.0009
F-/t-value	-3.60	0.75	0.97		
p-value	0.0032	0.53	0.41		

Larvae of the slender clupeoid species showed a faster average growth in length per day compared to the stout *T. capensis* larvae. At a similar length of 6 mm *SL*, larvae of *S. sagax* (0.50 mm d^{-1}) and *E. encrasicolus* (0.55 mm d^{-1}) grew almost at double speed compared to *T. capensis* (0.28 mm d^{-1}, Chapter III). However, expressing that growth in biomass, these relationships between species were opposite. *T. capensis* grew significantly faster (0.0655 mg d^{-1}) than *E. encrasicolus* (0.0250 mg d^{-1}) and *S. sagax* larvae (0.0090 mg d^{-1}, Chapter III). Increased food availability and temperature positively affect growth rate and feeding activity in fish larvae (Houde, 1989; Aldanondo *et al.*, 2008; Takahashi *et al.*, 2012), hence explaining the higher daily growth in biomass, i.e. feeding success in *T. capensis* larvae.

Trachurus larvae show a "hover and dart" foraging behaviour, as indicated by their comparatively high routine metabolic rates (Chapter I) and a high burst swimming capacity (Masuda, 2009), resembling the Scombriform foraging type described by Hunter (1980). Their better nutritional condition (*TFA*-content) and higher biomass growth rates suggest this strategy to be more effective than the "stalker" strategy of clupeoid larvae, which move less and dart with a highly sinuous feeding posture (Blaxter and Hunter, 1982). Feeding attacks of clupeoid larvae lack persistence, prey must be near to be perceived, and the volume of water searched for food is remarkably small (Hunter, 1980; Blaxter and Hunter, 1982).

Interspecific differences in digestive efficiency could be another reason for the observed differences in nutritional condition and growth rates. In clupeoid species, conversion efficiency is generally low (Brett and Groves, 1979). An interspecific comparison of the activity of digestion and digestive enzymes would permit further insights. Future determination of gut retention- and evacuation times and excretion rates could specify energy budgets for larvae, an important prerequisite for accurate food web- and biophysical models.

The comparison of nutritional condition factors (*k*) between cruises revealed significantly higher values during the peak spawning period in summer for all species (Chapter II and III). During February 2011, *k* was significantly lower in *S. sagax* and *S. aurita* larvae, as was the *TFA*-content in *S. sagax* larvae (Table 5). During that period, food competition among fish larvae around Walvis Bay, which was dominated by *S. sagax* (Fig. 4), probably led to the overall poor nutritional conditions of fish larvae. In the NBCE, the periods of maximum food availability (winter-spring) and shelf retention (summer) are separated, and peak spawning of sardines occurs under maximum shelf retention periods (Brochier *et al.*, 2011, Kreiner *et al.*, 2011). These specific conditions increase the risk of food limitation especially for the less efficiently feeding clupeoid larvae, and make a density effect in February 2011 likely, which has been rarely demonstrated for marine fish larvae to date (Houde, 2008). Interestingly, estimates of *S. sagax* recruitment, based on cohort analyses of length frequency data and

acoustic surveys, were higher for the years 2008-2010 than for 2011 and 2012 (Nadine Moroff, NatMIRC, pers. comm.). Thus, a quantitative comparison of fish larvae abundances only, appears insufficient to infer recruitment success. In lieu thereof, quality measures such as nutritional condition can provide higher predictive conclusions.

In contrast to *S. sagax* larvae, the nutritional condition of *T. capensis* was not significantly different between March 2008 and February 2011. Thus, *T. capensis* seems to be less affected by the proposed lower concentration of food organisms compared to *S. sagax*, probably because of advantages in its feeding ecology described above.

T. capensis larval nutritional condition was better under a shallow 2.5 mL O_2 L^{-1} oxypleth (Chapter III). Bertrand *et al.* (2011) hypothesised that shoaling of the Humboldt Current hypoxic zone leads to a concentration of plankton in the surface water layers and similar observations of copepod species concentrating above hypoxic layers were made in the NBCE (e.g. *Calanoides carinatus*: Verheye *et al.*, 2005; Auel and Verheye, 2007). Taking up this hypothesis, *T. capensis* may have benefitted from higher plankton densities, leading to its improved nutritional condition. Active behaviour and a robust body probably allows them to deal more successfully with negative consequences of higher plankton concentrations, e.g. increased encounters with potential predators, than the more fragile clupeoid larvae. An association of *Trachurus* larvae and juveniles with jellyfish has been described repeatedly (see Masuda, 2006 and 2009). For example, *T. japonicus* larvae (>11 mm) and juveniles associate with jellyfish, using them as shelter and prey collectors. Higher growth rates of larvae kept with jellyfish indicate the advantage of this relationship for fish larvae (Masuda, 2006 and 2009). In contrast, Japanese anchovy (*E. japonicus*) larvae were highly vulnerable to jellyfish predation (Masuda, 2011). If *T. capensis* behaved similar to their Japanese conspecifics, it might benefit from increasing jellyfish abundance in the NBCE (Lynam *et al.*, 2006; Flynn *et al.* 2012).

Trophic ecology – perspectives

I showed that the trophic position of larvae of coastal pelagic fish species in the NBCE is similar under the same environmental conditions and revealed their feeding preference for different copepod groups (Chapter II and III). However, differences in feeding preferences remain unaccounted for lower taxonomic levels of prey items. In this regard, Schukat (2012) discovered a highly diverse feeding ecology of calanoid copepods in the NBCE and time-series data revealed that abundances of different calanoid species in the NBCE did not follow parallel trends over the last ten years (Verheye and Kreiner, 2013). In addition, small or soft-bodied prey items (e.g. microzooplankton) are difficult to detect with gut content analysis. Thus, a higher taxonomic resolution of the prey groups "nauplia" and "calanoida" and screening for

small organisms (e.g. ciliates) via molecular tools (e.g. Vestheim *et al.*, 2005; Martin *et al.*, 2006; King *et al.*, 2008; Troedsson *et al.* 2009) has the potential to reveal important dietary differences among fish species.

Furthermore, organisms of the same prey species may constitute a variable biochemical composition at different times, e.g. relative to the successional state of the plankton community. A variation in protein- and lipid content and/or lipid composition of prey items can heavily affect the nutritional condition of fish larvae (Copeman and Laurel, 2010). Thus, in addition to density-dependent processes leading to food competition among and within species, and the potential influence of digestive efficiency discussed above, the biochemical composition of prey organisms may also be responsible for inter-specific and seasonal differences in nutritional condition of fish larvae. A concerted attempt, i.e. the determination of nutritive values of prey organisms and the analysis of indicators for larval nutritional conditions, can unravel small-scale tropho-dynamic interactions. The use of nucleic acid derived indices (reviewed by Chícharo and Chícharo, 2008) and lipid class composition (Håkanson, 1993; Osako *et al.*, 2003), in addition to the methods applied in this thesis, is suggested to broaden the foundation of interspecific comparisons.

Conclusion and Outlook

Considering their lower abundance, biomass and spatiotemporal patchiness, the direct effect of small and medium pelagic fish larvae on overall matter fluxes in the NBCE is likely negligible in comparison to other plankton groups, such as Copepoda (Schukat, 2012) and Euphausiacea (Thorsten Werner, AWI, pers. comm.). Nevertheless, they may influence zooplankton densities over locally and temporally restricted scales, when occurring in high numbers. The stronger but indirect impact of larval stages on the ecosystem is via recruitment success and subsequently adult stock size.

In this thesis, I showed that several ELH traits distinguish the four investigated species. The investigated ELH traits have the potential to explain the comparatively good recruitment of the *T. capensis* stock during the last two decades in the NBCE. My findings also contribute to a better understanding of the higher resilience of perciform species to smaller stock sizes and changing environmental conditions. They suggest an integration of ELH traits into life history and stock recovery theories, which have been mainly related to adult life history traits before (Rochet, 2000; Winemiller, 2005).

The four coastal pelagic fish species in the NBCE (Clupeiformes: *S. sagax*, *S. aurita* and *E. encrasicolus*; Perciformes: *T. capensis*) share important life history characteristics sensu Winemiller (2005). As "periodic strategists", their fitness is maximised when the influence of environmental variation on early life stages survival is periodic and large-scale (Winemiller and Rose, 1993). They share common traits, being schooling species, multiple batch spawners showing low parental investment with pelagic eggs and larvae that contain little yolk (Fréon *et al.*, 2005; Annex II and III). In contrast, adult feeding preferences and prey spectra are different, with *T. capensis* and *E. encrasicolus* being particle-feeders of larger prey compared to filter-feeding sardines (van der Lingen *et al.*, 2006a; Annex II and III). The potential life span distinguishes the longer-lived perciform *T. capensis* from the shorter-lived Clupeiformes (Annex II and III). However, under the current fully-exploited or collapsed stock conditions, both the *T. capensis* and *S. sagax* stocks in the NBCE show a trend towards earlier maturation and consist to a great part of small, young fish (Annex II and III; Kirchner *et al.*, 2010; Kreiner *et al.*, 2011; no information available for *S. aurita* and *E. encrasicolus*). *T. capensis* are, up to the age of two years, epipelagic and zooplanktivorous (Venter, 1976 as cited in: Boyer and Hampton, 2001), thus possessing traits that are also typical for Clupeiformes (Rochet, 2000; Fréon *et al.*, 2005).

A shorter life span and earlier maturation have been related to an amplification of the variability of fish populations and closer tracking of climate forcing (Perry *et al.*, 2010). Myers *et al.* (1999) determined a higher steepness parameter of the stock-recruitment function

(Beverton and Holt, 1957) for *Trachurus trachurus* (0.75)*, the sister species of *T. capensis*, than for *Sardina pilchardus* (0.34), *S. sagax* (0.59) and *E. encrasicolus* (0.47). This indicates a higher resilience of *Trachurus* species against a reduction of the spawner biomass. Following Rochet (2000), this is caused by a different life-history strategy of Perciformes and Clupeiformes, with Perciformes having a higher capacity to compensate for low spawner abundance by modulating their fecundity.

Importantly, this thesis revealed that early life history traits should serve as additional explanation for the higher resilience of *Trachurus* stocks to changing environmental conditions. *T. capensis* appears to follow a different strategy than clupeoid species. The scattered distribution of *T. capensis* larvae and lower maximum densities, together with a higher feeding success, make them less vulnerable to starvation. *T. capensis* larvae tolerated high water temperatures and low oxygen levels. They appeared to be voracious feeders under different plankton compositions, leading to a constantly high nutritional condition compared to clupeoid larvae. In addition, *Trachurus* larvae were more robust to physical damage making them less susceptible to predation (Masuda, 2009). Accordingly, *T. capensis* larvae in the NBCE may be favoured by the present "warm period", which is characterised by frequent intrusion of warm, tropical waters and quiescent upwelling conditions, shoaling of hypoxic zones during the peak spawning period in summer and changes in the zooplankton community towards small copepod species (Hutchings *et al.*, 2009, Verheye and Kreiner, 2009, and 2013).

E. encrasicolus's inferred tolerance of higher temperatures, when compared to *S. sagax* larvae, contrasts the temperature preferences at the adult stage. *E. encrasicolus*'s preference for colder conditions can be derived from high landing numbers during the "cold period" in the NBCE during the 1980s (Fig. 2; Hutchings *et al.*, 2009) and the comparison of the "mean temperature of the catch" of the two species (Cheung *et al.*, 2013b). Furthermore, the adaptation of adult *E. encrasicolus,* towards larger prey items, led to the hypothesis that they are nutritionally favoured under "cold conditions" (van der Lingen *et al.*, 2006a). Thus, in addition to the observed low nutritional condition of their larvae, *E. encrasicolus* may presently be limited in the NBCE due to unfavourable trophic condition the subsequent adult life history stage, leading to decreased numbers and quality of offspring.

In contrast, *S. sagax* adult stages should benefit from the present "warm period" in the NBCE. However, low egg and larval numbers observed during the last decade (Kreiner *et al.*, 2011) and GENUS cruises, together with the small adult stock size, indicate that environmental conditions have rather been unfavourable for sardines, hence limiting their recruitment success. At the adult stage, the small stock size and reduced body size of spawning females likely led to a reduced population fecundity (Kreiner *et al.*, 2011). In addition, high jellyfish

densities in adult feeding grounds between Walvis Bay and Lüderitz (Bakun and Weeks, 2006; Flynn *et al.*, 2011) may impede swarm formation and increase the energy demand for swimming. Furthermore, they could force sardines to exert evasive manoeuvers to avoid collisions and disturb their preferred filter-feeding mode. Such a disturbed energy budget may thus ultimately lead to inferior offspring quantity and quality. At the larval stage, high water temperatures probably prevented intense spawning or caused high mortalities in the north of the NBCE, restricting *S. sagax* larvae to the Walvis Bay region. There, extended periods of quiescent upwelling during the peak spawning season in summer may not provide sufficient food for high concentrations of sardine larvae, as observed during February 2011. Food limitation due to density effects is probably a more severe problem for clupeoids because their reproductive strategy is primarily focused on producing very high numbers of relatively fragile larvae with a poor feeding success (Hunter and Blaxter, 1982; Rochet, 2000; Fréon *et al.*, 2005).

Based on the findings of this thesis, the population sizes of coastal pelagic fishes observed in the NBCE are strongly influenced by processes during ELH stages. I assume that ELH traits play a similarly important rule in other EBUE, such as the northern Humboldt Current ecosystem off Peru. There, *S. sagax* disappeared while *T. murphyi* and *E. ringens* increased in fisheries landings around 2000, along with a warming of the system and shoaling of hypoxia (Chavez *et al.*, 2008; Bertrand *et al.*, 2011). Thus, further investigations of ELH traits to unravel fine-scale larvae-environment interactions, as outlined in the perspectives, together with modelling approaches to link those interactions to recruitment rates and adult stock sizes, should be the focus of future investigations in the NBCE and other upwelling systems.

As a prediction, the pelagic fish community composition in the NBCE will depend on the future development of upwelling intensity related environmental processes. If upwelling increases with global warming, as assumed by Bakun (1990), the resulting "cold period" will improve the chances of *S. sagax* and *E. encrasicolus* stocks to recover, whereas the continuation of the present "warm period" will mainly favour *T. capensis.* However, increased frequencies of severe Benguela Niño events would probably negatively affect *T. capensis* as well (Gammelsrød *et al.*, 1998). If shoaling of hypoxic conditions continued also in the "cold period", recovery of the presumably less hypoxia-tolerant clupeoid species would likely be hampered. In light of uncertain future development of environmental conditions during the next decades, conservative fishery quotas seem to be crucial to ensure a sustainable harvest of *T. capensis* and facilitate the recovery of depleted *S. sagax* and *E. encrasicolus* stocks in the NBCE. Furthermore, the integration of knowledge on ELH traits, gained through this thesis, into new ecosystem-based management models, provides an enormous potential to improve present management practices of fisheries resources.

References

Aldanondo, N., Cotano, U., Etxebeste, E., Irigoien, X., Álvarez, P., Mártinez de Murguía, A., and Herrero, D. L. 2008. Validation of daily increments deposition in the otoliths of European anchovy larvae (*Engraulis encrasicolus* L.) reared under different temperature conditions. Fisheries Research, 93: 257–264.

Alder, J., Campbell, B., Karpouzi, V., Kaschner, K., and Pauly, D. 2008. Forage Fish: From Ecosystems to Markets. Annual Review of Environment and Resources, 33: 153–166.

Alheit, J., and Niquen, M. 2004. Regime shifts in the Humboldt Current ecosystem. Progress in Oceanography, 60: 201–222.

Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V., and Wasmund, N. 2005. Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. ICES Journal of Marine Science, 62: 1205-1215.

Alheit, J. 2009. Consequences of regime shifts for marine food webs. International Journal of Earth Sciences, 98: 261–268.

Alheit, J., and Bakun, A. 2010. Population synchronies within and between ocean basins: Apparent teleconnections and implications as to physical–biological linkage mechanisms. Journal of Marine Systems, 79: 267–285.

Almeida-Val, V. M., Farias, I. P., Silva, M. N., Duncan, W. P., and Val, A.L. 1995. Biochemical adjustments to hypoxia by Amazon cichlids. Brazilian Journal of Medical and Biological Research, 28(11-12): 1257-1263.

Anderson, C. N. K., Hsieh, C.-H., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., May, R. M., and Sugihara, G. 2008. Why fishing magnifies fluctuations in fish abundance. Nature, 452: 835–839.

Arthur, D. K. 1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fishery Bulletin, U.S., 74(3): 517–530.

Assis, C. A. 1996. A generalised index for stomach contents analysis in fish. Scientia Marina, 60: 385-389.

Auel, H., and Verheye, H. M. 2007. Hypoxia tolerance in the copepod *Calanoides carinatus* and the effect of an intermediate oxygen minimum layer on copepod vertical distribution in the northern Benguela Current upwelling system and the Angola-Benguela Front. Journal of Experimental Marine Biology and Ecology, 352: 234–243.

Auel, H., and Ekau, W. 2009. Distribution and respiration of the high-latitude pelagic amphipod *Themisto gaudichaudi* in the Benguela Current in relation to upwelling intensity. Progress in Oceanography, 83: 237–241.

Axelsen, B. E., Krakstad, J.-O., and Bauleth-D'Almeida, G. 2004. Aggregation dynamics and behaviour of the Cape horse mackerel (*Trachurus trachurus capensis*) in the northern Benguela - implications for acoustic abundance estimation. In Namibia's fisheries: Ecological, economic and social aspects, pp. 135–164. Ed. by U. R. Sumaila, S. I. Steinshamn, M. D. Skogen, and D. Boyer. Eburon Publishers, Delft, Netherlands.

Bailey, G., Noli-Peard, K., and Tchipalanga, P. 2009. Monitoring of variability in the inshore environment in the Benguela system. In Benguela Environment Fisheries Interaction and Training Programme (BENEFIT) Research Projects, pp. 5-9. Ed. by I. Hampton, M. Barange, and N. Sweijd. GLOBEC Report 25, Plymouth, UK..

Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. Science, 247: 198–201.

Bakun, A. 1996. Patterns in the ocean: ocean processes and marine population dynamics. California Sea Grant, La Jolla, CA and Centro de Investigaciones Biológicas del Noroeste, La Paz, Mexico. 323 pp.

Bakun, A. 2006. Wasp-waist populations and marine ecosystem dynamics: Navigating the '*predator pit*' topographies. Progress in Oceanography, 68: 271–288.

Bakun, A. 2010. Linking climate to population variability in marine ecosystems characterized by non-simple dynamics: conceptual templates and schematic constructs. Journal of Marine Systems, 79: 361–373.

Bakun, A., and Weeks, S. J. 2006. Adverse feedback sequences in exploited marine systems: are deliberate interruptive actions warranted? Fish and Fisheries, 7: 316–333.

Bakun, A., and Weeks, S. J. 2008. The marine ecosystem off Peru: What are the secrets of its fishery productivity and what might its future hold? Progress in Oceanography, 79: 290–299.

Bakun, A., Babcock, E. A., Lluch-Cota, S. E., Santora, C., and Salvadeo, C. J. 2010a. Issues of ecosystem-based management of forage fisheries in 'open' non-stationary ecosystems: the example of the sardine fishery in the Gulf of California. Reviews in Fish Biology and Fisheries, 20: 9–29.

Bakun, A., Field, D. B., Redondo-Rodriguez, A., and Weeks, S. J. 2010b. Greenhouse gas, upwelling-favorable winds, and the future of coastal ocean upwelling ecosystems. Global Change Biology, 16: 1213–1228.

Barange, M., and Pillar, S. C. 1992. Cross-shelf circulation, zonation and maintenance mechanisms of *Nyctiphanes capensis* and *Euphausia hanseni* (Euphausiacea) in the northern Benguela upwelling system. Continental Shelf Research, 12: 1027–1042.

Bartholomae, C. H., and van der Plas, A. K. 2007. Towards the development of environmental indices for the Namibian shelf, with particular reference to fisheries management. African Journal of Marine Science, 29: 25–35.

Beddington, J. R., Agnew, D. J., and Clark, C. W. 2007. Current problems in the management of marine fisheries. Science, 316: 1713–1716.

Bertrand, A., Chaigneau, A., Peraltilla, S., Ledesma, J., Graco, M., Monetti, F., and Chavez, F. P. 2011. Oxygen: A fundamental property regulating pelagic ecosystem structure in the coastal southeastern tropical Pacific. PLoS ONE, 6: e29558.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fishery Investigations, Series 2, 19. United Kingdom Ministry of Agriculture and Fisheries. 533 pp.

Blaxter, J. H. S., and Hunter, J. R. 1982. The biology of clupeoid fishes. Advances in Marine Biology, 20: 1-223.

Bodungen, von, B., John, H.-Ch., Lutjeharms, J. R. E., Mohrholz, V., and Veitch, J. 2008. Hydrographic and biological patterns across the Angola-Benguela frontal zone under undisturbed conditions. Journal of Marine Systems, 74: 189–215.

Boyd, A. J. 1983. Seasonal distributions of temperature, salinity, oxygen, and nitrate off Soutwestern Africa in 1981/82 and their possible influence on anchovy catches. International Commission for the Southeast Atlantic Fisheries, Collection of scientific papers, 10, Part II: 41-73.

Boyd, A. J., Hewitson, J. D., Kruger, I., and Le Clus, F. 1985. Temperature and salinity off namibia from August 1982 to August 1984, and their relation to plankton abundance and the reproductive success of pelagic fish. International Commission for the Southeast Atlantic Fisheries, Collection of scientific papers, 12, Part I: 53-58.

Boyd, A. J., Salat, J., and Masó, M. 1987. The seasonal intrusion of relatively saline water on the shelf off northern and central Namibia. South African Journal of Marine Science, 5: 107–120.

Boyer, D. C., and Hampton, I. 2001. An overview of the living marine resources of Namibia. South African Journal of Marine Science, 23: 5–35.

Boyer, D. C., Boyer, H. J., Fossen, I., and Kreiner, A. 2001. Changes in abundance of the northern Benguela sardine stock during the decade 1990-2000, with comments on the relative importance of fishing and the environmment. South African Journal of Marine Science, 23: 67–84.

Boyer, D. C., and Hampton, I. (Eds.) 2007. Northern Benguela transboundary small pelagic and mid-water resources research planning workshop. A synthesis oft he scientific input, discussions and output from the workshop. Windhoek, Namibia. 52 pp.

Breitburg, D. L., Hondorp, D. W., Davias, L. A., and Diaz, R. J. 2009. Hypoxia, nitrogen, and fisheries: Integrating effects across local and global landscapes. Annual Review of Marine Science, 1: 329–349.

Brett, J. R., and Groves, T. D. D. 1979. Physiological energetics. In Fish Physiology, Vol. VIII, pp. 279-352. Ed. by W. S. Hoar, D. J. Randall, and J. R. Brett. Academic Press, New York.

Brochier, T., Lett, C., and Fréon, P. 2011. Investigating the 'northern Humboldt paradox' from model comparisons of small pelagic fish reproductive strategies in Eastern Boundary Upwelling Ecosystems. Fish and Fisheries, 12. 94-109.

Chavez, F. P., Ryan, J., Lluch-Cota, S. E., and Niquen M. C., 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science, 299: 217–221.

Chavez, F. P., and Messié, M. 2009. A comparison of Eastern Boundary Upwelling Ecosystems. Progress in Oceanography, 83: 80–96.

Checkley, D., Alheit, J., Oozeki, Y., and Roy, C. (Eds.). 2009. Climate change and small pelagic fish. Cambridge University Press, New York. 372 pp.

Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., and Pauly, D. 2009. Projecting global marine biodiversity impacts under climate change scenarios. Fish and Fisheries, 10: 235–251.

Cheung, W. W. L., Sarmiento, J. L., Dunne, J., Frölicher, T. L., Lam, V. W. Y., Palomares, M. L. D., Watson, R., and Pauly, D. 2013a. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. Nature Climate Change, 3: 254–258.

Cheung, W. W. L., Watson, R., and Pauly, D. 2013b. Signature of ocean warming in global fisheries catch. Nature, 497: 365-368.

Chícharo, M. A., and Chícharo, L. 2008. RNA : DNA ratio and other nucleic acid derived indices in marine ecology. International Journal of Molecular Sciences, 9: 1453–1471.

Collins, M., An, S.-I., Cai, W., Ganachaud, A., Guilyardi, E., Jin, F.-F., Jochum, M., Lengaigne, M., Power, S., Timmermann, A., Vecchi, G., and Wittenberg, A. 2010. The impact of global warming on the tropical Pacific Ocean and El Niño. Nature Geoscience, 3: 391–397.

Copeman, L. A., and Laurel, B. J. 2010. Experimental evidence of fatty acid limited growth and survival in Pacific cod larvae. Marine Ecology Progress Series, 412: 259–272.

Costalago, D., Tecchio, S., Palomera, I., Álvarez-Calleja, I., Ospina-Álvarez, A., and Raicevich, S. 2011. Ecological understanding for fishery management: condition and growth of anchovy late larvae during different seasons in the northwestern Mediterranean. Estuarine Coastal and Shelf Science, 93: 350–358.

Cram, D. L. 1977. Research and management in Southeast Atlantic pelagic fisheries. CalCOFI Reports, 19: 33-62.Crawford, R. J. M. 1987. Food and population variability in five regions supporting large stocks of anchovy, sardine and horse mackerel. South African Journal of Marine Science, 5: 735–757.

Cury, P. M., and Roy, C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Canadian Journal of Fisheries and Aquatic Sciences, 46(4): 670–680.

Cury, P. M., Roy, C., and Faure, V. 1998. Environmental constraints and pelagic fisheries in upwelling areas: the Peruvian puzzle. South African Journal of Marine Science, 19: 159–167.

Cury, P. M., Bakun, A., Crawford, R. J. M., Jarre, A., Quiñones, R. A., Shannon, L. J., and Verheye, H. M. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in 'wasp-waist' ecosystems. ICES Journal of Marine Science, 57: 603–618.

Cury, P. M., and Shannon, L. J. 2004. Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. Progress in Oceanography, 60: 223–243.

Cury, P. M., Shin, Y. J., Planque, B., Durant, J. M., Fromentin, J.-M., Kramer-Schadt, S., Stenseth, N. C., Travers, M. and Grimm, V. 2008. Ecosystem oceanography for global change in fisheries. Trends in Ecology and Evolution, 23: 338–346.

Cushing, D. H. 1974. The natural regulation of fish populations. In Sea fisheries research. pp. 399-412. Ed. by F. R. Harden Jones. Elek Science, London.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: An update of the Match/Mismatch hypothesis. Advances in Marine Biology, 26: 249–293.

Cushing, D. H. 1996. Towards a science of recruitment in fish populations. Ecology Institute, Oldendorf/Luhe. 175 pp.

Dalsgaard, J., St. John, M., Kattner, G., Müller-Navarra, D., and Hagen, W. 2003. Fatty acid trophic markers in the pelagic marine environment. Advances In Marine Biology, 46: 225–340.

Daskalov, G. M., Boyer, D. C., and Roux, J. P. 2003. Relating sardine *Sardinops sagax* abundance to environmental indices in northern Benguela. Progress in Oceanography, 59: 257–274.

Diaz, R. J., and Rosenberg, R. 2008. Spreading dead zones and consequences for marine ecosystems. Science, 321: 926–929.

Diaz, R. J., and Breitburg, D. L. 2009. The hypoxic environment. In Hypoxia, pp. 1-17. Ed. by J. G. Richards, A. P. Farell, and C. J. Brauner. Academic Press, Amsterdam.

Drinkwater, K. F., Beaugrand, G., Kaeriyama, M., Kim, S., Ottersen, G., Perry, R. I., Pörtner, H.-O., Polovina, J. J., and Takasuka, A. 2010. On the processes linking climate to ecosystem changes. Journal of Marine Systems, 79: 374–388.

Duncombe Rae, C. 2005. A demonstration of the hydrographic partition of the Benguela upwelling ecosystem at 26° 40'S. African Journal of Marine Science, 27: 617–628.

Ekau, W., and Verheye, H. M. 2005. Influence of oceanographic fronts and low oxygen on the distribution of ichthyoplankton in the Benguela and southern Angola currents. African Journal of Marine Science, 27: 629–639.

Ekau, W., Auel, H., Pörtner, H.-O., and Gilbert, D. 2010. Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). Biogeosciences, 7: 1669–1699.

Finney, B. P., Alheit, J., Emeis, K.-C., Field, D. B., Gutiérrez, D., and Struck, U. 2010. Paleoecological studies on variability in marine fish populations: A long-term perspective on the impacts of climatic change on marine ecosystems. Journal of Marine Systems, 79: 316–326.

FAO. 2010. The state of world fisheries and aquaculture 2010. Food and Agriculture Organization of the United Nations, Rome. 197 pp.

Flynn, B. A., Richardson, A. J., Brierley, A. S., Boyer, D. C., Axelsen, B. E., Scott, L., Moroff, N. E., Kainge, P. I., Tjizoo, B. M., and Gibbons, M. J. 2012. Temporal and spatial patterns in the abundance of jellyfish in the northern Benguela upwelling ecosystem and their link to thwarted pelagic fishery recovery. African Journal of Marine Science, 34: 131–146.

Folkvord, A., and Mosegaard, H. 2002. Some uses of individual age data. A. Age and growth analysis. In Manual of fish sclerochronology, pp. 146–166. Ed. by J. Panfili, H. Troadec, H. dePontual, and P. J. Wright. Ifremer, Brest.

Fréon, P., Cury, P. M., Shannon, L., and Roy, C. 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. Bulletin of Marine Science, 76: 385–462.

Fréon, P., Arístegui, J., Bertrand, A., Crawford, R. J. M., Field, J. C., Gibbons, M. J., Tam, J., Hutchings, L., Masski, H., Mullon, C., Ramdani, M., Seret, B., and Simier, M. 2009a. Functional group biodiversity in Eastern Boundary Upwelling Ecosystems questions the wasp-waist trophic structure. Progress in Oceanography, 83: 97–106.

Fréon, P., Barange, M., and Arístegui, J. 2009b. Eastern Boundary Upwelling Ecosystems: Integrative and comparative approaches. Progress in Oceanography, 83: 1–14.

Fréon, P., Werner, F. E., and Chavez, F. P. 2009c. Conjectures on future climate effects on marine ecosystems dominated by small pelagic fish. In Climate Change and Small Pelagic Fish, pp. 312–343. Ed. by D. Checkley, J. Alheit, Y. Oozeki, and C. Roy. Cambridge University Press, New York.

Fry, F. E. J. 1947. Effects of the environment on animal activity. University of Toronto Press, Canada. 62 pp.

Fry, F. E. J. 1971. The effect of environmental factors on the physiology of fish. In Fish Physiology, Vol. VI, pp. 1–98. Ed. by W. S. Hoar and D. J. Randall. Academic Press, New York.

Fuiman, L. A. 1994. The interplay of ontogeny and scaling in the interactions of fish larvae and their predators. Journal of Fish Biology, 45(Supplement A): 55–79.

Fuiman, L. A. 2002. Special considerations of fish eggs and larvae. In Fishery Science: The unique contributions of early life stages, pp. 1–32. Ed. by L. A. Fuiman and R. G. Werner. Blackwell Science, Oxford.

Fuiman, L. A., Cowan Jr., J. H., Smith, M. E., and O'Neal, J. P. 2005. Behavior and recruitment success in fish larvae: variation with growth rate and the batch effect. Canadian Journal of Fisheries and Aquatic Sciences, 62: 1337–1349.

Gammelsrød, T., Bartholomae, C. H., Boyer, D. C., Filipe, V., and O'Toole, M. J. 1998. Intrusion of warm surface water along the Angolan-Namibian coast in February-March 1995: The 1995 Benguela Niño. South African Journal of Marine Science, 19: 41–56.

Gibbons, M. 1999. An introduction tot he zooplankton of the Benguela Current region. Zoology Department, University of Western Cape, Belville, South Africa. 51 pp.

Gilly, W. F., Beman, J. M., Litvin, S. Y., and Robison, B. H. 2013. Oceanographic and biological effects of shoaling of the Oxygen Minimum Zone. Annual Review of Marine Science, 5: 393–420.

Griffiths, C. L., van Sittert, L., Best, P. B., Brown, A. C., Clark, B. M., Cook, P. A., Crawford, R. J. M., David, J. H. M., Griffiths, M. H., Hutchings, K., Jerardino, A., Kruger, N., Lamberth, S., Leslie, R. W., Melville-Smith, R., Tarr, R., and van der Lingen, C. D. 2004. Impacts of human activities on marine animal life in the Benguela, a historical overview. In Oceanography and Marine Biology, An Annual Review, 42, pp. 303-392. Ed. by R. N. Gibson, R. J. A. Atkinson, and J. D. M. Gordon. CRC Press, Boca Raton, USA.

Grote, B., Hagen, W., Lipinski, M. R., Verheye, H. M., Stenevik, E. K., and Ekau, W. 2011. Lipids and fatty acids as indicators of egg condition, larval feeding and maternal effects in cape hakes (*Merluccius paradoxus* and *M. capensis*). Marine Biology, 158: 1005–1017.

Grote, B., Ekau, W., Stenevik, E. K., Clemmesen, C., Verheye, H. M., Lipinski, M. R., and Hagen, W. 2012. Characteristics of survivors: growth and nutritional condition of early stages of the hake species *Merluccius paradoxus* and *M. capensis* in the southern Benguela ecosystem. ICES Journal of Marine Science, 69(4): 553-562.

Haigh, E. H. 1972. Development of *Trachurus trachurus* (Carangidae), the South African maasbanker. Annals of the South African Museum, 59(8): 139-150.

Hammer, C., Dorrien, von, C., Hopkins, C. C. E., Köster, F. W., Nilssen, E. M., St John, M., and Wilson, D. C. 2010. Framework of stock-recovery strategies: analyses of factors affecting success and failure. ICES Journal of Marine Science, 67: 1849–1855.

Hauss, H., Franz, J. M. S., and Sommer, U. 2012. Changes in N:P stoichiometry influence taxonomic composition and nutritional quality of phytoplankton in the Peruvian upwelling. Journal of Sea Research, 73: 74–85.

Håkanson, J. L. 1993. Nutritional condition and growth rate of anchovy larvae (*Engraulis mordax*) in the California Current: two contrasting years. Marine Biology, 115: 309-316.

Heincke, F. 1908. Bericht über die Untersuchungen der Biologischen Anstalt auf Helgoland zur Naturgeschichte der Nutzfische. Die Beteiligung Deutschlands an der Internationalen Meeresforschung, 4: 67–155.

Hilborn, R. 2010. Pretty Good Yield and exploited fishes. Marine Policy, 34: 193–196.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Conseil International pour l'Exploration de la Mer: Rapports et Proces-verbaux, 20: 1-228.

Hjort, J. 1926. Fluctuations in the year classes of important food fishes. Journal du Conseil pour l'Exploration de la Mer, 1: 5-38.

Hochachka, P. W., Buck, L. T., Doll, C. J., and Land, S. C. 1996. Unifying theory of hypoxia tolerance: molecular/metabolic defense and rescue mechanisms for surviving oxygen lack. Proceedings Of The National Academy Of Sciences, 93: 9493–9498.

Houde, E. D. 1987. Fish early life dynamics and recruitment variability[1]. American Fisheries Society Symposium, 2: 17–29.

Houde, E. D. 1989. Comparative growth, mortality, and energetics of marine fish larvae: Temperature and implied latitudinal effects. Fishery Bulletin, U.S., 87: 471–495.

Houde, E. D. 2008. Emerging from Hjort's Shadow. Journal of Northwest Atlantic Fishery Science, 41: 53–70.

Hunter, J. R. 1980. The feeding behavior and ecology of marine fish larvae. In Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, pp. 287-326. Ed. by J. E. Bardach, J. J. Magnuson, R. C. May and J. M. Reinhart. ICLARM, Manila.

Hutchings, J. A. 2000. Collapse and recovery of marine fishes. Nature, 406: 882–885.

Hutchings, J. A., and Reynolds, J. D. 2004. Marine fish population collapses: Consequences for recovery and extinction risk. BioScience, 54(4): 297–309.

Hutchings, L., Beckley, L. E., Griffiths, M. H., Roberts, M. J., Sundby, S., and van der Lingen, C. D. 2002. Spawning on the edge: spawning grounds and nursery areas around the southern African coastline. Marine and Freshwater Research, 53: 307–318.

Hutchings, L., van der Lingen, C. D., Shannon, L. J., Crawford, R. J. M., Verheye, H. M., Bartholomae, C. H., van der Plas, A. K., Louw, D., Kreiner, A., Ostrowski, M., Fidel, Q., Barlow, R. G., Lamont, T., Coetzee, J., Shillington, F., Veitch, J., Currie, J. C., and Monteiro, P. M. S. 2009. The Benguela Current: an ecosystem of four components. Progress in Oceanography, 83: 15–32.

Ibaibarriaga, L., Irigoien, X., Santos, M., Motos, L., Fives, J. M., Franco, C., Lago de Lanzós, A., Acevedo, S., Bernal, M., Bez, N., Eltink, G., Farinha, A., Hammer, C., Iversen, S. A., Milligan, S. P., and Reid, D. G. 2007. Egg and larval distributions of seven fish species in north-east Atlantic waters. Fisheries Oceanography, 16: 284–293.

Iles, A. C., Gouhier, T. C., Menge, B. A., Stewart, J. S., Haupt, A. J., and Lynch, M. C. 2011. Climate-driven trends and ecological implications of event-scale upwelling in the California Current System. Global Change Biology, 18: 783–796.

Inthorn, M., Wagner, T., Scheeder, G., and Zabel, M. 2006. Lateral transport controls distribution, quality, and burial of organic matter along continental slopes in high-productivity areas. Geology, 34(3): 205-208.

IPCC, 2007. Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Ed. by Core Writing Team, R. K. Pachauri and A. Reisinger. IPCC, Geneva, Switzerland. 104 pp.

John, H.-Ch., Mohrholz, V., Lutjeharms, J. R. E., Weeks, S., Cloete, R., Kreiner, A., and da Silva Neto, D. 2004. Oceanographic and faunistic structures across an Angola Current intrusion into northern Namibian waters. Journal of Marine Systems, 46: 1–22.

Jordan, A. R. 1994. Age, growth and back-calculated birthdate distributions of larval Jack Mackerel, *Trachurus declivis* (Pisces, Carangidae), from eastern Tasmanian coastal waters. Australian Journal of Marine and Freshwater Research, 45: 19–33.

Jury, M. 2006. Tropical South-East Atlantic response to ENSO as an ecosystem indicator for the southern Benguela. African Journal of Marine Science, 28(1): 41-50.

King, R. A., Read, D. S., Traugott, M., and Symondson, W. O. C. 2008. Molecular analysis of predation: a review of best practice for DNA-based approaches. Molecular Ecology, 17: 947–963.

Kirchner, C. H., Bartholomae, C. H., and Kreiner, A. 2009. Use of environmental parameters to explain the variability in spawnerrecruitment relationships of Namibian sardine *Sardinops sagax*. African Journal of Marine Science, 31: 157–170.

Kirchner, C. H., Bauleth-D'Almeida, G., and Wilhelm, M. R. 2010. Assessment and management of Cape horse mackerel *Trachurus capensis* off Namibia based on a fleet-disaggregated age-structured production model. African Journal of Marine Science, 32(3): 525–541.

Kirchner, C. H. 2011. Benguela Current Large Marine Ecosystem, State of fish stocks report 2011. The Secretariat of the Benguela Current Commission, Windhoek. 92 pp.

Kirchner, C. H. 2012. Benguela Current Large Marine Ecosystem, State of Stocks Report, report No. 2 (2012). The Secretariat of the Benguela Current Commission, Windhoek. 105 pp.

Kreiner, A., Stenevik, E. K., and Ekau, W. 2009. Sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* larvae avoid regions with low dissolved oxygen concentration in the northern Benguela Current system. Journal of Fish Biology, 74: 270–277.

Kreiner, A., Yemane, D., Stenevik, E. K., and Moroff, N. E. 2011. The selection of spawning location of sardine (*Sardinops sagax*) in the northern Benguela after changes in stock structure and environmental conditions. Fisheries Oceanography, 20: 560–569.

Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Conseil International pour l'Exploration de la Mer: Rapports et Proces-verbaux, 173: 212–230.

Lasker, R. 1981. The role of a stable ocean in larval fish survival and subsequent recruitment. In: Marine fish larvae: morphology, ecology, and relation to fisheries, pp. 80–87. Ed. by R. Lasker. University of Washington Press, Seattle.

Le Clus, F. 1991. Hydrographic features related to pilchard and anchovy spawning in the northern Benguela system, comparing three environmental regimes. South African Journal of Marine Science, 10: 103–124.

Legendre, L., and Rivkin, R. 2002. Pelagic food webs: Responses to environmental processes and effects on the environment. Ecological Research, 17: 143–149.

Lehodey, P., Alheit, J., Barange, M., Baumgartner, T., Beaugrand, G., Drinkwater, K., Fromentin, J.-M., Hare, S. R., Ottersen, G. Perry, R. I., Roy, C., van der Lingen, C. D., and Werner, F. 2006. Climate variability, fish, and fisheries. Journal of Climate, 19: 5009–5030.

Leterme, S. C., Edwards, M., Seuront, L., and Attrill, M. J. 2005. Decadal basin-scale changes in diatoms, dinoflagellates, and phytoplankton color across the North Atlantic. Limnology and Oceanography, 50(4): 1244-1253.

Lett, C., Veitch, J., van der Lingen, C. D., and Hutchings, L. 2007. Assessment of an environmental barrier to transport of ichthyoplankton from the southern to the northern Benguela ecosystems. Marine Ecology Progress Series, 347: 247–259.

Levin, L. A., Ekau, W., Gooday, A. J., Jorissen, F., Middelburg, J. J., Naqvi, S. W. A., Neira, C., Rabalais, N. N., and Zhang, J. 2009. Effects of natural and human-induced hypoxia on coastal benthos. Biogeosciences, 6: 2063–2098.

Litzow, M. A., Bailey, K. M., Prahl, F. G., and Heintz, R. 2006. Climate regime shifts and reorganization of fish communities: the essential fatty acid limitation hypothesis. Marine Ecology Progress Series, 315: 1–11.

Lluch-Belda, D., Lluch-Cota, D. B., Hernandez-Vazquez, S., Salinas-Zavala, C. A., and Schwartzlose, R. A. 1991. Sardine and anchovy spawning as related to temperature and upwelling in the California Current system. CalCOFI Reports, 32: 105–111.

Loick, N., Ekau, W., and Verheye, H. M. 2005. Water-body preferences of dominant calanoid copepod species in the Angola-Benguela frontal zone. African Journal of Marine Science, 27: 597–608.

Lutjeharms, J. R. E., Monteiro, P. M. S., Tyson, P., and Obura, D. 2001. The oceans around southern Africa and regional effects of global change. South African Journal of Science, 97: 119–130.

Lynam, C. P., Gibbons, M. J., Axelsen, B. E., Sparks, C. A. J., Coetzee, J. C., Heywood, B. G., and Brierley, A. S. 2006. Jellyfish overtake fish in a heavily fished ecosystem. Current Biology, 16(13): R492–493.

Martin, D. L., Ross, R. M., Quetin, L. B., and Murray, A. E. 2006. Molecular approach (PCR-DGGE) to diet analysis in young Antarctic krill *Euphausia superba*. Marine Ecology Progress Series, 319: 155–165.

Masuda, R. 2006. Ontogeny of antipredator behavior in hatchery reared jack mackerel *Trachurus japonicus* larvae and juveniles: patchiness formation, swimming capability, and interaction with jellyfish. Fisheries Science, 72: 1225–1235.

Masuda, R. 2009. Behavioral ontogeny of marine pelagic fishes with the implications for the sustainable management of fisheries resources. Aqua-Bio Science Monographs, 2: 1–56.

Masuda, R. 2011. Ontogeny of swimming speed, schooling behaviour and jellyfish avoidance by Japanese anchovy *Engraulis japonicus*. Journal of Fish Biology, 78: 1323–1335.

Matsuoka, M. 1997. Osteological development in the Japanese sardine, *Sardinops melanostictus*. Ichthyological Research, 44(3): 275–295.

Messié, M., Ledesma, J., Kolber, D. D., Michisaki, R. P., Foley, D. G., and Chavez, F. P. 2009. Potential new production estimates in four eastern boundary upwelling ecosystems. Progress in Oceanography, 83: 151–158.

Michalek, K. 2012. Activity of metabolic key enzymes in early life stages of cape horse mackerels, *Trachurus trachurus capensis* from the northern Benguela Current upwelling system. MSc thesis, Faculty of Biology and Chemistry, University Bremen, 56 pp.

Mitchell-Innes, B. A., and Pitcher, G. C. 1992. Hydrographic parameters as indicators of the suitability of phytoplankton populations as food for herbivorous copepods. South African Journal of Marine Science, 12: 355–365.

Mohrholz, V., Bartholomae, C. H., van der Plas, A. K., and Lass, H. U. 2008. The seasonal variability of the northern Benguela undercurrent and its relation to the oxygen budget on the shelf. Continental Shelf Research, 28: 424–441.

Mohrholz, V. 2012a-c. Hydrographic measurements in the Northern Benguela upwelling system during the cruise AFR258 (a), D356 (b), MSM17/3 (c). Leibniz-Institut für Ostseeforschung Warnemünde, unpublished datasets #784364 – 784366.

Monteiro, P. M. S., van der Plas, A. K., Mohrholz, V., Mabille, E., Pascall, A., and Joubert, W. 2006. Variability of natural hypoxia and methane in a coastal upwelling system: Oceanic physics or shelf biology? Geophysical Research Letters, 33: L16614.

Morote, E., Olivar, M. P., Villate, F., and Uriarte, I. 2008. Diet of round sardinella, *Sardinella aurita*, larvae in relation to plankton availability in the NW Mediterranean. Journal of Plankton Research, 30: 807–816.

Morote, E., Olivar, M. P., Villate, F., and Uriarte, I. 2010. A comparison of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) larvae feeding in the northwest Mediterranean: influence of prey availability and ontogeny. ICES Journal of Marine Science, 67: 897–908.

Mullon, C., Fréon, P., and Cury, P. M. 2005. The dynamics of collapse in world fisheries. Fish and Fisheries, 6: 111–120.

Murawski, S. A. 2010. Rebuilding depleted fish stocks: the good, the bad, and, mostly, the ugly. ICES Journal of Marine Science, 67: 1830–1840.

Myers, R. A., Bowen, K. G., and Barrowman, N. J. 1999. Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences, 56: 2404–2419.

Neill, W. H., Miller, J. M., van der Veer, H. W., and Winemiller, K. O. 1994. Ecophysiology of marine fish recruitment: a conceptual framework for understanding interannual variability. Netherlands Journal of Sea Research, 32: 135–152.

Olivar, M. P., and Barange, M. 1990. Zooplankton of the northern Benguela region in a quiescent upwelling period. Journal of Plankton Research, 12: 1023–1044.

Olivar, M.-P., and Fortuño, J. M. 1991. Guide to ichthyoplankton of the southeast Atlantic (Benguela Current region). Scientia Marina, 55: 1–383.

Osako, K., Kuwahara, K., Saito, H., Hossain, M. A., and Nozaki, Y. 2003. Effect of starvation on lipid metabolism and stability of DHA content of lipids in horse mackerel (*Trachurus japonicus*) tissues. Lipids, 38: 1263–1267.

Ottersen, G., Kim, S., Huse, G., Polovina, J. J., and Stenseth, N. C. 2010. Major pathways by which climate may force marine fish populations. Journal of Marine Systems, 79: 343–360.

Paulmier, A., and Ruiz-Pino, D. 2009. Oxygen minimum zones (OMZs) in the modern ocean. Progress in Oceanography, 80: 113–128.

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate change and distribution shifts in marine fishes. Science, 308: 1912–1915.

Perry, R. I., Cury, P., Brander, K., Jennings, S., Möllmann, C., and Planque, B. 2010. Sensitivity of marine systems to climate and fishing: Concepts, issues and management responses. Journal of Marine Systems, 79: 427–435.

Peterson, R. G., and Stramma, L. 1991. Upper-level circulation in the South Atlantic Ocean. Progress in Oceanography, 26: 1–73.

Pikitch, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., Sumaila, U. R., Dee Boersma, P., Boyd, I. L., Conover, D. O., Cury, P., Heppell, S. S., Houde, E. D., Mangel, M., Plagányi, É., Sainsbury, K., Steneck, R. S., Geers, T. M., Gownaris, N., and Munsch, S. B. 2012. The global contribution of forage fish to marine fisheries and ecosystems. Fish and Fisheries, DOI: 10.1111/faf.12004

Planque, B., Fromentin, J., Cury, P., Drinkwater, K. F., Jennings, S., Perry, R. I., and Kifani, S. 2010. How does fishing alter marine populations and ecosystems sensitivity to climate? Journal of Marine Systems, 79: 403-417.

Pörtner, H.-O. 2010. Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. The Journal of Experimental Biology, 213: 881–893.

Pörtner, H.-O., and Farrell, A. P. 2008. Physiology and Climate Change. Science, 322: 690–692.

Pörtner, H.-O., and Peck, M. A. 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. Journal of Fish Biology, 77: 1745–1779.

Richards, J. G. 2009. Metabolic and molecular processes of fish to hypoxia. In Fish Physiology, Vol. XXVII, pp. 443-485. Ed by J. G. Richards, A. P. Farrell and C. J. Brauner. Acacemic Press, London.

Richardson, A. J., Verheye, H. M., Herbert, V., Rogers, C., and Arendse, L. M. 2001. Egg production, somatic growth and productivity of copepods in the Benguela Current system and Angola-Benguela Front. South African Journal of Science, 97: 1-7.

Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C., and Pinnegar, J. K. 2009. Resolving the effect of climate change on fish populations. ICES Journal of Marine Science, 66: 1570–1583.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada, 11: 559-623.

Rochet, M.-J. 2000. A comparative approach to life-history strategies and tactics among four orders of teleost fish. ICES Journal of Marine Science, 57: 228–239.

Rombough, P. J. 1988. Respiratory gas exchange, aerobic metabolism, and effects of hypoxia during early life. In Fish Physiology, Vol. XI, the physiology of developing fish, pp. 59-161. Ed. by W. S. Hoar, and D. J. Randall. Academic Press, New York.

Rose, K. A., Cowan Jr, J. H., Winemiller, K. O., Myers, R. A., and Hilborn, R. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish and Fisheries, 2: 293–327.

Roux, J.-P., van der Lingen, C. D., Gibbons, M. J., Moroff, N. E., Shannon, L. J., Smith, A. D., and Cury, P. M. 2013. Jellyfication of marine ecosystems as a likely consequence of overfishing small pelagic fishes: Lessons from the Benguela. Bulletin of Marine Science, 89(1): 249–284.

Rykaczewski, R. R., and Checkley, Jr., D. M. 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. Proceedings Of The National Academy Of Sciences, 105: 1965–1970.

Sassa, C., and Tsukamoto, Y. 2012. Inter-annual comparison of diet and daily ration of larval jack mackerel *Trachurus japonicus* in the southern East China Sea. Journal of Plankton Research, 34: 173–187.

Schukat, A. 2012. Trophic interactions and energetics of key components in the Benguela Current Ecosystem: The role of calanoid copepods and pelagic decapods. PhD thesis, University of Bremen, Germany. 132 pp.

Schwartzlose, R. A., Alheit, J., Bakun, A., Baumgartner, T. R., Cloete, R., Crawford, R. J. M., Fletcher, W. J., Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota, S. E., MacCall, A. D., Matsuura, Y., Nevarez-Martínez, M. O., Parrish, R. H., Roy, C., Serra, R., Shust, K. V., Ward, M. N.,

and Zuzunaga, J. Z. 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. South African Journal of Marine Science, 21: 289–348.

Shackleton, L. Y. 1987. A comparative study of fossil fish scales from three upwelling regions. South African Journal of Marine Science.

Shannon, L. V. 1985. The Benguela ecosystem part I. Evolution of the Benguela, physical features and processes. In Oceanography and Marine Biology, An Annual Review, 23, pp. 105–182. Ed. by M. Barnes. Aberdeen University Press, Aberdeen.

Shannon, L. V., Agenbag, J. J., and Buys, M. E. L. 1987. Large-and mesoscale features of the Angola-Benguela front. South African Journal of Marine Science, 5: 11-34.

Shannon, L. V., Crawford, R. J. M., Brundrit, G. B., and Underhill, L. G. 1988. Responses of fish populations in the Benguela ecosystem to environmental change. Journal du Conseil pour l'Exploration de la Mer, 45: 5-12.

Shelton, P. A., Boyd, A. J., and Armstrong, M. J. 1985. The influence of large-scale environmental processes on neritic fish populations in the Benguela Current system. CalCOFI Reports, 26: 72–92.

Sherbourne, R. 2007. Namibia's fishing industry. IJG Securities (Pty) Ltd., Windhoek, 27 pp.

Sommer, U., Stibor, H., Katechakis, A., Sommer, F., and Hansen, T. 2002. Pelagic food web configurations at different levels of nutrient richness and their implications for the ratio fish production: primary production. Hydrobiologia, 484: 11–20.

Steele, J. H. 2004. Regime shifts in the ocean: reconciling observations and theory. Progress in Oceanography, 60: 135–141.

Stenevik, E. K., Skogen, M. D., Sundby, S., and Boyer, D. C. 2003. The effect of vertical and horizontal distribution on retention of sardine (*Sardinops sagax*) larvae in the northern Benguela-observations and modelling. Fisheries Oceanography, 12: 185–200.

Stenevik, E. K., Sundby, S., and Cloete, R. 2007. Diel vertical migration of anchovy *Engraulis encrasicolus* larvae in the northern Benguela. African Journal of Marine Science, 29: 127–136.

Stramma, L., Johnson, G. C., Sprintall, J., and Mohrholz, V. 2008. Expanding oxygen-minimum zones in the tropical oceans. Science, 320: 655–658.

Stramma, L., Prince, E. D., Schmidtko, S., Luo, J., Hoolihan, J. P., Visbeck, M., Wallace, D. W. R., Brandt, P. and Körtzinger, A. 2011. Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. Nature Climate Change, 2: 33–37.

Sumaila, U. R., Cheung, W. W. L., Lam, V. W. Y., Pauly, D., and Herrick, S. 2011. Climate change impacts on the biophysics and economics of world fisheries. Nature Climate Change, 1: 449–456.

Takahashi, M., Checkley Jr, D. M., Litz, M. N. C., Brodeur, R. D., and Peterson, W. T. 2012. Responses in growth rate of larval northern anchovy (*Engraulis mordax*) to anomalous upwelling in the northern California Current. Fisheries Oceanography, 21: 393–404.

Takasuka, A., Aoki, I., and Mitani, I. 2003. Evidence of growth-selective predation on larval Japanese anchovy *Engraulis japonicus* in Sagami Bay. Marine Ecology Progress Series, 252: 223–238.

Takasuka, A., Oozeki, Y., Kubota, H., and Lluch-Cota, S. E. 2008. Contrasting spawning temperature optima: Why are anchovy and sardine regime shifts synchronous across the north Pacific? Progress in Oceanography, 77: 225–232.

Thomas, R. M. 1986. Growth of larval pelagic fish in the south-east Atlantic from daily otolith rings in 1982/83 and 1983/84. South African Journal of Marine Science, 4: 61–77.

Timonin, A. G., Arashkevich, E. G., Drits, A. V. And T. N. Semenova. Zooplankton dynamics in the northern Benguela ecosystem, with special reference to the copepod *Calanoides carinatus*. South African Journal of Marine Science, 12(1): 545-560.

Tjizoo, M. B. 2008. Characterizing and comparing the spawning habitats of sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) in the northern Benguela Region. MSc thesis, University of Cape Town, South Africa. 117 pp.

Ton, C., Stamatiou, D., and Liew, C.-C. 2003. Gene expression profile of zebrafish exposed to hypoxia during development. Physiological genomics, 13: 97–106.

Troedsson, C., Simonelli, P., Nagele, V., Nejstgaard, J. C., and Frischer, M. E. 2009. Quantification of copepod gut content by differential length amplification quantitative PCR (dla-qPCR). Marine Biology, 156: 253–259.

Twatwa, N. M., van der Lingen, C. D., Drapeau, L., Moloney, C. L., and Field, J. G. 2005. Characterising and comparing the spawning habitats of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela upwelling ecosystem. African Journal of Marine Science, 27: 487–499.

van der Lingen, C. D., Hutchings, L., and Field, J. G. 2006a. Comparative trophodynamics of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela: are species alternations between small pelagic fish trophodynamically mediated? African Journal of Marine Science, 28: 465–477.

van der Lingen, C. D., Shannon, L. J., Cury, P. M., Kreiner, A., Moloney, C. L., Roux, J. P., and Vaz-Velho, F. 2006b. Resource and ecosystem variability, including regime shifts, in the Benguela Current system. Large Marine Ecosystems, 14: 147–184.

van der Lingen, C. D., Bertrand, A., Bode, A., Brodeur, R. D., Cubillos, L. A., Espinoza, P., Friedland, K., Garrido, S., Irigoien, X., Miller, T. Möllmann, C., Rodriguez-Sanchez, R., Tanaka, H., and Temming, A. 2009. Trophic dynamics. In Climate change and small pelagic fish, pp. 112-157. Ed. by D. M. Checkley Jr, J. Alheit, Y. Oozeki, and C. Roy. Cambridge University Press, New York.

Vander Zanden, M. J., and Rasmussen, J. B. 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: implications for aquatic food web studies. Limnology and Oceanography, 46(8): 2061–2066.

Verheye, H. M., Hagen, W., Auel, H., Ekau, W., Loick, N., Rheenen, I., Wencke, P., and Jones, S. 2005. Life strategies, energetics and growth characteristics of *Calanoides carinatus* (Copepoda) in the Angola-Benguela frontal region. African Journal of Marine Science, 27: 641–651.

Verheye, H. M., and Kreiner, A. 2009. Retrospective analysis of zooplankton community structure in the Benguela current large marine ecosystem. In: Benguela Environment Fisheries Interaction and Training Programme (BENEFIT) Research Projects, pp. 100–103. Ed. by I. Hampton, M. Barange, and N. Sweijd. GLOBEC Report 25, Plymouth, UK..

Verheye, H. M., and Kreiner, A. 2013. SCOR-WG125, Zooplankton abundance and biomass of the Northern Benguela Current, Walvis Bay 23S. http://www.st.nmfs.noaa.gov/nauplius/media/time-series/site__satl-walvis-bay-23s/, accessed: 20.4.2013.

Vert-pre, K. A., Amoroso, R. O., Jensen, O. P., and Hilborn, R. 2013. Frequency and intensity of productivity regime shifts in marine fish stocks. Proceedings of the National Academy of Sciences of the United States of America, 110: 1779–1784.

Vestheim, H., Edvardsen, B., and Kaartvedt, S. 2005. Assessing feeding of a carnivorous copepod using species-specific PCR. Marine Biology, 147: 381–385.

Waldron, M. E., and Kerstan, M. 2001. Age validation in horse mackerel (*Trachurus trachurus*) otoliths. ICES Journal of Marine Science, 58: 806–813.

Winemiller, K. O. 2005. Life history strategies, population regulation, and implications for fisheries management. Canadian Journal of Fisheries and Aquatic Sciences, 62: 872–885.

Winemiller, K. O., and Rose, K. A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences, 49: 2196-2218.

Xie, S., and Watanabe, Y. 2005. Hatch date-dependent differences in early growth and development recorded in the otolith microstructure of *Trachurus japonicus*. Journal of Fish Biology, 66: 1720–1734.

Xie, S., Watanabe, Y., Saruwatari, T., Masuda, R., Yamashita, Y., Sassa, C., and Konishi, Y. 2005. Growth and morphological development of sagittal otoliths of larval and early juvenile *Trachurus japonicus*. Journal of Fish Biology, 66: 1704–1719.

Young, J. W., and Davis, T. L. O. 1992. Feeding ecology and interannual variations in diet of larval jack mackerel, *Trachurus declivis* (Pisces: Carangidae), from coastal waters of eastern Tasmania. Marine Biology, 113: 11–20.

Zhang, J., Gilbert, D., Gooday, A. J., Levin, L., Naqvi, S. W., Middelburg, J. J., Scranton, M., Ekau, W., Peña, A., Dewitte, B., Oguz, T., Monteiro, P. M. S., Urban, E., Rabalais, N. N., Ittekot, V., Kemp, W.

M., Ulloa, O., Elmgren, R., Escobar-Briones, E., and van der Plas, A. K. 2010. Natural and human-induced hypoxia and consequences for coastal areas: synthesis and future development. Biogeosciences, 7: 1443-1467.

Zheng, J. 1996. Herring stock-recruitment relationships and recruitment patterns in the north Atlantic and northeast Pacific oceans. Fisheries Research, 26: 257–277.

Publications

Chapter I

Energy demand of larval and juvenile Cape horse mackerels,

Trachurus capensis,

and indications for hypoxia tolerance

as an advantage in a changing environment

Simon Joscha Geist[1*] (corresponding author)

Werner Ekau[1]

Andreas Kunzmann[1]

[1]Leibniz Center for Tropical Marine Ecology (ZMT)

28359 Bremen

Germany

*simon.geist@zmt-bremen.de

+49 421 23800124 (phone)

+49 421 2380030 (fax)

52

<u>key words</u>

fish; larvae; juveniles; respiration; energy demand; hypoxia; Benguela; upwelling; pelagic

1. Abstract

Trachurus capensis is an important pelagic fisheries resource in the degraded Namibian upwelling ecosystem. Food supply and shoaling of hypoxic zones are hypothesised to influence the species' recruitment success. This paper is the first to quantify energy requirements and hypoxia tolerance of larval and juvenile stages of a *Trachurus* species. We measured normoxic respiration rates of *T. capensis* with a size range from 0.001-20.8 g wet mass (*WM*) collected off Cape Town (33.9°S, 18.5°E, 12/2009) and in the northern Benguela (17-24°S, 11-15°E, 02/2011). Routine metabolic, *RMR*, and standard routine rates, *SRR*, (mg O_2 h^{-1}) followed the allometric functions $RMR = 0.418\ WM^{0.774}$ and $SRR = 0.275\ WM^{0.855}$, respectively. Larvae and juveniles had comparatively high metabolic rates, and the energy demand of juveniles at the upper end of the size range appeared too high to be fuelled by a copepod diet alone. *T. capensis*' early life stages showed a high tolerance to hypoxic conditions. *RMR* in larvae did not change until 30% O_2sat at 18°C. In juveniles, critical oxygen saturation levels were low (P_C for $SRR = 11.2 \pm 1.7\%$ O_2sat and P_C for $RMR = 13.2 \pm 1.6\%$ O_2sat at 20°C) and oxy-regulation effective (regulation index = 0.78 ± 0.09). A high hypoxia tolerance may facilitate the retention of larvae in near-shore waters providing favourable feeding conditions and allowing juveniles to exploit food resources in the oxygen minimum zone. These mechanisms seem to well adapt *T. capensis* to a habitat affected by spreading hypoxic zones and probably enhance its recruitment success.

2. Introduction

The expansion of hypoxic and anoxic zones in coastal seas and particularly upwelling systems is one of the major threats for ecosystem functioning (Grantham et al. 2004, Levin et al. 2009, Bakun et al. 2010b, Ekau et al. 2010, Gilly et al. 2013).

The Northern Benguela Current ecosystem (NBCE), situated off the Namibian coast and bounded by the perennial Lüderitz upwelling cell in the south and the Angola-Benguela Front in the north, is regarded as an example for negative future scenarios in coastal ecosystems (Bakun et al. 2010a). Overexploitation and environmental changes induced a regime shift in the 1970s and 1980s resulting in a new ecosystem state (Cury and Shannon 2004, van der Lingen et al. 2006). Before this shift typical small pelagic fishes of upwelling systems, sardines (*Sardinops sagax*) and anchovies (*Engraulis encrasicolus*), were the key species in the food web. To date, Cape horse mackerel (*Trachurus capensis*), hakes (*Merluccius capensis* and *M. paradoxus*), bearded goby (*Sufflogobius bibarbatus*) and jellyfish dominate the system (Cury and Shannon 2004, Hutchings et al. 2009, Flynn et al. 2011) with *T. capensis* being the major pelagic fisheries resource, however, without reaching the historic biomasses and catches recorded for sardines and anchovies (FAO 2012). The expansion of oxygen minimum zones

(OMZ) and a change in zooplankton composition have been suggested as major agents stabilizing the new ecosystem state (Hutchings et al. 2009, Bakun et al. 2010b, Ekau et al. 2010). Ekau and Verheye (2005) and Kreiner et al. (2009) suggested from their vertical distribution that larvae of pelagic fishes (*S. sagax*, *E. encrasicolus*, *T. capensis*) avoid low oxygenised waters (<2.5 mL O_2 L^{-1}). Thus, knowledge of their physiological capacity is crucial to understand the underlying mechanisms of recruitment success or failure (Neill et al. 1994).

Recruitment success is a major factor determining fish stock dynamics as planktonic early life history (ELH) stages are considerably vulnerable to changes in their environment (see reviews of Houde 2008, Bakun 2010, Drinkwater et al. 2010). Food limitation and narrow tolerance windows for environmental parameters, such as temperature, oxygen, pH, can negatively affect growth and survival in ELH stages in a changing environment (Hjort 1914, Houde 1987, Cushing 1990, Pörtner 2010).

In fishes, oxygen uptake (MO_2) can be used as proxy for energy use (Winberg 1956, Fry 1971) and oxygen consumption determined in respiration measurements, depending on the activity level of the fish. According to Fry (1971), it ranges from the standard metabolic rate (*SMR*) which is the minimal energy required to keep a resting, unfed fish alive, to the maximum metabolic rate (*MMR*). Within this range, the routine metabolic rate (*RMR*) is the average *MO2* of an unfed fish at normal or spontaneous activity level. The active metabolic rate (AMR) is defined as the oxygen uptake at maximum sustained swimming (Behrens and Steffensen 2007). The metabolic scope allows an estimation of the amount of energy available for investments other than maintenance of basic body functions. Its factorial form allows a comparison over large size ranges (Killen et al. 2007). It is defined as the difference between *SMR* and *MMR* and marks the scope for activity, which is reduced at lower oxygen levels (Fry 1971, Neill et al. 1994). A common measure of the metabolic response to hypoxia is the critical partial pressure of oxygen (P_C) defined as the "level of no excess activity", when aerobic scope is zero (Fry 1971).

The first physiological evidence for the restructuring potential of hypoxia in the NBCE came from respiration experiments with adult *S. bibarbatus* (P_C = 5.5 ± 0.3 % O_2sat at 12°C). Their high tolerance of extremely low oxygen levels favours their role in the current ecosystem state (Utne-Palm et al. 2010). Despite of the high and worldwide ecological and economic importance of *Trachurus* species (FAO 2012), physiological studies have been carried out on adults only (*T. trachurus*: Wardle et al. 1996, Shulman and Love 1999, Herrmann and Enders 2000; *T. japonicus*: Ikeda 1970; *T. murphyi*: Chekunova and Naumov 1978). Here, we present energy requirements and hypoxia tolerance levels of larval and juvenile stages of a *Trachurus* species for the first time.

This study is an integral part of the larger GENUS research program (Geochemistry and Ecology of the Namibian Upwelling System), which aims to investigate and model energy and material fluxes of important players to understand the mechanisms and driving forces behind the changes in the Benguela upwelling ecosystem.

We address the following major questions:

1)   What is the energy demand of larval and juvenile *T. capensis* under normoxic conditions and how does this transfer in units of typical prey items?

2)   How well are early life stages of *T. capensis* adapted to exposure of hypoxic water conditions of short- to mid-term durations (hours to two days)?

3. Materials and Methods

3.1 Collection and maintenance of fish

The majority of *T. capensis* larvae and juveniles used in our experiments were caught in the NBCE (26° 40' S to 11° 10' S) during Cruise No. 17-3 of the research vessel *Maria S. Merian* (*MSM*) in February/March 2011. They were caught in the upper 50 m of the water column with different types of plankton nets trawled at a maximum ship speed of 1 m s^{-1} (Ekau et al. 2012). A ring net (mouth area: 2 m^2, mesh size: 1000 μm), deployed in the upper 30 m of the water column for 1-5 min per haul with the ship drifting, yielded the best results in terms of numbers and quality of live larvae when jellyfish were not too abundant. Live *Trachurus* were isolated immediately after capture and kept in separate aquaria (0.5-20 L, depending on fish size). The aquaria were maintained with aerated, pre-filtered seawater at a constant temperature of 18°C, which closely corresponded to the *in-situ* temperature at the catching depth (± 2°C). Juvenile fish being in good condition at the end of the cruise were transferred to the Leibniz Center for Tropical Marine Ecology (*ZMT*) in Bremen, Germany, to continue experiments. There, they were kept in tanks equipped with a biofilter and filled with artificial seawater reflecting in-situ salinities at 18°C for up to seven months after catch. On board *MSM* and at *ZMT*, fish were fed either with wild-caught copepods or reared *Artemia* enriched with DHA-Selco and kept under a 12 h/12 h artificial light/dark regime.

In addition, larger juveniles were caught with a sink net operated from a pier in Cape Town during December 2009. Fish were kept in two 500 L tanks containing filtered seawater at 19 ± 1°C at the Marine Research Aquarium (*MRA*) in Sea Point, Cape Town. Facilities there allowed the fish to acclimatize and readapt normal schooling patterns under natural light conditions (14 h/10 h).

3.2 Normoxia experiments

In total 58 respiration experiments were conducted. 45 experiments took place directly on board the *MSM* during February/March 2011. Seven experiments on juveniles were done at *ZMT* from May to September 2011, and six at *MRA* during December 2009. Experiments were conducted on a 12 h/12 h day/night light regime at salinity 35. Experimental water temperatures were kept constant by submersing the respiration chamber in a temperature-controlled water bath. The respirometer was screened off with black plastic material to prevent external disturbance, and a miniature camera remotely recorded the behaviour of the fish. To reduce microbial activity, seawater was micro-filtered (ACROPAK 1000 filter cartridge, 0.8/0.2 µm) and all components of the respirometry setups were carefully cleaned, using 70% Ethanol and rinsed in distilled water after each experiment. Metabolic rate measurements were conducted on animals in a post-absorptive state to minimize the effect of specific dynamic action. Therefore, larvae were not fed for 24 h and juveniles for 36 to 48 h prior to an experiment, taking into account increasing gut evacuation times with body size. Due to the limited duration of a research cruise, the minimum time period between catch and experiment for larvae on board *MSM* was set to two days, thus allowing the larvae to recover from catching stress. Only larvae showing normal swimming and feeding behaviour were chosen for experiments. Juveniles were kept for at least 15 d between catch and experiments on board *MSM* and at *MRA*. Time span between transport and experiment at *ZMT* was at least two months. At the end of the experiments, wet body mass (*WM*) of larvae was obtained using a fine balance (Sartorius ME36S, accuracy: 0.1 mg) after blotting larvae on precision wipes to remove any water. Juvenile fish were weighed alive right after an experiment (Kern 572, accuracy: 0.1 g).

3.2.1 Data collection

Individual respiration rates (*MO2*, mg O_2 h^{-1}) were measured in two different respirometry systems. Respiration rates of larvae of 1.0-8.4 mg *WM* were determined in a <u>closed system</u> consisting of a 20 mL glass vial equipped with a temperature-compensated optical oxygen sensor spot (PreSens). A slowly rotating, glass-coated magnetic stirrer guaranteed good mixing in the respiration chamber, shielded by a gauze housing to prevent direct contact with the larva. 19 experiments were conducted under normoxic conditions (100-70% O_2sat = dissolved oxygen saturation in the respirometer) at temperatures from 15.9 to 18.1°C. At 70% O_2sat, 50% of the water in the respirometer was exchanged by fresh, fully saturated water to allow experiments between 244-1091 min. Respiration rates of older larvae and juveniles (8 mg to 20.8 g) were measured in an automated <u>intermittent-flow system</u> described by Zimmermann and Kunzmann (2001) in 39 normoxia experiments. Here, the desired upper and lower oxygen

saturation levels of the measuring phase were set to 90 and 70% O_2sat prior to the experiment. Whenever the lower oxygen limit was reached, the respirometer automatically opened a valve to flush aerated seawater into the system. The valve closed again upon reaching the upper oxygen limit. The mixing phase (Herrmann and Enders 2000) was excluded from MO2 calculations. Three setups were used to account for differences in fish size, all equipped with optical oxygen sensor probes (Online Resource 1). In both systems, O_2sat was logged in the respirometer continuously every minute.

3.2.2 Data analysis

Individual MO2 were calculated for subsequent 10 min intervals via the slope of the linear regression describing the rate of decrease in % O_2sat per unit time (Δ%O_2sat Δt^{-1}). The standard formula for closed-system respirometry (Schurmann and Steffensen 1997) was used:

MO2 (mg O_2 h^{-1}) = c * V_{resp} * α,

where c = slope, V_{resp} = volume of the respirometer corrected for the volume of the fish; and α = solubility of oxygen in the water. α was calculated using Garcia and Gordon's (1992) Equation 8 and a conversion factor from mL to mg O_2 L^{-1} of 1.429 (0°C and 101.325 kPa). To correct for bacterial background respiration, all post-blanks were plotted against the duration of the respective experiment, separately for each of the four respirometer setups. For each setup, an exponential function was fitted to the plotted data to estimate the temporal development of background respiration, assuming an exponential bacterial growth after an initial lag phase. Every individual MO2 measured during an experiment was corrected accordingly. MO2-values were standardised to 18°C, the mean temperature of all experiments, using a Q_{10}-value of 2.2 determined for Black Sea horse mackerel (Shulman and Love 1999) to adjust for temperature differences between setups:

MO2 at T1 = MO2 at T2 * Q_{10} $^{((T1 - T2)/10)}$

We used the quantile method to deduce metabolic rates of standard routine (*SRR*), routine (*RMR*) and active routine (*ARR*) metabolism, a procedure robust to different sample sizes and the presence and number of outliers (van den Thillart et al. 1994, Daoud et al. 2007, Dupont-Prinet et al. 2010). *RMR* was determined as the median of the frequency distribution including all 10-min-MO2 of an experiment. The 5%-quantile reflected standard metabolism best and was termed *SRR*, to distinguish it from *SMR*. The 95%-quantile was defined as the *ARR*, reflecting the maximum spontaneous activity (Rombough 1988, van den Thillart et al. 1994). Representative examples of the temporal development of MO2 in the closed and the intermittent system with indications of *SRR*, *RMR* and *ARR* are given in Fig. 1. First experiments (Kunzmann unpubl. data) confirmed that the *SRR* is already achieved after ca. 200
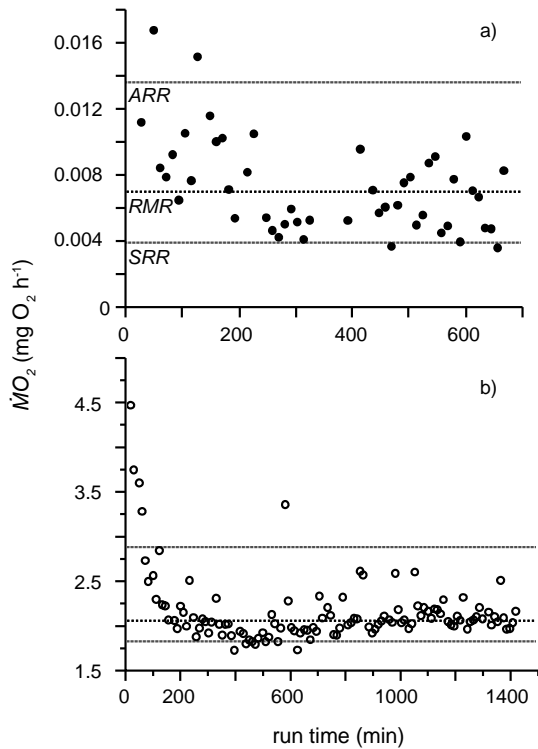
Fig. 1: Variation in respiration rates (*M*O2) in two representative experiments and levels for standard routine (*SRR*, lower dashed line), routine metabolic (*RMR*, broken line) and active routine (*ARR*, upper dashed line) rates calculated as the 0.05, 0.5 and 0.95 quantiles. (a) larva (7.7 mg) in closed system, (b) juvenile (15 g) in intermittent system

min and does not significantly change within the next 24 h. Experiments in the current study were carried out at different times of the day. In 14 experiments with significantly lower *M*O2 during dark conditions (Wilcoxon tests), *SRR* was calculated solely with the respective 10-min-*M*O2.

The relationships between *WM* and *SRR* and *RMR* were analysed by least-squares linear regressions of log-transformed data (log *SRR* and log *RMR* = $A + b$ log *WM*, with A = metabolic coefficient and b = weight exponent). The linear fits were compared with quadratic fits (log *SRR* and log *RMR* = $A + b$ log *WM* $+ c$ log *WM*^{2}, with A, b, c as constants) by use of the adjusted Akaike information criterion (AICc) and the Bayesian Information Criterion (BIC). Homogeneity of slopes test was applied to compare the slopes of the linear regressions

of *RMR* and *SRR* with body mass. The ratio of *ARR SRR*$^{-1}$ was calculated as an estimate of the "aerobic scope for spontaneous activity" (SSA) (Rombough 1988, van den Thillart et al. 1994).

3.2.3 Calculation of prey requirements

Metabolic rates of *T. capensis* were converted into units of carbon (mg C h^{-1}) and prey requirements were estimated based on the average carbon content of their preferred prey organisms for an evaluation of their influence on energy and matter fluxes in the planktonic food web in the northern Benguela. The diet of young *T. capensis* is mainly based on copepods (Geist et al. 2013) that are rich in lipids (Schukat et al. 2013a). Therefore carbon requirements (*CR*) were calculated as: *CR* (mg C h^{-1}) = (*SSR* or *RMR* * 1.429^{-1}) * *RQ* * (12/22.4), with the respiratory quotients (*RQ*) of lipid (0.71) (Ikeda et al. 2000). The carbon content of different copepod groups from the northern Benguela was estimated for individuals of average dry mass (*DM*) determined from freeze-dried, pooled samples. Relative carbon content (% *DM*) in Calanoida species was determined in another study within the GENUS project (Schukat et al.

2013b). Carbon values for Cyclopoida, Poecilostomatoida and Harpacticoida were assumed to be similar to those of Calanoida, i.e. 44% *DM*.

3.3 Hypoxia experiments

3.3.1 Development of *RMR* at lowered oxygen saturations in larvae

In ten experiments with larvae, the normoxic phase was extended to a hypoxic phase. In the closed system oxygen saturation declined constantly and experiments were stopped at a level of 20% O_2sat before larvae showed severe stress behaviour (increase in movements as indicator). *RMR* was calculated as described above for subsequent steps of oxygen saturation intervals (69-60%, 59-50%, 49-40%, 39-30%, 29-20% O_2sat) and the development of *RMR* under decreasing oxygen saturation was tested via a univariate ANOVA for repeated measurements.

3.3.2 Critical oxygen partial pressures (P_C) for *RMR* and *SRR* and regulation index (*RI*) for *RMR* in juveniles

Seven experiments with juveniles were extended to oxygen levels below 20% O_2sat, with *M*O2 calculated for subsequent oxygen saturation intervals (> 40% O_2sat in 10%-increments, < 40% O_2sat in 5%- and 2%-increments) instead of the time-based (10 min intervals) calculation. The first 200 min of an experiment were excluded to account for elevated *M*O2 due to initial stress responses. In these experiments, *RMR* and *SRR* were calculated with all MO_2 >30% O_2sat. The critical oxygen pressures for *RMR* (P_C2) and *SRR* (P_C1) were estimated according to Yeager and Ultsch's (1989) definition as PO_2 below which an animal can no longer maintain a given rate of O_2- consumption. In addition, the regulation index (*RI*), a new method for assessing the relationship between oxygen consumption and environmental oxygen (Mueller and Seymour 2011), was determined referring to *RMR*. In all seven experiments the one-phase-decay model of *M*O2 plotted against % O_2sat displayed the better fit, judged by Akaike's corrected information criterion (AICc). Consequently, this fit and two lines visualizing the theoretical shape of perfect oxyregulation and oxyconformity were constructed. The ratio of the areas below the curve fit and below the oxyconformity line was defined as *RI*, ranging between 0 (perfect oxyconformity) and 1 (perfect oxyregulation, Mueller and Seymour 2011).

Analyses of regulation index and P_C were calculated with GraphPad Prism 5. All other statistical analyses were performed using the software package JMPpro 10.0.0. Notations in the form X ± Y refer to mean ± standard deviation, if not explicitly stated.

4. Results

4.1 Normoxic conditions

Respiration rates of larval and juvenile *T. capensis* (0.001-20.8 g *WM*, 4.3-21.0 mm standard length, *SL*) were measured in 58 experiments under normoxic conditions (100-70% O_2sat). Allometric relations of routine metabolic (*RMR*) and standard routine (*SRR*) rates showed an increase with body mass (Fig. 2, Table 1). Linear and quadratic regression fits on log-transformed data *RMR* and *SRR* to body mass had similar r^2-values. For both *RMR* and *SRR*, the linear models were preferentially selected based on the BIC and the AICc (Table 1). The weight exponent *b* increased significantly from *RMR* to *SRR* (Table 1; $F_{(1,116)} = 4.65$, p = 0.0331).
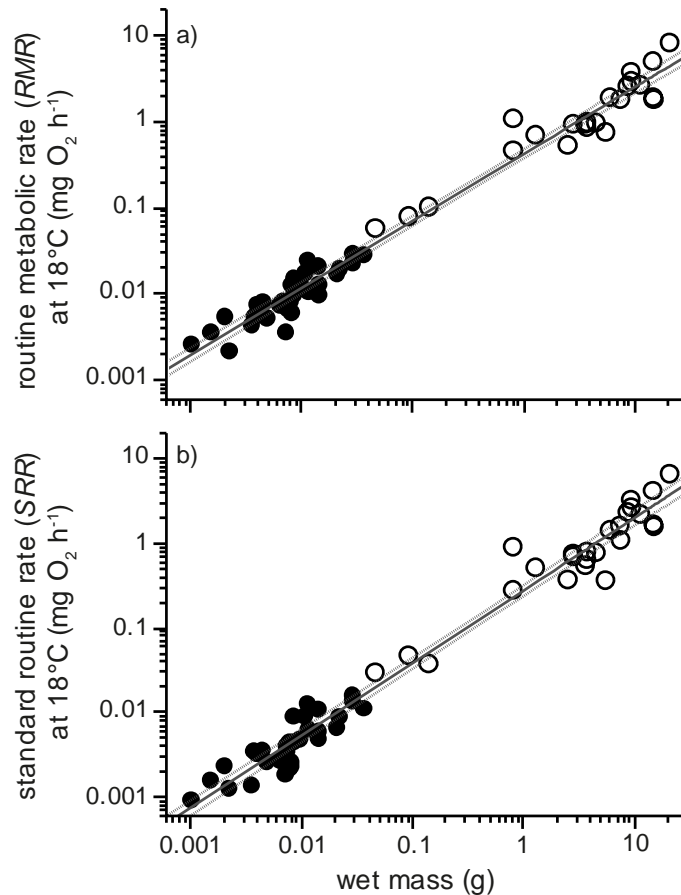
Fig. 2: Allometric relationship of a) routine (*RMR*) and b) standard routine (*SRR*) metabolic rates with wet mass during early ontogenetic development of *Trachurus capensis* at 18°C as power-law fits (y = a * x^b) and 95% confidence lines shown on logarithmic axes. Each symbol represents one single-fish-experiment (N = 58). Different markers indicate larvae (closed) and juveniles (open)
a) SRR = 0.275 *WM*$^{0.855}$ and
b) *RMR* = 0.418 *WM*$^{0.774}$

Table 1: Ontogenetic development of standard routine (*SRR*) and routine metabolic (*RMR*) rates of *T. capensis* larvae and juveniles (0.001-20.8 g wet mass, 43–1320 mm standard length, N = 58) at 18°C water temperature.

Metabolic rates (mg O_2 h^{-1})	model	*A*	*b*	*c*	N	No. of parameters	r^2	RMSE	AIC_c	AIC_c weight	BIC
RMR	linear	-0.8719 ±0.0600	0.7738 ±0.0152		58	2	0.98	0.37	54.12	0.76	59.86
	quadratic	-0.8564 ±0.0903	0.7675 ±0.0315	-0.0019 ±0.0084	58	3	0.98	0.38	56.38	0.24	63.86
SRR	linear	-1.2895 ±0.0728	0.8549 ±0.0185		58	2	0.98	0.45	76.91	0.76	82.64
	quadratic	-1.3086 ±0.1100	0.8627 ±0.0383	0.0024 ±0.0102	58	3	0.98	0.46	79.16	0.24	86.65

SRR and *RMR* defined as the 5% and the 50% quantile of the frequency distribution of all 10 min interval $M$$O_2$ in the respective respirometry experiment. For both measures linear (log *RMR* and log SRR = A + b log *WM*) and quadratic (log *RMR* and log SRR = A + b log *WM* + c log WM^2) fits of log-transformed data were compared. The parameters *A*, *b* and *c* are given as estimate ± standard error. RMSE = root mean square error; AIC_c = corrected Akaike information criterion; BIC = Bayesian information criterion
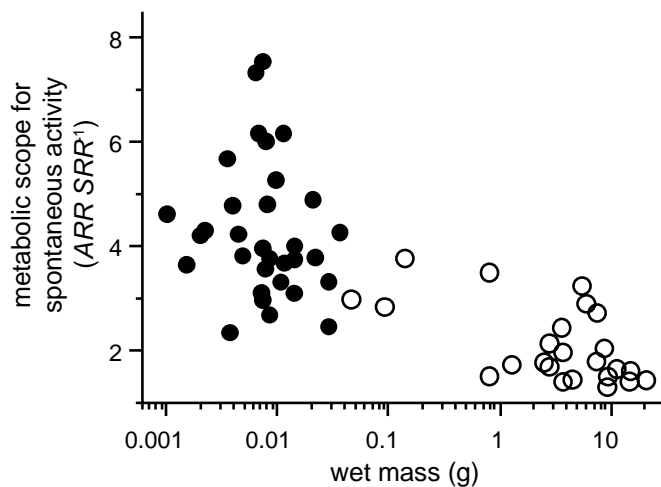
Fig. 3: Ontogenetic development of the "factorial aerobic scopes for spontaneous activity" (*ARR SRR*[-1]) in young *Trachurus capensis* at 18°C. Different markers indicate larvae (closed) and juveniles (open). Outlier at x = 0.008, y = 11.16 not shown

Scope for spontaneous activity (*ARR SRR*[-1]) was higher in larvae (<0.04 g *WM*, <15 mm *SL*) than in juveniles (Fig. 3; $\chi^2_{(1,58)}$ = 34.21, P<0.001).

RMR increased by a factor of 5.9 and *SRR* by a factor of 7.2 for body mass increments of one order of magnitude. Within the investigated size range of four orders of magnitude (0.001-10 g *WM*), *RMR* and *SRR* increased more than 1000- and 2000-fold, respectively (Table 2a).

Copepods are the main prey of *T. capensis* larvae and early juveniles (Geist et al. 2013). Based on their average carbon contents they split into three size groups (small, medium, large) (Table 2b). This led to marked differences in the estimated prey items required to satisfy the energy demand for *RMR* and *SRR* (Table 2a).

Table 2a: Daily routine metabolic (*RMR*) and standard routine (*SRR*) rates at five standard sizes of *T. capensis* larvae and juveniles at 18°C in oxygen, carbon and prey equivalents (individuals) of different copepod groups. Estimations based on the power function models of metabolic rate to body mass relationships. Conversions into carbon requirements were done according to Ikeda et al. (2000) assuming a lipid-based metabolism. Estimation of prey equivalents were calculated with values given in Table 2b

		0.001 g	0.01 g	0.1 g	1 g	10 g
RMR	mg O_2 d^{-1}	0.048	0.284	1.690	10.037	59.620
	mg C d^{-1}	0.013	0.076	0.450	2.674	15.885
	Small copepods (Cyclopoida, Harpacticoida, Calanoida small)	0.5-0.9	3-5	18-30	107-178	635-1059
	Calanoida medium		1.0	6	36	211
	Calanoida large				9	56
SRR	mg O_2 d^{-1}	0.018	0.129	0.923	6.610	47.323
	mg C d^{-1}	0.005	0.034	0.246	1.761	12.608
	Small copepods (Cyclopoida, Harpacticoida, Calanoida small)	0.2-0.3	1.3-2.4	10-17	69-125	490-892
	Calanoida medium		0.5	3	23	168
	Calanoida large				6	44

Table 2b: Estimated carbon content of average representatives (mg *DM*) of major copepod groups from the northern Benguela system derived from samples taken during the GENUS-research-project. Calanoida groups incorporate the following species: small: *Metridia lucens*, *Nannocalanus minor*; medium: *Calanoides carinatus*, *Aetideopsis carinata*; large: *Rhincalanus nasutus*, *Eucalanus hyalinus*, *Euchirella rostrata*, *Pleuromamma ziphias*. Data: [a]Schickenberg (2012) and [b]Schukat et al. (2013b)

Copepod group		*DM* (μg ind.$^{-1}$)	Carbon content (mg C ind.$^{-1}$)
Cyclopoida[a]	*Oncaea* sp.	35	0.015
	Oithona sp.	49	0.022
Harpacticoida[a]	*Microsetella* sp.	45	0.020
Calanoida[b]	small	63	0.025
	medium	155	0.075
	large	658	0.285

4.2 Responses to decreasing oxygen levels

T. capensis larvae (4.4-28.6 mg *WM*, N = 10) tolerated low oxygen levels and did not show a significant decrease in *RMR* until 29-20% O_2sat (ANOVA R, $F_{(5, 49)}$ = 0.50, P = 0.77). Juveniles (6.0-20.8 g *WM*, N = 7) were robust to very low oxygen saturations exposure, as expressed by a P_C *for RMR* = 13.23 ± 1.62% O_2sat., a P_C *for SRR* of 11.15 ± 1.66% O_2sat., and a *RI* of 0.78 ± 0.09 at 20°C (Fig. 4). Detailed calculation and results are given in Online Resource 2.
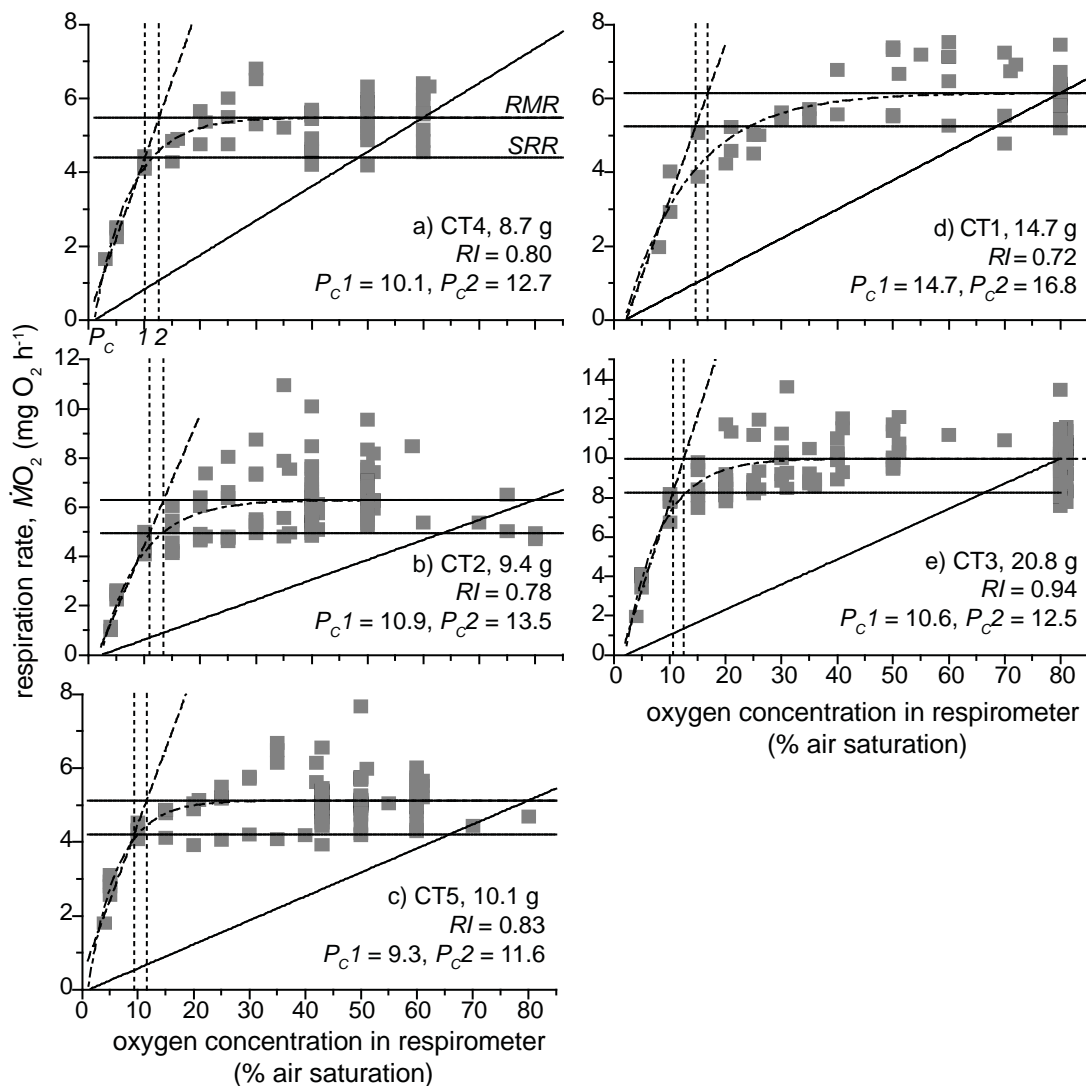
Fig. 4: Response of MO₂ (grey) to decreasing oxygen concentrations in five selected experiments with *T. capensis* juveniles at 20°C (a-f). In each plot, solid horizontal lines identify *RMR* and *SRR*, the broken line reflects the linear regression fit of MO₂ at low oxygen concentrations. The two vertical dotted lines mark P_C for *SRR* and P_C for *RMR* estimated as the x-values of the respective intersections. *RI for RMR* was calculated as the area enclosed by the slope of *RMR* at decreasing oxygen levels (broken-dotted line), the solid diagonal line reflecting a perfect oxyconformer

5. Discussion

5.1 Methodology

A number of methods exist to determine standard metabolic rate in fishes (Nelson and Chabot 2011) and possible constraints originating from different methods should be considered as source of variation in inter-study comparisons. For larvae, the classic extrapolation method to zero swimming speed is difficult to apply. Thus, defining *SMR* as a quantile (5-15%) derived from a frequency distribution of measurement intervals is a more promising approach. However, experiment durations <24 h and a short recovery time after catch in our experiments might have led to an overestimation of *SMR*. To account for this uncertainty and to minimize potential error, we named the standard rate *SRR* and chose the 5% quantile as threshold. At the upper end, we defined the 95% quantile of all measured intervals, including the initial ones affected by handling stress, as *ARR* (van den Thillart et al. 1994). For larvae, this is a good approximation to determine the scope for spontaneous activity (Rombough 1988). However, the decrease in aerobic scope from larvae to juveniles indicated that maximum metabolic rate was not satisfactorily reflected for juveniles.

5.2 Metabolic rates and energy demand under normoxia

5.2.1 Metabolic scaling exponent *b* during ontogeny

The allometric scaling exponent *b* of metabolic rate (*RMR* and *SMR*) to body mass relations is an important parameter for bioenergetics and physical modelling studies in fishes (Buckley et al. 2000, Hinrichsen et al. 2002). Winberg (1956) showed the validity of the general ¾-power-law for the scaling of metabolic rates with body mass (Kleiber 1932) for juvenile and adult fish. Thereafter, a change in *b* during ontogeny (from *b* ~1 in larvae to *b* ~0.75 in adults) was measured in several fish species and related to changes in e.g. growth efficiencies (Rombough 1988, Post and Lee 1996, Bochdansky and Leggett 2001, Moran and Wells 2007, Killen et al. 2007). Recently, an additional effect of a fish's lifestyle on *b* was proposed by Killen et al. (2010), i.e. pelagic fish species were more constrained by surface area limitations (*b*-values closer to 0.67-0.75) compared to benthic species (*b*-value close to 1). The exponent *b* for the *SRR* to body mass relation (0.855 ± 0.019) was higher in *T. capensis* early life stages than in *T. trachurus* adults (0.725 ± 0.003, Hermann and Enders 2000). Although b-values we obtained were not close to 1, this decrease in *b* from *T. capensis* larvae to *T. trachurus* adults is in accordance with the ontogenetic change of *b* reported in other species, considering their close taxonomic relationship (*T. capensis* was long regarded as a subspecies of *T. trachurus*). In contrast, *b* for the *RMR* - body mass relation was close to the ¾-power-law in *T. capensis* larvae and juveniles (0.774 ± 0.015, mean ± S.E.) and also in *T. trachurus* juveniles and adults

64

(0.752 ± 0.003, Herrmann and Enders 2000). This can be explained by the relatively continuous development from larval to juvenile stages in *T. capensis*, in contrast to the pronounced changes during metamorphosis occurring e.g. in flatfishes, and thus supporting the hypothesis of Killen et al. (2010).

5.2.2 Energy demand and resulting consequences for feeding ecology

Metabolic rates of *T. capensis* juveniles (5 and 10 g *WM*) were similar to those of *T. trachurus* from the North Sea (Hermann and Enders 2000), when standardised to the same temperature (Table 3). This indicates similar energy requirements for the two taxonomically closely related species. In comparison to another member of Carangidae, the yellowtail kingfish *Seriola lalandi (*Moran and Wells 2007), *T. capensis* had lower *RMR* throughout the investigated size range with the differences in values increasing over size (Table 3). Larvae of both species are morphologically similar (Olivar and Fortuno 1991). However adults of *S. lalandi* are regarded as more active species compared to members of *Trachurus* (Wardle et al. 1996, Herrmann and Enders 2000, Clark and Seymour 2006). Thus the observed differences in *RMR* may reflect these different life styles already at early life stages.

Comparison of metabolic rates of key fish species in the NBCE shows species-specific differences, which may explain different recruitment success rates. Since there are no previous studies on larval stages of fishes from the NBCE, we included studies on the juveniles of the bearded goby *Sufflogobius bibarbatus* from the NBCE (Utne-Palm et al. 2010), the Cape anchovy *Engraulis encrasicolus* from the southern Benguela Current ecosystem (James and Probyn 1989), and of the larval dover sole *Solea solea* from the North-Eastern Atlantic (McKenzie et al. 2008) as representative of Pleuronectiformes (Table 3) to compare our results on *T. capensis*. After standardization to 18°C and using the average Q_{10}-value of marine fishes (2.4, Clarke and Johnston 1999), *T. capensis* metabolic rates appeared to be high although different methodologies in the measurements were considered. The lower *RMR* of *S. bibarbatus* juveniles likely reflects their calmer lifestyle as bentho-pelagic species. Interesting is the difference between the juveniles of the two truly pelagic species, with a lower *RMR* in *E. encrasicolus* compared to *T. capensis*. A similar difference was found in a study in the California Current, where *Trachurus symmetricus* showed higher metabolic rates compared to *Engraulis mordax*, in this case measured in white and red muscles (Gordon 1972a, b). Thus, *T. capensis* appears to have a more active metabolism resulting in a comparatively high energy demand already at the larval stage, as can be estimated from the higher *RMR* values of unfed *T. capensis* larvae compared to fed *S. solea* (Table 3). In a comparison of larvae from pelagic fish species from Japan, Masuda (2011) distinguished two strategies in fish larvae. One group is characterised by passive predator avoidance through a transparent and less conspicuous body

Table 3: Interspecific comparison of routine (*RMR*) and standard (*SRR and SMR*) metabolic rates (mg O$_2$ h^{-1}) of *T. capensis* with taxonomically related species and species representing functional groups of the northern Benguela fish community (* = Benguela species) at six standard sizes (g wet mass). A factor 1.429 was applied to convert from ml O$_2$ to mg O$_2$, and a factor of 6 was applied to convert from dry- to wet mass. Metabolic rates are given for original temperatures and standardised to 18°C (18s) with a Q$_{10}$ of 2.2 for *T. trachurus* (Shulman and Love 1999) and 2.4 for the other other species (Clarke and Johnston 1999). [1] =estimations based on allometric fits, [2] =estimations based on mass specific metabolic rates in the same size range

species	T (°C)		0.001 g	0.01 g	0.1 g	1 g	5 g	10 g	reference
Trachurus capensis*	**18**	**RMR**	2.00 E-3	1.19 E-2	7.04 E-2	4.18 E-1	1.45	2.48	**this study[1]**
	18	**SRR**	7.50 E-4	5.37 E-3	3.85 E-2	2.75 E-1	1.09	1.97	
Trachurus trachurus	13	RMR	–	–	–	–	0.93	1.56	Herrmann and Enders (2000)[1]
	18s	RMR	–	–	–	–	1.38	2.31	
	13	SMR	–	–	–	–	0.76	1.28	
	18s	SMR	–	–	–	–	1.13	1.90	
Seriola lalandi	20	RMR	3.18 E-2	3.95 E-2	1.16 E-1	8.79 E-1	4.24	8.73	Moran and Wells (2007)[1]
	18s	RMR	2.67 E-2	3.32 E-2	9.74 E-2	7.38 E-1	3.56	7.33	
*Sufflogobius bibarbatus***	12	RMR					0.35-0.45	0.7-0.9	Utne-Palm et al. (2010)[2]
	18s	RMR					0.59-0.76	1.18-1.52	
*Engraulis encrasicolus***	16	RMR					0.56	1.11	James and Probyn (1989)[2]
	18s	RMR	–	–	–	–	0.67	1.32	
	16	SMR					0.30	0.60	
	18s	SMR					0.36	0.72	
Solea solea	19	RMR	5.18 E-04	3.31 E-3					McKenzie et al. (2008)[2]
	18s	RMR	4.75 E-04	3.03 E-3					

66

and slow development of swimming potential, such as in *Engraulis japonicus*. The other strategy is characterised by having a more conspicuous robust body and higher agility expressed by a faster development of cruise- or burst- swimming capacities, e.g. *Scomber japonicus* and *Trachurus japonicus* (Masuda 2009, 2011). If this difference is genera-specific it can explain the observed high metabolic rates and high numbers of prey requirements of *T. capensis*. A high burst swimming capacity of *T. capensis* larvae, which probably led to the high scope for spontaneous activity in some of the larval experiments, likely ensures a high feeding success. Indeed, a parallel study on the feeding ecology of *T. capensis* larvae and juveniles from the NBCE showed a high feeding incidence and a high voracity (Geist et al. 2013). The prey requirements in units of copepods estimated for *T. capensis* juveniles appear too high to be met in nature. It can be argued that at this size, *T. capensis* needs to start feeding on larger organisms such as euphausiids to satisfy its energy demands. Euphausiids are known to be an important diet component in adults (Pillar and Barange 1998).

5.3 Hypoxia tolerance

5.3.1 Response of metabolic rates to decreased oxygen levels in larvae

During the past ten years, increasing abundances of *T. capensis* larvae have been observed in ichthyoplankton catches in the NBCE, whereas numbers of the formerly dominant pelagic species were low (Werner Ekau unpub. data). Kreiner et al. (2009) suggested an avoidance of oxygen saturation levels of <2.5 mL L^{-1} by *S. sagax* and *E. encrasicolus* larvae. Thus hypoxia tolerance of *T. capensis* may explain the observed differences in larval abundance. And indeed, *T. capensis* larvae tolerated oxygen saturations below 2.5 mL L^{-1} ≈ 50% O$_2$sat, expressed by their constant *RMR* down to ~30% O$_2$sat. Assuming that clupeiform larvae are less hypoxia tolerant, *T. capensis* is likely advantaged under the present environmental conditions of shoaling of hypoxic zones as their recruitment success is potentially less affected. A hypothetical mechanism can be deduced from Stenevik et al. (2003), who report that fish larvae in the NBCE can actively prolong their retention time in coastal waters with high food densities via vertical migration into onshore currents below the Ekman layer. High hypoxia tolerance of *T. capensis* larvae would allow them to use this retention mechanism even when hypoxic zones extend to shallow water layers, as frequently observed especially during the main spawning period in summer and autumn (Bartholomae and van der Plas 2007, Hutchings et al. 2009, Ekau et al. 2010). To understand the underlying mechanisms in more detail, information on threshold levels, such as P_C and lethal oxygen concentrations, are required for larvae. Knowledge of gill and haemoglobin development (Rombough 1988) or behavioural responses (Chapman and McKenzie 2009) during the larval phase will provide additional information.

5.3.2 Response of metabolic rates to hypoxia in juveniles

Small pelagic fishes are thought to be intolerant to hypoxic conditions as inferred from their depth distribution and behavioural responses (Moss and McFarland 1970, Bertrand et al. 2006, Taylor et al. 2007, Ludsin et al. 2009, Bertrand et al. 2008, Herbert et al. 2012). However the metabolic responses of upwelling species have not been investigated to present. In contrast to this generally accepted hypothesis, we showed that the metabolism of *T. capensis* juveniles tolerates extremely low hypoxic conditions. The critical oxygen saturation of *T. capensis* juveniles (P_C for SRR = 11% O_2sat at 20°C) was even lower than in some demersal fishes, which probably experience hypoxia more frequently e.g. *S. solea*: P_C for SMR = 27-32% at 17°C (Coutourier et al. 2007) and P_C for SMR = 20% at 19°C (van den Thillart et al. 1994), and *Paralichthys dentatus* with P_C for SMR = 27% at 22°C (Capossela et al. 2012). However, recorded P_C of *T. capensis* juveniles is still higher than that of e.g. *S. bibarbatus* (5.5 ± 0.3 % at 12°C), which is probably one of the best hypoxia-adapted fish species in the northern Benguela system (Utne-Palm let al. 2010). In addition, the difference between P_C for SMR and for RMR defines the oxygen concentrations of a restricted aerobic scope, which can lead to elevated predation risk and lower growth rates. In *T. capensis* juveniles this difference was only 2% O_2sat, further indicating their high hypoxia tolerance. As an ecological consequence, *T. capensis* juveniles should be able to briefly enter hypoxic zones and exploit hiding food resources, similar to a behaviour exhibited by *Gadus morhua* from the Baltic Sea (Neuenfeld et al. 2009). Potential prey organisms of *T. capensis,* such as some larger copepod and krill species, are physiologically adapted to enter hypoxic waters and inhabit the OMZ in the NBCE (Auel and Verheye 2007, Schukat et al. 2013b, Werner and Buchholz 2013). The *RI* of *T. capensis* juveniles (0.78 ± 0.09 at 20°C) is similar to *Euphausia hanseni* (0.74 ± 0.16 at 20°C, Werner 2012); a krill species that regularly enters hypoxic zones in the northern Benguela. This indicates that the predator species *T. capensis* has developed similar physiological adaptations to hypoxic conditions as its potential prey species.

5.4. Conclusion

We demonstrated that early life stages of *T. capensis* are characterised by high metabolic rates, allowing for an agile behaviour and consequently causing a high energy demand. We also showed that *T. capensis* tolerate hypoxic conditions both as larvae and juveniles, which probably constitutes an advantage compared to other small pelagic species under the observed shoaling of hypoxic zones in the NBCE.

6. Acknowledgements

7. Ethical standards declaration

Hereby the authors declare that the conducted experiments complied with the current laws of the country in which they were performed (South Africa, Germany, and Namibia).

8. References

Auel H, Verheye HM (2007) Hypoxia tolerance in the copepod *Calanoides carinatus* and the effect of an intermediate oxygen minimum layer on copepod vertical distribution in the northern Benguela Current upwelling system and the Angola-Benguela Front. J Exp Mar Biol Ecol 352:234-243

Bakun A (2010) Linking climate to population variability in marine ecosystems characterized by non-simple dynamics: conceptual templates and schematic constructs. J Mar Syst 79:361-373

Bakun A, Babcock EA, Lluch-Cota SE, Santora C, Salvadeo CJ (2010a) Issues of ecosystem-based management of forage fisheries in "open" non-stationary ecosystems: the example of the sardine fishery in the Gulf of California. Rev Fish Biol Fish 20: 9-29

Bakun A, Field DB, Redondo-Rodriguez A, Weeks SJ (2010b) Greenhouse gas, upwelling-favorable winds, and the future of coastal ocean upwelling ecosystems. Glob Change Biol 16:1213-1228

Bartholomae CH, van der Plas AK (2007) Towards the development of environmental indices for the Namibian shelf, with particular reference to fisheries management. Afr J Mar Sci 29:25-35

Behrens JW, Steffensen JF (2007) The effect of hypoxia on behavioural and physiological aspects of lesser sandeel, Ammodytes tobianus (Linnaeus, 1785). Mar Biol 150:1365-1377

Bertrand A, Barbieri MA, Gerlotto F, Leiva F, Cordova J (2006) Determinism and plasticity of fish schooling behaviour as exemplified by the South Pacific jack mackerel *Trachurus murphyi*. Mar Ecol Prog Ser 311:145-156

Bertrand A, Gerlotto F, Bertrand S, Gutierrez M, Alza L, Chipollini A, Díaz E, Espinoza P, Ledesma J, Quesquén R, Peraltilla S, Chavez FP (2008) Schooling behaviour and environmental forcing in relation to anchoveta distribution: An analysis across multiple spatial scales. Prog Oceanogr 79:264-277

Bochdansky AB, Leggett WC (2001) Winberg revisited: convergence of routine metabolism in larval and juvenile fish. Can J Fish Aquat Sci 58:220–230

Buckley LJ, Lough R, Peck MA, Werner FE (2000) Comment: Larval Atlantic cod and haddock growth models, metabolism, ingestion, and temperature effects. Can J Fish Aquat Sci 57:1957-1960

Capossela KM, Brill RW, Fabrizio MC, Bushnell PG (2012) Metabolic and cardiorespiratory responses of summer flounder *Paralichthys dentatus* to hypoxia at two temperatures. J Fish Biol 81:1043-1058

Chapman LJ, McKenzie DJ (2009) Chapter 2 Behavioral responses and ecological consequences. In: Richards JG, Farell AP, Brauner CJ (eds) Fish Physiology Series 27, Hypoxia. Academic Press, Amsterdam, pp 25-77

Chekunova VI, Naumov AG (1978) Energy metabolism of the horse mackerel, *Trachurus murphyi*, and the butterfish, *Stromateus maculatus*, from the south-eastern part of the Pacific Ocean. J Ichthyol 18:468-474

Clark TD, Seymour RS (2006) Cardiorespiratory physiology and swimming energetics of a high-energy-demand teleost, the yellowtail kingfish (*Seriola lalandi*). J Exp Biol 209:3940-3951

Clarke A, Johnston NM (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. J Anim Ecol 68:893-905

Couturier CS, Rouault A, McKenzie D, Galois R, Robert S, Joassard L, Claireaux G (2007) Effects of water viscosity upon ventilation and metabolism of a flatfish, the common sole *Solea solea* (L.). Mar Biol 152:803-814

Cury P, Shannon L (2004) Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. Prog Oceanogr 60:223-243

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26: 249-293

Daoud D, Chabot D, Audet C, Lambert Y (2007) Temperature induced variation in oxygen consumption of juvenile and adult stages of the northern shrimp, *Pandalus borealis*. J Exp Mar Biol Ecol 347:30–40

Drinkwater KF, Beaugrand G, Kaeriyama M, Kim S, Ottersen G, Perry RI, Pörtner HO, Polovina JJ, Takasuka A (2010) On the processes linking climate to ecosystem changes. J Mar Syst 79:374–388

Dupont-Prinet A, Chatain B, Grima L, Vandeputte M, Claireaux G, McKenzie DJ (2010) Physiological mechanisms underlying a trade-off between growth rate and tolerance of feed deprivation in the European sea bass (*Dicentrarchus labrax*). J Exp Biol 213:1143–1152

Ekau W, Verheye H (2005) Influence of oceanographic fronts and low oxygen on the distribution of ichthyoplankton in the Benguela and southern Angola Currents. Afr J Mar Sci 27 (3):629–639

Ekau W, Auel H, Pörtner H-O, Gilbert D (2010) Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). Biogeosciences 7:1669–1699

Ekau W, Geist S, von Waldthausen C, Verheye H (2012) 5.7 Ichthyoplankton, fish studies and copepod studies (GENUS SP-4) In: Lahajnar, N (ed) RV MARIA S. MERIAN Cruise Report MSM17/L3, Geochemistry and Ecology of the Namibian Upwelling System 2011. DFG Senatskommission für Ozeanographie, Bremen, pp 28-32

FAO (2012) The state of world fisheries and aquaculture 2012. Rome

Flynn BA, Richardson AJ, Brierley AS, Boyer DC, Axelsen BE, Scott L, Moroff NE, Kainge PI Tjizoo MB, Gibbons MJ (2012) Temporal and spatial patterns in the abundance of jellyfish in the northern Benguela upwelling ecosystem and their link to thwarted pelagic fishery recovery. Afr J Mar Sci 34:131-146

Fry FEJ (1971) 1 The effect of environmental factors on the physiology of fish. In: Hoar WS, Randall DJ (eds) Fish Physiology 6. Academic Press, New York, pp 1-98

García HE, Gordon LI (1992) Oxygen solubility in seawater: Better fitting equations. Limnol Oceanogr 37:1307-1312

Geist SJ, Kunzmann A, Verheye HM, Ekau W (2013) Early life history traits determine success of Cape horse mackerel, *Trachurus capensis* Castelnau, 1861, in the degraded northern Benguela upwelling ecosystem off Namibia ICES J Mar Sci: (under review)

Gilly WF, Beman JM, Litvin SY, Robison BH (2013) Oceanographic and Biological Effects of Shoaling of the Oxygen Minimum Zone. Annu Rev Mar Sci 5:393-420

Gordon, MS (1972a) Comparative studies on the metabolism of shallow-water and deep-sea marine fishes I. White-muscle metabolism in shallow-water fishes. Mar Biol 13:222-237

Gordon, MS (1972b) Comparative studies on the metabolism of shallow-water and deep-sea marine fishes II. Red-muscle metabolism in shallow-water fishes. Mar Biol 15:246-250

Grantham B, Chan F, Nielsen K, Fox D, Barth J, Huyer A, Lubchenco J, Menge B (2004) Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. Nature 429:749-754

Herbert NA, Goodman M, Kunzmann A (2012) The low O_2 avoidance strategy of the Cape silverside *Atherina breviceps* (Teleostei). Mar Freshw Behav Phy 45:199-208

Herrmann J-P, Enders EC (2000) Effect of body size on the standard metabolism of horse mackerel. J Fish Biol 57:746-760

Hinrichsen HH, Möllmann C, Voss R, Köster FW, Kornilovs G (2002) Biophysical modeling of larval Baltic cod (*Gadus morhua*) growth and survival. Can J Fish Aquat Sci 59:1858-1873

Hjort J (1914) Fluctuations in the great fisheries of northern Europe. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 20:1-228

Houde ED (1987) Fish early life dynamics and recruitment variability. Am Fish Soc Symp 2:17-29

Houde ED (2008) Emerging from Hjort's shadow. J Northw Atl Fish Sci 41:53-70

Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM, Verheye HM, Bartholomae CH, van der Plas AK, Louw D, Kreiner A, Ostrowski M (2009) The Benguela Current: an ecosystem of four components. Prog Oceanogr 83:15-32

Ikeda T (1970) Relationship between respiration rate and body size in marine plankton animals as a function of the temperature of habitat. Bull Fac Fish Hokkaido Univ 21(2):91-112

Ikeda T, Torres JJ, Hernández-León S, Geiger SP (2000) 10 Metabolism. In: Harris RP, Wiebe PH, Lenz J, Skjoldal HR, Huntley M (eds) ICES zooplankton methodology manual. Academic Press, London, pp 455-532

James AG, Probyn T (1989) The relationship between respiration rate, swimming speed and feeding behavior in the cape anchovy *Engraulis capensis* Gilchrist. J Exp Mar Biol Ecol 131:81-100

Killen SS, Costa I, Brown JA, Gamperl AK (2007) Little left in the tank: metabolic scaling in marine teleosts and its implications for aerobic scope. P Roy Soc Lond B Bio 274:431-438

Killen SS, Atkinson D, Glazier DS (2010) The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. Ecol Letters 13:184-193

Kleiber M (1932). Body size and metabolism. Hilgardia 6: 315-351

Kreiner A, Stenevik EK, Ekau W (2009) Sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* larvae avoid regions with low dissolved oxygen concentration in the northern Benguela Current system. J Fish Biol 74:270-277

Levin LA, Ekau W, Gooday AJ, Jorissen F, Middelburg JJ, Naqvi SWA, Neira C, Rabalais NN, Zhang J (2009) Effects of natural and human-induced hypoxia on coastal benthos. Biogeosciences 6:2063-2098

Ludsin SA, Zhang X, Brandt SB, Roman MR, Boicourt WC, Mason DM, Costantini M (2009) Hypoxia-avoidance by planktivorous fish in Chesapeake Bay: Implications for food web interactions and fish recruitment. J Exp Mar Biol Ecol 381:121-131

Masuda R (2009) Behavioral ontogeny of marine pelagic fishes with the implications for the sustainable management of fisheries resources. Aqua-Bio Science Monographs 2:1-56

Masuda R (2011) Ontogeny of swimming speed, schooling behaviour and jellyfish avoidance by Japanese anchovy *Engraulis japonicus*. J Fish Biol 78:1323-1335

McKenzie DJ, Lund I, Pedersen PB (2008) Essential fatty acids influence metabolic rate and tolerance of hypoxia in Dover sole (*Solea solea*) larvae and juveniles. Mar Biol 154:1041-1051

Moran D, Wells RMG (2007) Ontogenetic scaling of fish metabolism in the mouse-to-elephant mass magnitude range. Comp Biochem Phys A 148:611-620

Moss SA, McFarland WN (1970) The influence of dissolved oxygen and carbon dioxide on fish schooling behavior. Mar Biol 5:100-107

Mueller CA, Seymour RS (2011) The Regulation Index: A new method for sssessing the relationship between oxygen consumption and environmental oxygen. Physiol Biochem Zool 84:522-532

Neill WH, Miller JM, Van Der Veer HW, Winemiller KO (1994) Ecophysiology of marine fish recruitment: a conceptual framework for understanding interannual variability. Neth J Sea Res 32:135-152

Nelson G, Chabot D (2011) General energy metabolism. In: Farrell AP (ed in chief) Encyclopedia of fish physiology, Vol. 3. Academic Press, London, pp 1566-1572

Neuenfeldt S, Andersen KH, Hinrichsen HH (2009) Some Atlantic cod *Gadus morhua* in the Baltic Sea visit hypoxic water briefly but often. J Fish Biol 75:290-294

Olivar MP, Fortuño JM (1991) Guide to ichthyoplankton of the southeast Atlantic (Benguela Current region). Sci Mar 55:1-383

Pillar S, Barangé M (1998) Feeding habits, daily ration and vertical migration of the Cape horse mackerel off South Africa. S Afr J Mar Sci 19:263-274

Pörtner, H-O (2010) Oxygen- and capacity limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. J Exp Biol 213:881-893

Post J, Lee JA (1996) Metabolic ontogeny of teleost fishes. Can J Fish Aquat Sci 53:910-923

Rombough PJ (1988) 2 Respiratory gas exchange, aerobic metabolism, and effects of hypoxia during early life. In: Hoar WS, Randall DJ (eds) Fish physiology Vol. XI The physiology of developing fish, Part A: Eggs and larvae. Academic Press, Burlington, pp 59-161

Rosa R, Seibel BA (2010) Metabolic physiology of the Humboldt squid, *Dosidicus gigas*: Implications for vertical migration in a pronounced oxygen minimum zone. Prog Oceanogr 86:72-80

Schukat A, Auel H, Teuber L, Lahajnar N, Hagen W (2013a) Complex trophic interactions of calanoid copepods in the Benguela upwelling system. J Sea Res (in press). doi: 10.1016/j.seares.2013.04.01

Schukat A, Teuber L, Hagen W, Wasmund N, Auel H (2013b) Energetics and carbon budgets of dominant calanoid copepods in the northern Benguela upwelling system. Journal of Experimental Marine Biology and Ecology 442:1-9

Schurmann H, Steffensen JF (1997) Effects of temperature, hypoxia and activity on the metabolism of juvenile Atlantic cod. J Fish Biol 50:1166-1180

Shulman GE, Love RM (1999) Advances in marine biology Vol. 36, The biochemical ecology of marine fishes. Academic Press, London

Stenevik, EK, Skogen M, Sundby S, Boyer D (2003) The effect of vertical and horizontal distribution on retention of sardine (*Sardinops sagax*) larvae in the northern Benguela - observations and modelling. Fish Oceanogr 12 (3):185-200

Taylor JC, Rand PS, Jenkins J (2007) Swimming behavior of juvenile anchovies (*Anchoa* spp.) in an episodically hypoxic estuary: implications for individual energetics and trophic dynamics. Mar Biol 152:939-957

Utne-Palm AC, Salvanes AGV, Currie B, Kaartvedt S, Nilsson GE, Braithwaite VA, Stecyk JAW, Hundt M, van der Bank M, Flynn B, Sandvik GK, Klevjer TA, Sweetman AK, Brüchert V, Pittmann K, Peard KR, Lunde IG, Strandabø RAU, Gibbons MJ (2010) Trophic structure and community stability in an overfished ecosystem. Science 329:333-336

van den Thillart G, DallaVia J, Vitali G, Cortesi P (1994) Influence of long-term hypoxia exposure on the energy metabolism of *Solea solea* I. Critical O_2 levels for aerobic and anaerobic metabolism. Mar Ecol Prog Ser 104:109-117

van der Lingen CD, Shannon LJ, Cury P, Kreiner A, Moloney CL, Roux J-P, Vaz-Velho F (2006) 8 Resource and ecosystem variability, including regime shifts, in the Benguela Current system. In: Shannon V, Hempel G, Malanotte-Rizzoli P, Moloney C, Woods J (eds) Large Marine Ecosystems Series 14, Benguela: Predicting a large marine ecosystem. Elsevier, Amsterdam, pp 147-184

Wardle CS, Soofiani NM, O'Neill FGO, Glass CW, Johnstone, ADF (1996) Measurements of aerobic metabolism of a school of horse mackerel at different swimming speeds. J Fish Biol 49:854-862

Werner T (2012) Trophic positioning, diel vertical migration behavior and physiological traits in euphausiid species of the Namibian Upwelling system. Dissertation, Universität Hamburg

Werner T, Buchholz F (2013) Diel vertical migration behaviour in Euphausiids of the northern Benguela current: seasonal adaptations to food availability and strong gradients of temperature and oxygen. Journal of Plankton Research 35(4):792-812

Winberg GG (1956) Rate of metabolism and food requirements of fishes. Belorussian State University, Minsk (translated from Russian by Fish Res Bd Can Transl Ser 194:1-202, 1960)

Yeager DP, Ultsch GR (1989) Physiological regulation and conformation: a BASIC program for the determination of critical points. Physiol Zool 62(4):888-907

Zimmermann C, Kunzmann A (2001) Baseline respiration and spontaneous activity of sluggish marine tropical fish of the family Scorpaenidae. Mar Ecol Prog Ser 219:229-239

Online Resource 1: Overview of the three different intermittent flow setups. Equipment used and main parameters of respective normoxia experiments (100-70% O$_2$sat)

setup		small	medium	large		
respirometer volume	(L)	0.05	0.31	3.0		
oxygen probe		PreSens Microx FTC	PreSens Fibox DP	Hamilton Visiferm DO120		
pump		Ismatec Reglo Digital MS-4/6	Heidolph PD5201 C8	Ismatec Reglo Z		
Tygon tubing Ø (cm)		0.21	0.64	0.95		
fish	wet mass range (g)	0.008-0.036	0.09-0.21	MSM: 0.8-7.4	ZMT: 2.8-15.0	MRA: 6.0-20.8
Number of experiments		14	3	MSM: 9	ZMT: 7	MRA: 6
temperature range	(°C)	16.7-20.8	17.4-18.8	MSM: 17.2-17.9	ZMT: 18.6-20.1	MRA: 19.5-20.4
duration range	(min)	450-1484	1086-2070	MSM: 463-1359	ZMT: 996-1473	MRA: 299-922

Online Resource 2: Model parameters to calculate *RI* and *Pc*

1) decay models: Y=(Y0 - Plateau)*exp(-K*X) + Plateau

exp. Nr.	Y0	SE Y0	plateau	K	SE K	df	r^2	S S	Sy.x = sqrt (SS df^{-1})
ct1	-1.059	1.811	6.155	0.0855	0.0183	45	0.63	23.84	0.73
ct2	-2.262	1.539	6.300	0.1396	0.0264	109	0.51	151.20	1.18
ct3	-3.663	2.183	9.995	0.1594	0.0235	122	0.58	161.40	1.15
ct4	-0.9276	1.109	5.490	0.1554	0.0291	48	0.72	16.07	0.58
ct5	-1.108	1.744	5.130	0.1917	0.0481	98	0.48	35.59	0.60
ct6	-1		2.140	0.1432	0.0221	13	0.55	1.08	0.29
ct7	0		7.960	0.1235	0.0034	154	0.69	47.66	0.56

2) regulation index (RI) = ("area model"-"area conformer") "area conformer"$^{-1}$

exp. Nr.	area model	area conformer	area regulator	RI
ct1	414.5	240.5	481	0.723
ct2	437.1	245.1	490.2	0.783
ct3	754.9	390	780	0.936
ct4	292	161.9	323.9	0.804
ct5	370.1	202.6	405.2	0.827
ct6	143.3	82.74	165.5	0.732
ct7	326.2	199	676.6	0.639

3) calculation of P_c step 1: linear regressions through x-axis-intersection of decay models and MO_2s at pO_2-≤ 10% saturation y = e + fx

exp. Nr.	e	f	N	r^2
ct1	-0.8970 ± 0.8281	0.4196 ± 0.1013	4	0.896
ct2	-0.8067 ± 0.4551	0.5282 ± 0.06361	10	0.896
ct3	-1.1030 ± 0.5312	0.8863 ± 0.07164	9	0.956
ct4	0.0996 ± 0.2380	0.4263 ± 0.03431	8	0.963
ct5	0.3853 ± 0.3502	0.4095 ± 0.04870	10	0.898
ct6	-0.5010 ± 0.2779	0.2218 ± 0.04023	3	0.968
ct7	-0.03891 ± 0.2702	0.6106 ± 0.02879	21	0.960

4) calculation of critical oxygen partial pressure for *RMR* (P_C2) and *SRR* (P_C1) derived from respective MO_2 > 30% O_2 saturationa as the x-intersection of linear regression model (step3) and *RMR* or *SRR*: P_C = ("*RMR* or *SRR*" - "e") "f"$^{-1}$

exp. Nr.	*WM* (g)	*RMR* (mg O_2 h^{-1})	P_C2 (% O_2sat.)	SRR (mg O_2 h^{-1})	P_C1 (% O_2sat.)
ct1	14.7	6.16	16.81	5.25	14.65
ct2	9.4	6.30	13.45	4.96	10.93
ct3	20.8	10.00	12.52	8.25	10.55
ct4	8.7	5.49	12.65	4.40	10.09
ct5	10.1	5.13	11.59	4.21	9.34
ct6	6.0	2.14	11.91	1.75	10.16
ct7	6.2	7.96	13.67	7.12	12.3

<u>Chapter II</u>

Larval feeding ecology of clupeoid fish in the degraded northern Benguela

Current upwelling system and its implications for stock recruitment

processes

GEIST SJ[1], corresponding author

simon.geist@zmt-bremen.de

KUNZMANN A[1]

andreas.kunzmann@zmt-bremen.de

VERHEYE HM[2]

hverheye@environment.gov.za

EKAU W[1]

werner.ekau@zmt-bremen.de

[1] *Leibniz Center for Tropical Marine Biology, ZMT*

Fahrenheitstr. 6

D-28359 Bremen

[2] *Oceans and Coasts Research, Department of Environmental Affairs,*

and Marine Research Institute, University of Cape Town

- Cape Town, South Africa

ABSTRACT

Clupeoid fish are important members of most high-productive marine ecosystems in the world, but for the last three decades the northern Benguela Current has been an exception with persistently low stocks of these formerly dominating species. To improve our understanding of underlying factors influencing their recruitment success, we investigated the spatial distribution, feeding ecology, growth rates and nutritional conditions of *Sardinops sagax, Engraulis encrasicolus* and *Sardinella aurita* larvae in relation to ambient conditions (water temperature, plankton density and composition). Compared to *S. sagax, E. encrasicolus* and the tropical species *S. aurita* occurred at a wider temperature range shifted towards warmer temperatures. This may infer an advantage in times of frequent warm water events, caused by low upwelling intensities and/or pole-ward warm-water intrusions from the Angola Current. All three species were rather similar in their feeding ecology by preferring developmental stages of copepods grown in a diatom-based food web. At high larval densities, this might lead to food competition that manifests in poor nutritional conditions and lower growth rates likely leading to enhanced larval mortality and reduced recruitment success.

KEYWORDS

INTRODUCTION

Small pelagic fish are important in terms of biomass in many shelf sea ecosystems, occupying a key position in their food webs (Pikitch *et al.*, 2012). Members of the Clupeoidea, typically anchovy and sardine species, alternately dominate small pelagic fish communities of eastern boundary current upwelling ecosystems in abundance and biomass, which makes them key components in the food web and attractive for fisheries (Cury *et al.*, 2000). These species naturally show large fluctuations in stock size (Schwartzlose *et al.*, 1999) and long-term trends are associated with changes in the environmental properties of the ecosystems (Houde, 1987). Temperature (Takasuka *et al.*, 2008) and oxygen concentration (Bertrand *et al.*, 2011) are regarded as the key abiotic triggers of these regime shifts with potential direct impacts on fish via changes in growth and survival. Environmental changes may also alter the food web structure and functioning as well as the availability of prey promoting either sardine or anchovy species, which differ in their feeding ecology (van der Lingen *et al.*, 2006). The interaction of temperature and food availability as important factors for spawning success of clupeoids has been shown in modelling studies for e.g. the southern Benguela (Richardson *et al.*, 1998; Mullon *et al.*, 2003). Environmental factors appeared to have a higher influence on regime shifts than fishing impact (Shannon *et al.*, 2004).

The Benguela Current in the South-East Atlantic is one of four major eastern boundary upwelling systems and is divided into separated northern and southern subsystems (Duncombe Rae, 2005). The northern subsystem, ~16°S to ~27°S off Namibia, displays seasonality in upwelling activity, with lower intensity during austral summer (Bartholomae and van der Plas, 2007). It used to be dominated by sardines in the middle of the last century until sardine and subsequently anchovy stocks decreased around the 1970s, due to the combined effect of unsustainable fishery practices and detrimental environmental changes (Cury and Shannon, 2004; Bakun and Weeks, 2006). Since then clupeoid stocks have remained persistently low (Heymans *et al.*, 2004, Kreiner *et al.*, 2011), although this species group possesses a high recovery potential compared to others (Hutchings, 2000). Today, the northern Benguela is perceived as a warning example for possible future developments of upwelling ecosystems with the causes for its long-lasting degradation largely remaining unanswered (Bakun *et al.*, 2010).

The recovery potential of a fish population depends on a variety of factors (Hutchings and Reynolds, 2004) with recruitment processes forming a bottleneck, because early life history stages are particularly vulnerable to environmental fluctuations (reviewed by Bakun, 2010). For instance, increased temperatures and lowered oxygen concentrations presumably constrain the spawning habitat of small pelagic fish and impact on the development and survival of their

early life history stages in the northern Benguela ecosystem (NBCE) (Ekau and Verheye, 2005; Kreiner *et al.*, 2011). Temperature preference of the NBCE sardine population evaluated by recruitment strength appears to have changed in the period from 1961 to 1999, being negatively linked to sea surface temperature (*SST*) and positively linked to wind stress from the mid-1980s onwards (Daskalov *et al.*, 2003).

Furthermore, differences in the feeding ecology of adult sardine and anchovy are regarded as important triggers for regime shifts (van der Lingen *et al.*, 2006). In larval stages, feeding success is crucial for individual survival and growth and for recruitment success; it is influenced by the availability and composition of potential prey organisms (Lasker, 1978; Cushing, 1996). Comparative studies from the California (Arthur, 1976) and the Humboldt Current systems (Muck *et al.*, 1989) have shown that food preferences of larvae of the two species diverge from a size of about 9 mm with anchovies feeding on larger items than sardines. Given that interspecific differences in the feeding ecology exist already at the larval stage, a dominance of larger copepods under cooler, active upwelling conditions and a predominance of smaller prey items under warmer, quiescent conditions could link the effects of temperature and trophic ecology to differential recruitment success of clupeoid species (Cole 1999). However, to date no detailed study on the feeding ecology of clupeoid larvae has been done in the Benguela Current (van der Lingen *et al.*, 2009) and the influence of temperature remains controversial (Shannon *et al.*, 1988; Cole, 1999; Tjizoo, 2008; Kreiner *et al.*, 2011).

One of the aims of GENUS (Geochemistry and Biology of the Namibian Upwelling System), a Germany-funded interdisciplinary research project focusing on the northern Benguela, is to understand and quantify current energy and matter fluxes in the NBCE. Forming an integral part of GENUS, this study investigates the larval ecology of sardine, *Sardinops sagax* (Jenyns, 1842), anchovy, *Engraulis encrasicolus* (L., 1758), and round sardinella, *Sardinella aurita* Valenciennes, 1847, to understand how environmental conditions influence recruitment success of formerly dominating fish species in the severely degraded upwelling system of the NBCE. Based on the outlined theories and with a focus on potential interspecific differences, we investigate (1) their feeding ecology by combining three methodological approaches (gut content, stable isotopes, fatty acid trophic markers) operating at different times scales and (2) their spatial distribution in regard to in-situ temperatures during different seasons and discuss their combined effect on larval condition and growth.

MATERIAL AND METHODS

Fish larvae and data on prevailing environmental conditions were collected in the NBCE off Namibia (~16°S to ~27°S) during four research cruises at different times of the year. Sampling was conducted during February/March 2009 and 2011 (*FS Maria S. Merian*, cruises MSM 7-2/3 and 17-3), December 2009 (*FRS Africana,* cruise Afr258) and in September/October 2010 (*RRV Discovery*, cruise D356). Quantitative ichthyoplankton collections in the upper 200 m were made at 94 stations using a MultiNet type Midi (Hydrobios) (mouth area: 0.25 m^2, mesh size: 500 µm) equipped with five nets and hauled obliquely from 200 m to the surface (Fig. 1 and SuppInfo 1).
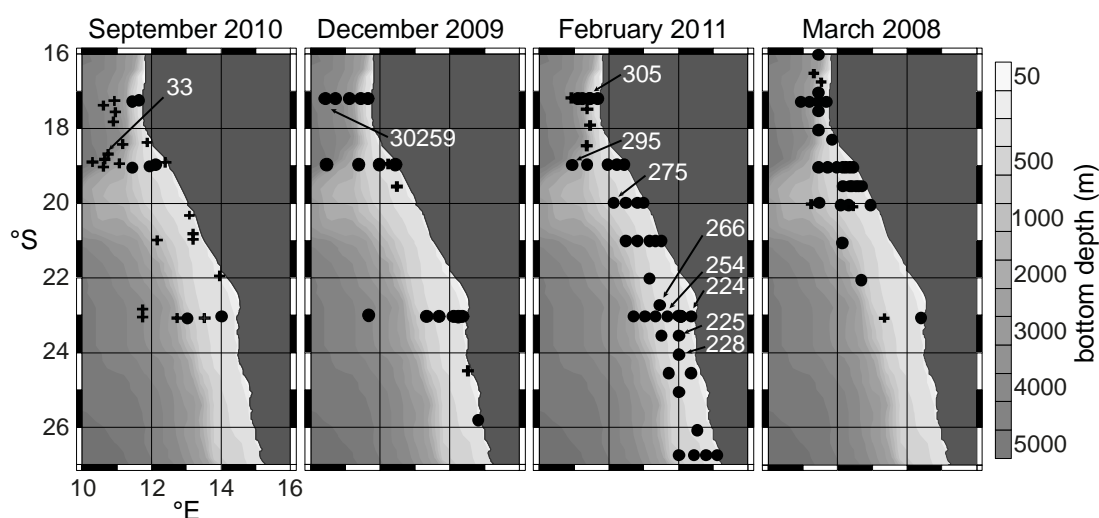
Fig. 1: Station grid of ichthyoplankton hauls during four research cruises arranged by season from austral spring to late summer. Black dots indicate quantitative sampling with a MultiNet and crosses indicate stations of exclusively qualitative hauls. Stations referred to in the manuscript are indicated. Bathymetry as greyscale

The nets were sampling in depth strata according to water column structure in terms of temperature and dissolved oxygen identified from CTD-casts (Mohrholz 2012a, b, c and unpublished data). Two of the nets were equipped with net-inlays (mouth diameter: 10 cm, mesh size: 55 µm) for the sampling of microzooplankton in the two uppermost depth strata. Additional hauls with a trawled or drifting Ring net (mouth area: 2m^2, mesh size: 1000 µm), a Tucker Trawl (mouth area: 1m^2, mesh size: 1000µm) and a MOCNESS (mouth area: 1- and 2-m^2) were made to increase the number of fish larvae available for stomach content, growth and biochemical analyses, which were sorted and kept deep-frozen at -80°C immediately after catching, until further analyses in the laboratory. The remaining catch was preserved in a 4% formalin-seawater-solution for community composition analyses. Phyto- and zooplankton samples were conserved for biochemical and community composition analyses in the same way as fish larvae.

Fish larvae were identified using Olivar and Fortuno (1991). Length was measured as standard length (*SL*; notochord length in early larvae). Body mass was determined as dry mass (mg *DM*) of the larva with empty intestinal tract, using a high-precision balance after freeze-drying. Larval densities were calculated from the MultiNet catches for each single net (ind. 100 m^{-3}) and standardised per unit area (ind. 10 m^{-2}) for each station. Based on the observed depth distribution of the larvae, water temperature at 20 m was chosen to optimally compare the thermal regime of stations.

To study the trophic ecology, we used an integrated approach combining gut content-, stable isotope- (*SI*) and fatty acid- (*FA*) analyses. Gut content analysis (intestinal tract) provides information about the ingested food items at the time of catch and allows for a high taxonomic resolution, but can be biased towards hard structured items that are more easily identifiable. We endeavoured to minimize the potential error introduced by regurgitation during catching by keeping net deployments of the Ring net short (<5 min) and towing at a ship speed of <1 knots (1 knot = ~ 0.5 m s^{-1}). In the home laboratory, frozen larvae were thawed, their feeding incidence was recorded, the digestive tracts were carefully removed and every food item was identified to the lowest possible taxonomic level under a dissecting microscope. Prey items were measured to the nearest 0.1 µm from digital images using a Zeiss AxioCam Icc1 and Axiovision software. The bio-volume of each item was estimated according to its respective shape: the volume of a cylinder was used for copepods and calyptopes larvae (prosome length and width) and for centric diatoms (height and diameter) and the volume of a sphere for eggs. The generalised importance index (*%GII*; Assis, 1996) was calculated using the relative values of abundance and bio-volume and the frequency of occurrence for each taxonomic group to compare the dietary composition between larval species and size classes. Prey selectivity was estimated using the selectivity index (*C*) of Pearre (1982) when larvae contained ≥ 5 prey items and data on *in-situ* microzooplankton composition from MultiNet-inlay catches were available. A positive or negative sign of the index indicates positive or negative selection.

SI-compositions, $\delta^{15}N$ and $\delta^{13}C$, of larval muscle tissue and potential food organisms (phytoplankton and Copepoda) were analysed in 209 samples to obtain an intermediate to long-term record of metabolised food (Van der Zanden and Rasmussen 2001). Phytoplankton was sampled with a 55 µm net when blooms were encountered and the different functional groups were separated from the rest of the seston based on their buoyancy (centric diatoms, *Coscinodiscus wallesii*, were sinking to the bottom and the dinoflagellate, *Noctiluca* sp., floated at the surface). SI data for Copepoda were obtained from Schickenberg (2011) for Harpacticoida (*Microsetella* sp.) and Cyclopoida (*Oithona* sp. and *Oncaea* sp.) and from Schukat *et al.* (2013) for Calanoida, and only those species were selected that were either recorded in the gut content analyses or when they were of a suitable size to be putative prey.

Additional phyto- and zooplankton samples were collected in August (cruise MSM 18) and October (cruise MSM 19) 2011 at stations with strong upwelling activity.

All samples were rinsed with distilled water, freeze-dried and ground to a homogenous powder prior to transfer into tin capsules for elemental micro-analysis. If the individual body mass was too small to be measured, specimens of a similar size and from the same location were pooled. *SI*-compositions were analysed in a gas isotope ratio mass spectrometer (Thermo Finnigan, Delta Plus) after high-temperature combustion in an elemental analyser (Thermo Finnigan, Flash EA 1112) at ZMT Bremen with atmospheric air ($\delta^{15}N$) and PDB carbonate ($\delta^{13}C$) as reference standards. For the estimation of trophic levels (TL), we estimated the $\delta^{15}N$-baseline separately for each cruise using direct measurements of phytoplankton (trophic level=1) when available. For cruises MSM 7 and 17 a trophic level of 2 was assigned to the copepod species with the lowest $\delta^{15}N$-signature and used as baseline (for details see: Schukat *et al.*, 2013). We used an enrichment factor of 3.4‰ per trophic level (Peterson and Fry 1987). Trophic level of the consumer was calculated as:

$$\textit{Trophic level} = \lambda + (\delta^{15}N_{consumer} - \delta^{15}N_{base})\, \Delta_n^{-1} \tag{1}$$

where λ is the trophic level of the organism used to estimate $\delta^{15}N_{base}$ and Δ_n is the enrichment in $\delta^{15}N$ per trophic level.

As a third method for investigating trophic ecology, we used fatty acid trophic markers (*FATM)* as a medium- to long-term record of metabolised food (Dalsgaard *et al.*, 2003) to reveal the relative importance of diatom- and autotroph-dinoflagellate-based prey in the larval food. We used 16:1ω7, 18:1ω7 and 16:4ω1 as markers for diatoms, 18:4ω3 as dinoflagellate marker, and 18:1ω9, 20:1ω9 and 22:1ω11 as markers for heterotroph organisms indicating carnivory (Dalsgaard *et al.*, 2003).

In addition to the *FATM* analysis, we used the following lipid-based condition measures: (1) contribution of total fatty acids (*TFA*) to tissue dry weight (St. John and Lund, 1996), and (2) the contributions of docosahexaenoic acid (*DHA*) 22:6ω3 and its precursor eicosapentaenoic acid (*EPA*) 20:5ω3, both of which are membrane components and thus important for the development of fish larvae and thus affecting recruitment success (Masuda, 2003). *FA*-content and composition were analysed in (i) 34 complete fish larvae with empty stomachs and (ii) in 67 samples of muscle tissue. Sample processing followed Peters *et al.* (2006). The internal standard, tricosanic acid (23:0), was added at the beginning of the extraction process to determine absolute amounts of *FA* (Grote *et al.*, 2011). Gas chromatography measurements were conducted in the BreMarE laboratories, University of Bremen with settings described in Schukat *et al.* (2013).

The morphometric condition factor (Heincke, 1908) adjusted for species-specific length-body mass relations were calculated as:

$$k = GDM\ SL^{-b}\ 10^{-5} \tag{2}$$

where GDM is gutted dry mass (mg), SL is standard length (mm) and b is derived from species-specific potential length-weight regressions.

We used daily increments in otoliths of sardine and anchovy larvae to assess growth potential of the different species. Daily increments have been validated in sardine and anchovy in the Benguela Current by Thomas (1986) and we presumed the same for round sardinella. Daily growth rates (DGR) during the first month of life were estimated using back-calculations from growth increment readings of sagittal otoliths. Following the procedure described by Grote *et al.* (2012) the model of Folkvord and Mosegaard (2002) was applied:

$$SL_i = (OR_i\ OR_c^{-1})^w\ SL_c \tag{3}$$

where SL_i is standard length (mm) at increment i, OR_i is the otolith radius (mm) at increment i, OR_c is the otolith radius (mm) at capture, w is the exponent of the potential regression of SL_c and OR_c (SuppInfo 2) and SL_c is the standard length (mm) at catch. For each analysed larva, the mean DGR ($mDGR$) at two size classes (5-7 mm and 8-12mm SL_i) were calculated with the respective individual DGR.

Superimposed surface plots of larval abundance at sampling stations and water temperatures (30‰-DIVA-gridding) were constructed using Ocean Data View 4.5.0 software. All statistical tests were performed using JMPpro 10.0.0 software. Categorical groups were tested either by Student's t-tests and Welch-ANOVAs or their non-parametric analogues of Wilcoxon tests (Mann-Whitney and Kruskal-Wallis), depending if preconditions were met. *TFA*-proportions were arcsin-square-root-transformed for all analyses, which require normal distribution. Statistical results are given in the form: "Value of test statistic$_{(\text{degrees of freedom, sample size})}$ = X.XX". Graphs were post- processed using Adobe Illustrator CS 5.1 software.

RESULTS

Spatial distribution of water temperature

Overall, water temperatures were coldest during September 2010 and warmest during February 2011 (Fig. 2). Surface temperatures (*SST*) at sampling stations did not exceed 18°C during 09/2010. *SST* >19°C at stations over the shelf (< 500m depth) extended further southward during 02/2011 (19.1°C at 23.5°S) and 03/2008 (21.4°C at 22°S), than during 12/2009 (19.4°C at 19°S). The 14°C isotherms at stations with bottom depths of 65–250 m at 23°S were shallower during 09/2010 (at 0% and 25% of total depth) and 12/2009 (n = 3, 25%, 14-31% of total depth as median and range) compared to 03/2008 (n = 4, 33%, 29-56% respectively) and 02/2011 (n = 7, 45%, 30-100% respectively). Temperatures usually increased with distance off the coast (Fig. 2).

Temperature preferences, spatio-temporal distributions and seasonal comparisons of condition indices and growth rates

In total, 1675 *Sardinops sagax*, 633 *Engraulis encrasicolus* and 304 *Sardinella aurita* larvae were caught in quantitative MultiNet hauls at 94 stations during the four research cruises. Together with qualitative hauls, 109 stations were sampled, and sardines were present at 29, anchovies at 51 and round sardinella at 25 of these stations. At 20 stations sardine and anchovy and at 12 stations all three species co-occurred (SuppInfo 1).

Larval abundance was low with the exception of 02/2011 (Fig. 2). Correspondingly, larval densities in single nets were usually <250 ind. 100 m^{-3}, sardines exceeded this value at the stations (Stat.) 224, 228, 254 and 266 and anchovy at Stat.225 during 02/2011 (Fig. 1 & 3). The majority of larvae were caught within the upper 50 m of the water column (Fig. 3). In contrast to round sardinella, larvae of sardine and anchovy also occurred below 100 m (median of the depth range of the respective net, Fig. 3).

Larvae were mainly caught over the shelf (77% of positive stations, bottom depths of 32-250 m). The maximum distance from shore of a positive catch was 165 km (Stat.33, 09/2010) and the maximum bottom depth 3240 m (Stat.30259, 12/2009). Sardine larvae concentrated around the Walvis Bay region (22.7-24.0°S). In contrast, larvae of anchovy and round sardinella occurred along most of the Namibian shelf from Kunene (17°S) to near Lüderitz (26°S) and Walvis Bay (23°S), respectively (Fig. 2).
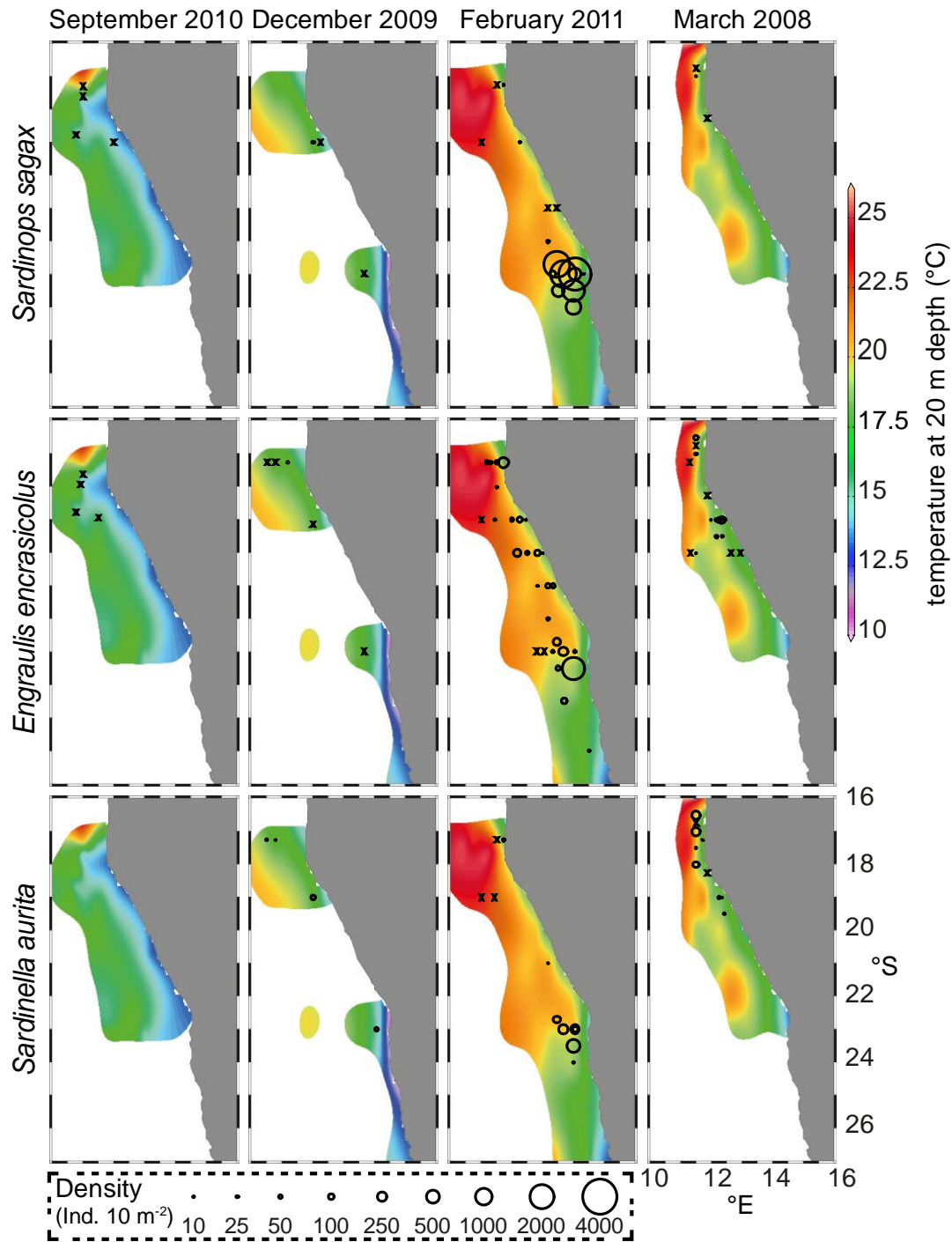
Fig. 2: Spatio-temporal distribution of *S. sagax* (row 1), *E. encrasicolus* (row 2) and *S. aurita* (row 3) larvae and water temperature in sequence of season from different years. The size of the black rings is proportional to larval density (Ind. 10m⁻²). Crosses indicate the presence of larvae in qualitative catches when no parallel positive catch was made in quantitative hauls. Colours indicate temperature distribution at 20 m depth taken from CTD-casts (Mohrholz 2012 a, b, c, unpublished data) extrapolated with 30‰-DIVA-gridding (ODV version 4.5)

Sardine larvae mainly occurred at water temperatures between 15 and 20 °C (Fig. 3 with temperatures at median depth of the respective net, Fig. 2 with T_{20m}). In contrast, larvae of anchovy and round sardinella were commonly present at water temperatures >20°C (Fig. 2 and 3).
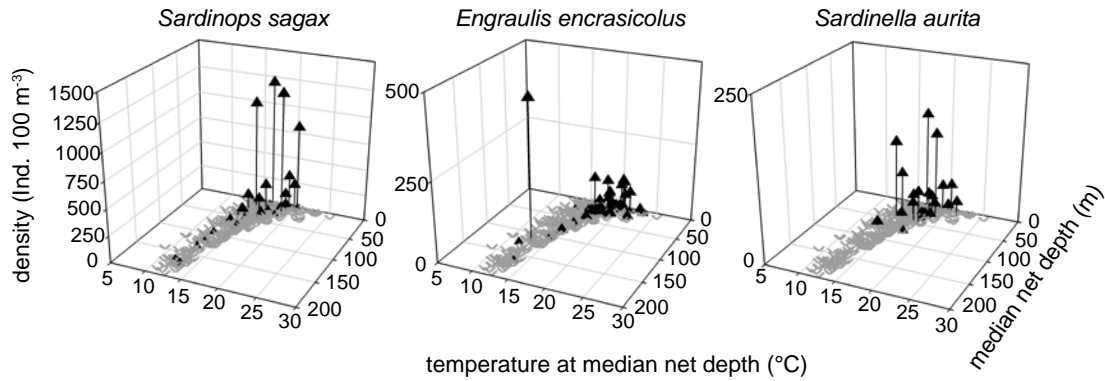
Fig. 3: Densities of sardine, anchovy and round sardinella larvae (left to right) for each quantitative net (z-axis) in relation to the median of the depth range (y-axis) covered by the net in which they were caught and the temperature at respective depth (x-axis) (black triangles). Grey crosses indicate median depths and corresponding temperature of nets with zero catch. Ranges of z-axes are different for the three species, gridline scale the same. Temperature taken from CTD casts (Mohrholz, 2012 a, b, c, unpublished data)

a) E.e. ┄┄┄┄   b) S.s. ┄┄┄┄   c) S.a. ━━━
a = 0.0011 ± 0.1639   a = 6.62 E^{-6} ± 0.4269   a = 8.13 E^{-7} ± 1.3173
b = 3.585 ± 0.061   b = 4.489 ± 0.164   b = 5.249 ± 0.080
$n = 237$, R^2 = 0.94 $n = 150$, R^2 = 0.83 $n = 26$, R^2 = 0.82
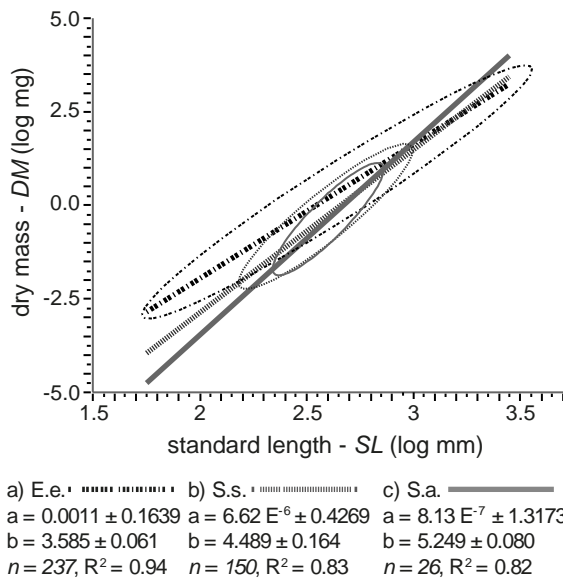
Fig. 4: Plots and confidence ellipsoids as well as significant regression equations of length-weight relationships of *Engraulis encrasicolus* (E.e.), *Sardinops sagax* (S.s.) and *Sardinella aurita* (S.a.) larvae caught during four research cruises in the northern Benguela Current between 2008 and 2011. Species-specific weight exponents *b,* sample size (n) and goodness of fit (R^2) are given only for significant linear regressions

The relationships between standard length and dry body mass were different between the clupeid species *S. sagax* and *S. aurita*, which showed a higher biomass increase per length unit, compared to the engraulid species *E. encrasicolus* (Fig. 4). Hence, condition factor *k* was calculated with a species-specific exponent *b*. *k* of sardine and anchovy differed between seasons. In anchovy larvae they were lower during 09/2010 compared to 02/2011 and 03/2008 ($\chi^2_{(3, 238)}$ = 10.96, p = 0.0119) and in sardine larvae they were lower in 09/2010 than in 03/2008 ($\chi^2_{(2, 148)}$ = 33.60, P < 0.0001; Fig. 5). During the same season, *k* was higher in 03/2008 than in 02/2011 in sardine ($\chi^2_{(2, 148)}$ = 33.60, P < 0.0001) and round sardinella larvae ($\chi^2_{(1, 25)}$ = 8.53, P = 0.0035; Fig. 5).
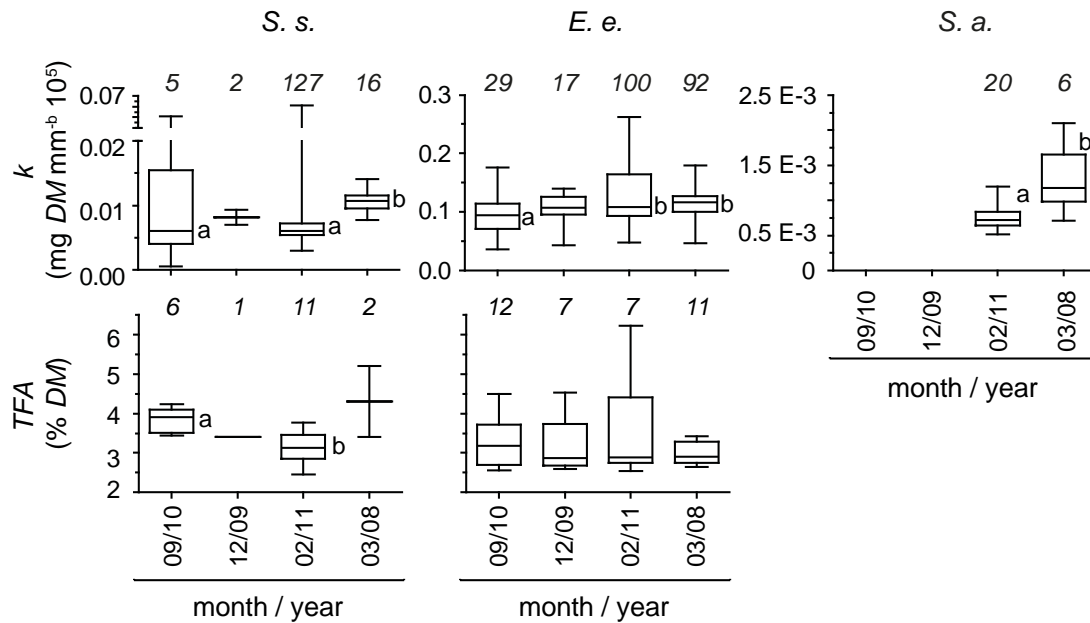
Fig. 5: Seasonal differences of condition factor (*k*, row 1) and total fatty acid content (*TFA*, row 2) in *Sardinops sagax* (S. s.), *Engraulis encrasicolus* (E. e.) and *Sardinella aurita* (S. a.) larvae in sequence of season as box whisker plots with mid-line, box and whiskers showing median, 1st and 3rd quartiles, and range respectively. *k* calculated with species-specific weight exponents *b* (see Fig.4), *TFA* relates to dry mass (*DM*) of muscle tissue. The italic number above the respective box indicates sample size. Lower case letters to the right of the boxes indicate significant differences tested for *k* by Wilcoxon- and subsequent Dunn's post-hoc tests and for *TFA* by general linear models on arcsin-square-root transformed data with "month/year" as categorical and "standard length" as continuous factors

In terms of the biochemical condition measure *TFA*-content in muscle tissue, anchovy larvae did not show seasonal differences (Fig. 5). Sardine larvae had a higher *TFA*-content during 09/2010 than during 02/2011 (2-way GLM on arcsin-square-root-transformed data with "cruise" as categorical and "standard length" as continuous independent factors, $F_{(2, 17)} = 8.80$, P = 0.0044 with "standard length": t = 1.78, P = 0.1 and "cruise": t = 3.81, P = 0.0025).

mDGR of anchovy larvae differed between seasons in the size class of 8-12 mm SL_i ($\chi^2_{(3, 49)} = 22.10$, P < 0.0001; Fig. 6), they grew faster during 02/2008 than during 09/2010 and 02/2011. In the smaller size class, 4-7mm SL_i, no significant differences were observed (Fig. 6).

Fig. 6: Seasonal differences in mean daily growth rates (*mDGR*) of *Engraulis encrasicolus* larvae at two different size classes derived from back-calculated data (*SL_i*, standard length back-calculated) in sequence of season from austral spring to late summer as box-whisker-plots with mid-line, box and whiskers showing median, 1st and 3rd quartiles, and range, respectively

Trophic ecology

The trophic ecology was investigated combining three methodological approaches, gut content-, *SI-* and *FATM*-analyses.

Gut contents were analysed in 927 larvae to investigate prey numbers, species and size composition of ingested prey items. Feeding incidence was 6.4% for sardines (n = 376), 2.0% for anchovies (n = 502) and zero for round sardinella (n = 49). In sardines, filled guts occurred more frequently during daytime and dusk (08:00 to 19:59 UTC) than during night-time (20:00-4:59 UTC) (Table 1, likelihood ratio: $\chi^2_{(2, 376)}$ = 47.68, P < 0.0001). In anchovies, less empty guts were encountered during dawn and daytime (05:00-16:59 UTC) (Table 1, likelihood ratio: $\chi^2_{(3, 665)}$ = 13.36, P < 0.0039).

Table 1: Diel changes of feeding incidence in sardine and anchovy larvae. The first number shows the relative amount in % and the second (in parentheses) gives the actual number, time in UTC

		Dawn 05:00-7:59	Day 8:00-16:59	Dusk 17:00-19:59	Night 20:00-4:59
S. sagax	empty	-	21 (12)	47 (7)	2 (5)
	full	-	79 (46)	53 (8)	98 (298)
E. encrasicolus	empty	50 (1)	7 (3)	0 (0)	2 (6)
	full	50 (1)	93 (41)	100 (123)	98 (492)

Prey characteristics changed with body size from 8 to 30 mm *SL* in both sardine and anchovy larvae (Fig. 7). Trophic niche breadth was not related to larval body size over the investigated range. Maximum and mean prey width, individual prey volume and the total prey volume per gut increased with body size whereas voracity decreased. In sardine larvae, a shift in prey size was observed around 15 mm *SL*. In contrast, a certain threshold size could not be determined for anchovies, due to the lack of intermediate sized larvae (Fig. 7).

Consequently, two size groups were defined for each of the two species for the gut content composition analyses (Fig. 8). 22 of the respective sardine larvae were caught around Walvis Bay (~ 23°S) in 02/2011 and one larva each was caught at 19°S and 17.5°S in 09/2010. The respective anchovy larvae were mainly caught at 20°S (n = 5 in 03/2008 and n = 2 in 02/2011), one larvae each was caught at 23°S in 02/2011 and at 17.25°S in 12/2009. In both species, Crustacea (Copepoda) dominated the gut content with a change of important groups with body size (Fig. 8). In the smaller size groups (<15mm) Harpacticoida (notably *Microsetella* sp., n = 41, prosome length and width in mm as mean ± SD: 0.27 ± 0.06 and 0.65 ± 0.28, respectively) and copepod nauplii (n = 67, 0.15 ± 0.03 and 0.09 ± 0.02, respectively) were the dominant

prey groups. Calanoida (n = 6, 1.96 ± 0.99 and 0.68 ± 0.28, respectively) dominated in guts of larger anchovies. In larger sardines, Calanoida (n = 11, 1.49 ± 0.86 and 0.63 ± 0.29, respectively) and euphausiid larvae (calyptopes, n = 11, 0.76 ± 0.08 and 0.51 ± 0.03, respectively) were the two most important prey groups (Fig. 8). Dinoflagellates,
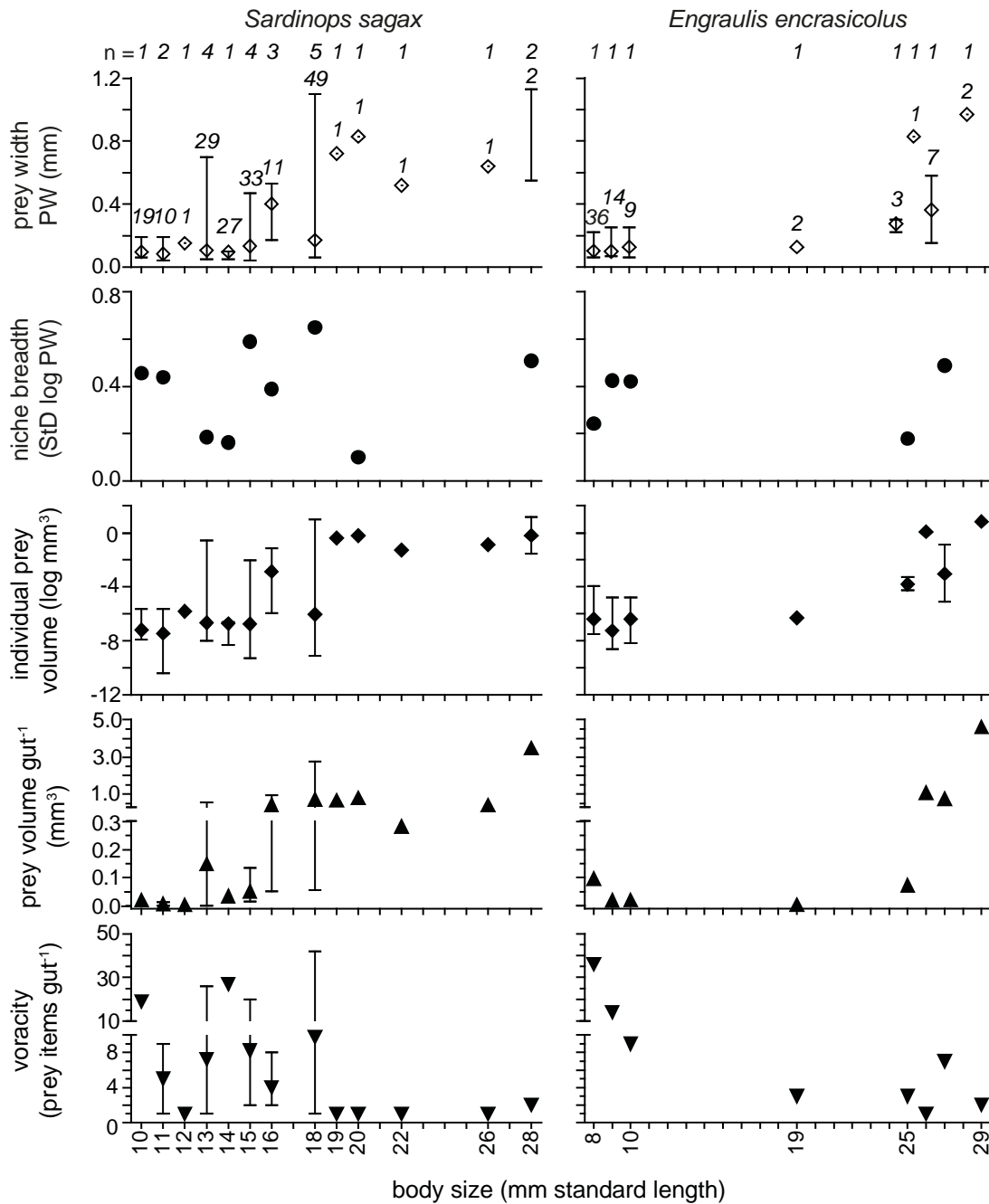
Fig. 7: Development of prey characteristics of sardine and anchovy larvae at body size ranging from 8-30 mm *SL*. Data are shown as means and range, except in the graphs of row 2. Italic numbers on top refer to numbers of guts analysed. In row 1, numbers above the whiskers relate to respective prey item counts

(*Peridinium.*sp., n = 10, 0.11 ± 0.03 and 0.09 ± 0.03, max. length and width respectively), were found in one anchovy (9 mm *SL*) and two sardine larvae (15 and 18 mm *SL*). Three anchovy larvae (19, 27 and 38 mm *SL*) contained centric diatoms (*Coscinodiscus* sp., Ø = 0.34 mm).
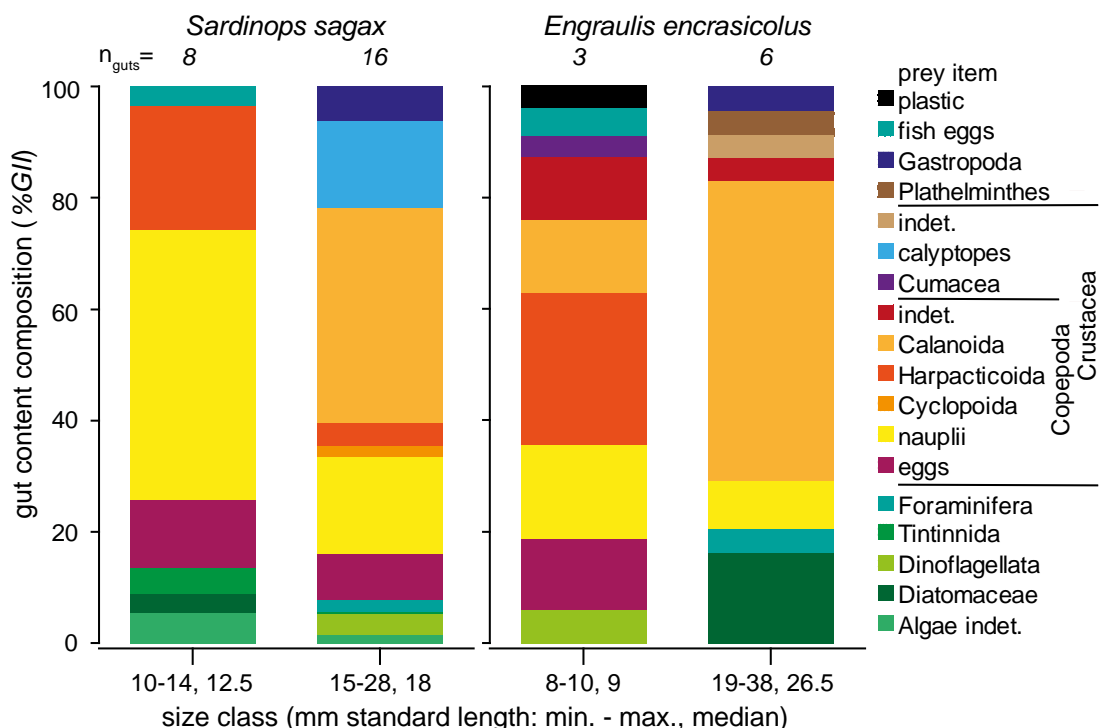
Fig. 8: Taxonomic composition of gut contents of sardine and anchovy larvae in two size classes, each calculated as generalised importance index *(%GII*, Assis 1996), incorporating abundance, volume and frequency of occurrence of the different prey item groups. Phytoplankton in shades of green and Copepoda in shades of yellow and red. Italic numbers on top refer to numbers of guts analysed

Pearre's selectivity index (*C*) was calculated for three sardine and two anchovy larvae caught in 02/2011 (Table 2). 4 of the 5 larvae selected positively for copepod nauplii and negatively for Harpacticoida. Copepod eggs were selected positively by the anchovy and negatively by the sardine larvae.

Table 2: Prey selection of individual *S. sagax* (*S. s.*) and *E. encrasicolus* (*E.e.*) anchovy larvae caught during 02/2011 expressed as Pearre's selectivity index (*C*) ranked by body size. The sign indicates positive or negative selection. Empty cells reflect absence of the respective prey group in both the ambient plankton and the gut samples

Species	*SL* (mm)	Station	Prey items	Selectivity (*C*) for: Harpac-ticoida	Copepod nauplii	Copepod eggs
S. s.	11	266	8	0.216	0.102	-0.056
	13	254	24	-0.396	0.458	
	15	266	18	-0.014	0.335	-0.523
E. e.	9	276	8	-0.432	0.410	0.378
	9	276	5	-0.816	-0.146	0.827

The *SI*-composition ($\delta^{13}C$ and $\delta^{15}N$) of larval muscle tissue was analysed to obtain information on metabolised food integrated over a longer time span in 148 fish larvae and 45 samples of potential prey items (Fig. 9). An overall increase in the $\delta^{15}N$-signatures from phytoplankton via copepods to fish larvae was observed (Fig. 9; SuppInfo 3: $F_{(7, 193)} = 249.09$, $P > 0.0001$). Over the investigated size ranges, the size of the larvae (mm *SL*) had no effect on their $\delta^{15}N$-signatures in any of the three species, when analysed separately per sampling station. In sardine and round sardinella larvae, $\delta^{15}N$-values were higher during 02/2011 compared to 03/2008 ($\chi^2_{(1, 32)} = 23.15$, $P = 0.0023$ and $\chi^2_{(1, 11)} = 7.0015$, $P = 0.0082$, respectively).
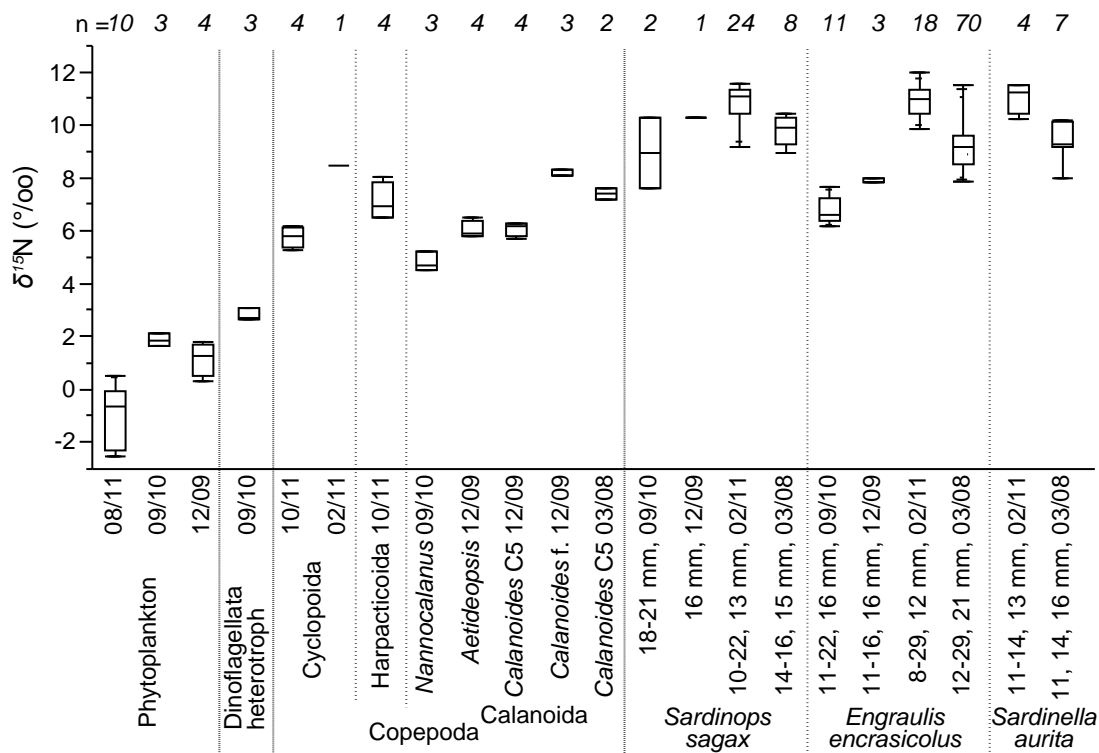
Fig. 9: $\delta^{15}N$-signatures of larvae of *S. sagax*, *E. encrasicolus*, *S. aurita* and potential prey items with mid-line, box and whiskers showing median, 1st and 3rd quartiles, and range. Potential prey groups and clupeoid species are separated by dotted, vertical lines and ordered in sequence of season. Size distribution of fish larvae as min.-max., median (mm *SL*). "Phytoplankton" are mixed plankton samples dominated by diatoms (*Coscinodiscus wallesii*), "Dinoflagellata heterotroph" are samples dominated by *Noctiluca* sp., "Cyclopoida" are *Oncaea* sp. and *Oithona* sp., and "Harpacticoida" is *Microsetella* sp. The data of calanoid copepods were taken from Schukat *et al.* (2012)

Anchovy larvae from 02/2011 showed higher values than those from the other three cruises ($\chi^2_{(3, 102)} = 56.60$, $P < 0.0001$). In 03/2008, $\delta^{15}N$-signatures of sardine and anchovy larvae were linearly correlated with T_{20m} (n = 8; $R^2 = 0.85$; a = 2.81 ± 1.19, P = 0.0565; b = 0.34 ± 0.06, P = 0.0011; and n = 65; $R^2 = 0.81$, a = -1.40 ± 0.64, P = 0.0319; b = 0.61 ± 0.04, P < 0.0001, respectively). "Phytoplankton" from 12/2009 showed a similar trend (n = 3; $R^2 = 0.77$; b = 0.63). In 02/2011, fish larvae signatures were not correlated with T_{20m}. Sardine larvae from

Stat.295 (T_{20m} = 23.7°C) had lower values than those from Stat.266 (T_{20m} = 18.4°C) and Stat.305 (T_{20m} = 20.7°C; $\chi^2_{(3,\ 22)}$ = 12.36, P = 0.063). Anchovy larvae had higher values at Stat.266 (T_{20m} = 18.4°C) than at Stat.275 (T_{20m} = 20.9°C; $\chi^2_{(3,\ 16)}$ = 9.97, P = 0.0188). Gross estimates for trophic levels of the larvae from the three species resolved to cruise level ranged between 2.4 to 3.5 (SuppInfo 3).

The contributions of *FATM* (% *TFA* of muscle tissue) indicating diatom- and dinoflagellate-based food webs and direct predation on heterotroph-organisms did not differ between cruises in sardine (n = 18) and anchovy (n = 41) larvae. The contributions of diatom (6.35 ± 1.63% in sardine and 6.38 ± 1.41% in anchovy) and dinoflagellate (1.37 ± 0.46% and 1.53 ± 0.51%, respectively) markers were similar in both species. In contrast, heterotrophy markers were higher in larvae of anchovy (6.28 ± 1.38%) than sardine (5.70 ± 2.61%; $\chi^2_{(1,\ 59)}$ = 6.85, P = 0.0089).

Interspecific comparisons under the same environmental conditions and intraspecific comparison between a southern and northern station in 02/2011

Two stations sampled during 02/2011 were selected (i) to examine interspecific differences in feeding ecology, condition measures and *DGR* of sardine, anchovy and round sardinella larvae under the same environmental conditions and (ii) to assess whether these parameters varied intra-specifically under different environmental conditions (Table 3). The two stations were located at the latitudinal limits of the spawning region, Stat.266 was situated north-west of

Table 3: Ambient conditions at stations Stat.266 and Stat.305 during cruise 02/2011 selected for (1) interspecific comparisons of condition, trophic ecology and growth parameters in sardine, anchovy and sardinella larvae and (2) intraspecific comparisons between the two latitudinally separated stations

Station °S bottom depth	depths (m) temperature (°C), salinity, dissolved oxygen (mL L^{-1})				total	diatoms	dinoflagellates	Microzooplankton	Zooplankton	Total fish larvae	*S. sagax*	*E. encrasicolus*	*S. aurita*
	0 m	20 m	50 m	100 m									
266 22.7 251	20.6, 35.22, 5.6	18.5, 35.23, 5.3	15.3 35.31 4.3	13.6 35.30 0.9	2657	2594	56	0.39	30.8	3068	2214	205	169
305 17.3 150	20.7, 35.92, 4.7	20.7, 35.92, 4.7	16.6 35.78 2.2	15.1 35.55 1.00	280	180	93	0.25	19.3	940	present	47	present

Phytoplankton biomass (mg m^{-3}) in upper 30 m sampled from Niskin bottles, only autotroph dinoflagellates included (courtesy of Wasmund and Hansen, IOW-Warnemünde). Microzooplankton taken from 55 µm mesh net-inlays of the surface net from MultiNet hauls reflecting upper ~ 30 m (g wet mass per 100 m towing distance). Zooplankton biomass (g wet mass 10 m^{-2}) and fish larvae densities (Ind. 10 m^{-2}) taken from MultiNet hauls (500 µm-mesh), present = occurring only in qualitative catches

Walvis Bay and Stat.305 was located off the Kunene River mouth (Fig. 1). *SST* was similar at both stations, but thermal stratification in the upper 100 m was more pronounced and concentrations of dissolved oxygen at 50 m depth were lower at Stat.305 (Table 3). Phytoplankton and zooplankton biomass was higher at Stat.266, as was also ichthyoplankton abundance with a high proportion of clupeoid larvae. In contrast, fish eggs were more abundant at Stat.305. The two stations also differed in their microzooplankton composition: copepod eggs (42.9%), Harpacticoida (29.0%), Cyclopoida (18.4%) and copepod nauplii (6.5%) were the most important groups at Stat.266, whereas Calanoida (37.8%), copepod nauplii (20.0%), Cyclopoida (14.7%), Harpacticoida (12.9%), and Appendicularia (11.0%) were important at Stat.305 in terms of abundance.

Larvae of sardine, anchovy and round sardinella were similar in their *SI-* and their *FA*-compositions (Table 4). Poly-unsaturated *FA*s (*PUFA*s, ≈ 50% *TFA*) were more important than saturated (*SFA* ≈ 35% *TFA*) and mono-unsaturated *FA*s (*MUFA* ≈ 14% *TFA*, Table 4). Three single *FA*s dominated and made up for > 60% of *TFA*: docosahexaenoic acid (*DHA*, 22:6ω3), its precursor eicosapentaenoic acid (*EPA*, 20:5ω3) and palmitic acid (16:0). *FATM*s of diatoms and heterotroph organisms (Copepoda) fell in a similar range but were higher than those of a dinoflagellate-based diet. With regard to interspecific differences, sardine larvae contained higher amounts of *DHA* and a higher proportion of stearic acid (18:0) than anchovy at Stat.266. *mDGR* of 4-7 mm SL_i-larvae were lower in sardine than in round sardinella at Stat.266 (Table 4). Anchovy larvae showed higher proportions of *MUFA*s and *EPA* at Stat.266 and a higher proportion of palmitoleic acid (16:1ω7) at both stations compared to sardine larvae. No interspecific differences were found for *FATM* and $\delta^{15}N$-signatures.

Intraspecific comparisons of condition measures and trophic markers between Stat.266 and Stat. 305 revealed significant differences in sardine and anchovy larvae (Table 4, SuppInfo 4). Sardine larvae had a higher total amount of *EPA* at Stat.305. In anchovy larvae, the amounts of *TFA*, *EPA* and *DHA* and the *FATM* of diatom-based diet as well as the $\delta^{13}C$-signatures were all significantly higher at Stat.305. In contrast, the *FATM* for heterotroph plankton (copepods) were higher at Stat.266. Average *mDGR* of sardine and anchovy larvae were higher at Stat.305, however not significantly due to high individual variation (Table 4).

Table 4 (right): Inter- and intra-specific comparisons of condition measures, trophic markers and daily growth rates of sardine, anchovy and round sardinella larvae from two selected sampling stations in the northern Benguela that differed in their environmental parameters (see Table 3) sampled during 02/2011. For each type of analysis, sample size (n) and body size (mm standard length, *SL*) and mass (mg dry mass, *DM*) are given as mean, minimum-maximum at the top of every section. All values are mean ± standard deviation. Bold typing indicates significant differences and superscript letters indicate different groups (statistical analysis results are given in SuppInfo 4). Intraspecific differences in sardines are indicated by a & b and in anchovies by c & d. Interspecific differences at Stat.266 are indicated by e & f and at Stat.305 by k & m

		Sardinops sagax		*Engraulis encrasicolus*		*Sardinella aurita*	
	Station	266	305	266	305	266	305
Condition	Sample size	6	4	5	5	4	3
	Size (mm *SL*)	12.5, 9.3-15.3	11.3, 9.9-15.1	13.2, 7.6-16.3	11.3, 9.6-13.7	14.8, 13.7-16.1	13.6, 13.6-13.7
	Mass (mg *DM*)	0.63, 0.14-1.30	0.36, 0.15-0.80	1.16, 0.17-2.2	0.72, 0.30-1.58	0.94, 0.70-1.14	0.69, 0.56-0.76
	TFA (% *DM*)	4.18 ± 0.40	5.01 ± 0.67	**3.44 ± 0.68[c]**	**4.54 ± 0.42[d]**	3.86 ± 0.30	4.26 ± 0.21
	EPA (µg mg DM^{-1})	**0.325 ± 0.029[a]**	**0.468 ± 0.096[b]**	0.302 ± 0.063[c]	0.484 ± 0.021[d]	0.393 ± 0.101	0.335 ± 0.021
	DHA (µg mg DM^{-1})	**1.243 ± 0.103[e]**	1.478 ± 0.200	0.984 ± 0.170[c, f]	1.178 ± 0.088[d]	1.123 ± 0.115	1.263 ± 0.106
Lipid analysis	ΣSFA	36.51 ± 1.53	35.65 ± 1.52	35.65 ± 0.91	36.09 ± 1.55	36.02 ± 0.58	36.11 ± 0.33
	ΣMUFA	14.46 ± 1.02	**13.36 ± 0.67[k]**	14.74 ± 0.69	**15.12 ± 0.65[l]**	14.71 ± 0.73	**13.71 ± 0.50[k]**
	ΣPUFA	49.04 ± 2.35	51.00 ± 1.93	49.61 ± 1.38	48.80 ± 1.81	49.27 ± 0.92	50.17 ± 0.80
	16:0	23.20 ± 0.57	22.58 ± 1.20	23.54 ± 0.47	23.71 ± 0.46	23.72 ± 0.47	23.47 ± 0.55
	18:0	**8.83 ± 1.75[e]**	8.58 ± 1.34	**6.69 ± 1.17[f]**	7.67 ± 0.82	6.97 ± 0.50	7.76 ± 0.83
	16:1ω7	**3.08 ± 0.46[e]**	**3.36 ± 1.18[k]**	**3.92 ± 0.62[c, f]**	**5.79 ± 0.35[d, m]**	3.71 ± 0.34	4.02 ± 1.36
	18:1ω9	7.18 ± 1.19	5.93 ± 1.53	**6.35 ± 0.80[c]**	**4.63 ± 0.49[d]**	6.18 ± 0.61	5.90 ± 2.68
	20:4ω6 (*AA*)	1.37 ± 0.16	1.33 ± 0.13	1.36 ± 0.13	1.24 ± 0.15	1.55 ± 0.08	1.42 ± 0.06
	20:5ω3 (*EPA*)	**7.74 ± 0.59[a, e]**	**9.27 ± 1.06[b]**	**8.80 ± 0.66[c, f]**	**10.74 ± 0.82[d]**	8.74 ± 0.79	9.27 ± 2.06
	22:6ω3 (*DHA*)	29.84 ± 1.86	29.55 ± 3.11	**28.77 ± 1.70[c]**	**26.03 ± 1.43[d]**	29.07 ± 1.39	29.75 ± 3.08
FATM	Diatoms	5.51 ± 0.81	5.91 ± 1.75	**6.52 ± 0.93[c]**	**9.12 ± 0.24[d]**	6.69 ± 0.57	6.13 ± 13.07
	Dinoflagellates	0.81 ± 0.24	0.98 ± 0.18	0.81 ± 0.16	0.88 ± 0.09	0.68 ± 0.12	0.93 ± 0.31
	Heterotrophs	7.22 ± 1.20	5.98 ± 1.49	**6.47 ± 0.83[c]**	**4.72 ± 0.53[d]**	6.32 ± 0.63	5.94 ± 2.64
Stable isotopes	Sample size	10	6	6	4	0	3
	Size (mm *SL*)	13.9, 10.0-18.4	13.6, 11.0-16.9	18.0, 13.0-28	10.5, 10.3-10.9		13.3, 12.9-13.6
	Mass (mg *DM*)	0.91, 0.15-1.96	0.85, 0.31-1.48	4.42, 0.80-13.71	0.43, 0.37-0.50		0.70, 0.48-0.98
	$δ^{15}N$	11.17 ± 0.18	11.20 ± 0.46	11.48 ± 0.36	10.82 ± 0.61		11.03 ± 0.71
	$δ^{13}C$	-20.14 ± 0.45	-19.29 ± 1.25	**-20.40 ± 0.78[c]**	**-16.84 ± 0.94[d]**		-18.42 ± 2.10
Condition factor	Sample size	90	26	18	26	11	9
	Size (mm *SL*)	13.2, 8.3-18.1	12.7, 8.6-16.9	14.0, 6.57-28.00	11.0, 7.9-13.7	13.5, 10.7-16.1	13.1, 10.9-13.7
	Mass (mg *DM*)	0.76, 0.06-2.84	0.60, 0.12-1.48	2.21, 0.08-13.71	0.54, 0.14-1.58	0.69, 0.20-1.17	0.59, 0.24-0.98
	k (mg $DM\,mm^{-b}$)	$6.27E^{-3}$ ± $0.18E^{-3}$	$6.22E^{-3}$ ± $0.14E^{-3}$	0.093 ± 0.028	0.093 ± 0.018	$7.27E^{-4}$ ± $1.55E^{-4}$	$7.49E^{-4}$ ± $2.53E^{-4}$
mDGR (mm d^{-1})	Sample size	26	7	7	8	17	6
	Size (mm *SL*)	13.4, 8.3-18.0	14.6, 13.6-16.9	14.1, 8.4-16-3	11.4, 8.6-13.4	14.0, 11.4-16.1	13.3, 10.9-15.6
	at 4-7 mm *SLᵢ*	**0.48 ± 0.15[e]**	0.62 ± 0.18	0.48 ± 0.08	0.52 ± 0.09	**0.58 ± 0.14[f]**	0.60 ± 0.24
	at 8-12 mm *SLᵢ*	0.47 ± 0.12	0.56 ± 0.11	0.42 ± 0.08	0.49 ± 0.14	0.47 ± 0.10	0.42 ± 0.10

Abbreviations and explanations in Table 4:

Lipid analysis: values are proportions (%) of total fatty acids (*TFA*), except condition markers related to dry body mass). *EPA:* eicosapentaenoic acid, *DHA:* docosahexaenoic acid, *SFA:* saturated fatty acids, *MUFA*: mono-unsaturated fatty acids, *PUFA*: poly-unsaturated fatty acids, AA: arachidonic acid. Nomenclature of single fatty acids: No. before the colon = number of carbon atoms, No. after the colon = number of double bonds, No. after ω = position of first double bond. Fatty acid trophic markers (*FATM*) include the following fatty acids: diatoms: Σ(16:1ω7. 18:1ω7. 16:4 ω1), dinoflagellates: 18:4 ω3, heterotrophs: Σ(18:1 ω9. 20:1ω9. 22:1ω11). $δ^{15}N$- and $δ^{13}C$-signatures were measured in muscle tissue. Condition factor *k* was calculated using species-specific exponents *b*. *mDGR*: mean daily growth rates calculated with all respective single *DGR* back-calculated from daily otolith growth increments.

DISCUSSION

This study investigates the traits of larval sardine *Sardinops sagax* (Jenyns, 1842), anchovy *Engraulis encrasicolus* (L. 1758), and round sardinella *Sardinella aurita* Valenciennes, 1847 in the northern Benguela ecosystem (NBCE) in terms of temperature preferences and feeding ecology and discusses their influence on daily growth rates and larval condition as indicators for the probability of successful recruitment in the light of potential competition.

Water temperature is recognised as one of the most important factors regulating clupeoid populations (e.g. Schwartzlose *et al.*, 1999) and temperature preferences can be contrasting in sibling species (Takasuka *et al.*, 2008) as well as between different populations (Shannon *et al.*, 1988). Temperatures at the sea surface (*SST*) and at 20 m (T_{20m}) can serve as simple indicators of upwelling intensity with T_{20m} reflecting the larval ambient conditions better (Håkanson, 1993). A normal seasonality of upwelling activity in the NBCE was observed during the four cruises, with higher upwelling intensities during austral spring and lower intensities during austral summer (Bartholomae and van der Plas, 2007). This was reflected by higher T_{20m}, a larger southward extension of the *SST*-19°C-isotherm, and a deeper 14°C-isotherm at 23°S during 02/2011 and 03/2008 compared to 09/2010 and 12/2009. The deep 14°C-isotherms during 02/2011, extending close to the seabed, are indicators for a pronounced warm-water event (Bartholomae and van der Plas, 2007).

Larvae of all three species avoid newly upwelled waters indicated by the same lower thermal limit of occurrence (16.5°C). The common occurrence of anchovy and round sardinella larvae at water temperatures >20°C suggest a wider temperature tolerance window compared to sardine larvae. This interspecific difference is evident when comparing larval densities in depth strata with in-situ conditions, reflecting the relevant environmental conditions governing physiological processes best. Preference of lower in-situ temperatures by sardine compared to anchovy larvae corroborates most previous findings (e.g. Cram, 1977; Daskalov *et al.*, 2003) and is in agreement with a better recruitment success of sardines under colder conditions identified for the periods from 1952-1987 and 1992-2007 (Kirchner *et al.*, 2009). However, it is not in support of Cole's (1999) results.

Sardine larvae were most abundant in the region around Walvis Bay (22.7°S-24°S), its traditional and currently major spawning ground in Namibia (Kreiner *et al.*, 2011). Further northwards (up to 17.25°S) they were only encountered occasionally and in small numbers. An avoidance of warmer water by sardines possibly limits their dispersal towards the northern part of the NBCE. Intrusions of warm tropical waters from the Angola Current frequently occurred during late summer in the past twenty years (John *et al.*, 2004; Bartholomae and van der Plas, 2007; Mohrholz *et al.*, 2008) and were also indicated for the cruises in 2011 and 2008. In

contrast, anchovy larvae distributed more widely over the Namibian shelf, from Walvis Bay (23°S) up to the Kunene River (17.25°S), thus they seem to be less affected by warm water intrusions. Under moderate upwelling conditions during late summer as encountered at Stat.266 in 02/2011 (22.7°S), sardine larvae might have an advantage over anchovy larvae as indicated by the higher content of the fatty acid DHA, which serves as a biochemical condition marker due to its importance for larval development (Masuda, 2003). The encountered warm conditions during late summer 2011 might have facilitated the southward extension of round sardinella spawning to the Walvis Bay region. High daily growth rates of their early larvae (4-7 mm SL_i) at Stat.266 indicate favourable ambient conditions. However larval densities were low compared to both sardine and anchovy.

The availability of sufficient and suitable food in time and space is an important factor determining survival and growth of larvae. The application of a multi-methodological approach enhances the ability to elucidate trophic relationships over different time-scales and reduce potential limitations of single methods. Gut content analyses indicated that larvae of sardine and anchovy display similarity in many aspects of their feeding ecology. They feed during the day, preferentially ingesting copepods. Prey-width and -volume are similar at a similar size of larvae and increases with larval body size, whereas trophic niche breadth does not change over the investigated size range. Voracity is low and decreases with body size. In these respects, clupeoid larvae in the NBCE behave in a similar way to species in other world regions (reviewed by: van der Lingen *et al.*, 2009; Catalan *et al.*, 2010; Morote *et al*, 2010). As lined out before, we confirmed information derived from a limited amount of gut content analyses with the results obtained from stable isotope- (*SI*) and fatty acid trophic marker- (*FATM*) analyses. A diet based on primary consumers like copepods is also indicated by the δ^{15}N-signatures leading to trophic level estimates around three. The high amount of *FATM* of heterotroph organisms (copepods) is further evidence for the elevated importance of copepods in the diet. Further indications for a similar feeding ecology of the three species during the larval phase are similar proportions of *FATM* and similar δ^{15}N- and ^{13}C-signatures when sampled at the same ambient conditions. This result contrasts with findings in clupeoid larvae from other upwelling systems (Arthur, 1976; Muck *et al.*, 1999), where differences in food composition were already observed at larval sizes between 10 and 20 mm. For the NBCE species this could mean, that the similar dietary preferences lead to interspecific competition for the same food sources, even when bulk zooplankton densities are high. Members of the small copepods Cyclopoida and Harpacticoida were both abundant in the ambient plankton at most sampling stations (Schwinghammer, 2011 and unpublished data), but the importance of cyclopoid copepods in the diet of sardine and anchovy larvae was low. This suggests a negative selection of cyclopoids, which was also found in Japanese anchovy *Engraulis*

japonicus (Islam and Tanaka, 2009). A negative selection of these small copepods could be a disadvantage for clupeoid larvae under stable conditions with low upwelling intensities and warmer temperatures, if small copepods dominate under these conditions as hypothesised by van der Lingen *et al.* (2006). The large contributions of essential FAs built up by diatoms emphasize the importance of a diatom-based food web for clupeoid larvae and direct feeding on diatoms was observed in post-larvae anchovy (25-30 mm *SL*).

The strong inter- and intra-seasonal variations in the δ^{15}N-signatures of fish larvae could indicate a seasonal shift in prey composition, but might also be caused by a changing baseline. Such a change is suggested by the positive correlations of $\delta^{15}N$-signatures of sardine and anchovy larvae during 03/2008 and of phytoplankton in 12/2009 with water temperature (T_{20m}). Thus it appears that the baseline increases from active upwelling to quiescent conditions, taking T_{20m} as a simple proxy for the "age of upwelled water". The exceptions of low $\delta^{15}N$-signatures of fish larvae at two stations with high water temperatures (Stat.275 and Stat.295 in 02/2011) are explained by their geographical position. Both stations were at the offshore end of the respective sampling transects and were likely affected by oceanic and tropical water, with a stable isotope stoichiometry that differed from upwelling water. A similar change in the baseline was observed during the succession of a phytoplankton bloom in the North Sea (Malzahn and Boersma, 2009). The recycling of nutrients and an increased importance of the microbial loop for the food web (Wu *et al.*, 1997) are possible underlying mechanisms. Tintinnida, present in sardine and anchovy larvae guts, could represent a link to the microbial food web, as previously suggested by van der Lingen *et al.* (2006). Constant proportions of *FATM* over the four cruises are an additional indicator that no major seasonal shift in the diet occurs, at least from a biochemical perspective. However, this does not exclude small-scale differences in prey compositions. A changing prey spectrum of the larvae and/or their prey, e.g. Calanoida of the NBCE are mostly omnivorous with a higher affinity for herbivory in smaller species (Schukat *et al.* 2013), likely explains the variability of $\delta^{15}N$-signatures at smaller scales. Accordingly, the differences in trophic markers of anchovy larvae ($\delta^{13}C$, diatom and heterotroph *FATM*) between Stat.266 and Stat.305 can be attributed to differences in their ambient plankton composition. This point to a high trophic plasticity of anchovy larvae, similar to a quick adaption to a changing prey field found in the Adriatic Sea by Conway et *al.* (1998).

Unfavourable temperatures or sub-optimum food levels can negatively influence growth rates (Håkanson, 1993; Takahashi and Checkley, 2008; Takahashi *et al.,* 2012) and a poor nutritional condition and slow growth affect developmental stage duration and thus likely increase mortality rate of fish larvae (Houde, 1987). The average daily growth rates (*mDGR*) of anchovy (0.55 mm d^{-1}) and sardine (0.50 mm d^{-1}) larvae are within the range determined in

earlier laboratory (King *et al.*, 1978; Brownell, 1983) and field studies (Thomas, 1986) in the Benguela and those reported for sibling species elsewhere, e.g. in the western Iberian upwelling system (Santos *et al.*, 2007), Australia (Gaughan *et al.*, 2001) and the East-China Sea (Chiu and Chen, 2001). Similar to *E. japonicus* (Chiu and Chen, 2001), anchovy larvae grew faster during the warmer conditions in 03/2008 compared to the colder conditions in 09/2010 and 12/2009.

In addition to the temperature effect, favourable feeding conditions allowed for higher growth rates during 03/2008 as indicated by better nutritional conditions of anchovy and sardine larvae (higher *k*). In contrast to late summer 2008, the nutritional conditions of sardine and round sardinella during 02/2011 were low, with sardine larvae containing less *TFA* than in 09/2010. Anchovy larvae grew slower during 02/2011 although temperature was higher. Further indications for an insufficient food supply during 02/2011 are the low feeding incidences of larvae, which were notably lower than reported for sardine and anchovy (Morote *et al.*, 2010) and round sardinella larvae (Morote *et al.*, 2008) from the Mediterranean Sea. The influence of a systematic error, caused by regurgitation during catching (Arthur, 1976), is assumed to be low since similar sampling protocols were used. Within 02/2011, a poorer nutritional condition at Stat.266 compared to Stat.305 was indicated for sardine and anchovy larvae. Together with higher *mDGR* of sardine larvae at Stat.305, this points to a suboptimal food supply in the region around Walvis Bay, where the highest larval densities were recorded. The higher density of zooplankton at Stat.266 seems to contradict food limitation; however the plankton composition is crucial in this regard. Likewise, the lower proportion of copepod nauplii and the high proportion of Harpacticoida at Stat.266, the first positively and the second negatively selected by four of five sardine and anchovy larvae, may have led to intra- and interspecific food competition at Stat.266. In addition, high zooplankton densities may also enhance predation pressure on clupeoid larvae (Agostini *et al.*, 2007) may result in elevated predation mortality.

In conclusion, we showed that anchovy larvae in the NBCE have an expanded temperature range of occurrence towards higher water temperatures compared to sardine and round sardinella larvae. This may be an advantage at times when warm water events in the NBCE increase in frequency. Larval feeding ecology of sardine, anchovy and round sardinella in the NBCE are similar in many aspects, which implies a potential for trophic competition. The extraordinarily high larval abundances encountered around Walvis Bay in 02/2011 suggest that especially sardines still possess the potential to produce high larval densities, a precondition for high recruitment. However, at such high numbers a likely food-mediated density effect might hamper recruitment success. Future experiments on temperature preference and tolerance ranges of larvae could clarify whether our field observations reflect their bioclimatic

envelope based on species-specific eco-physiological traits. Analyses of prey nutritional values and tropho-dynamic experiments that simultaneously investigate responses to different upwelling conditions at different trophic levels would further improve our understanding of the underlying processes affecting growth and condition of clupeoid larvae in the NBCE.

ACKNOWLEDGEMENTS

REFERENCES

Agostini, V.N., Bakun, A., Francis, R.C. (2007) Larval stage controls on Pacific sardine recruitment variability: high zooplankton abundance linked to poor reproductive success. Mar Ecol Prog Ser **345:** 237–244.

Arthur, D.K. (1976) Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fish Bull U.S. **74:** 517–530.

Assis, C.A. (1996) A generalised index for stomach contents analysis in fish. Sci Mar **60:** 385–389.

Bakun, A., Weeks, S.J. (2006) Adverse feedback sequences in exploited marine systems: are deliberate interruptive actions warranted? Fish Fish **7:** 316–333.

Bakun, A., Babcock, E.A., Lluch-Cota, S.E., Santora, C., Salvadeo, C.J. (2010) Issues of ecosystem-based management of forage fisheries in "open" non-stationary ecosystems: the example of the sardine fishery in the Gulf of California. Rev Fish Biol Fisheries **20:** 9–29.

Bakun, A. (2010) Linking climate to population variability in marine ecosystems characterized by non-simple dynamics: conceptual templates and schematic constructs. J Marine Syst **79:** 361–373.

Bartholomae, C.H., van der Plas, A.K. (2007) Towards the development of environmental indices for the Namibian shelf, with particular reference to fisheries management. Afr J Mar Sci **29**: 25–35.

Bertrand, A., Chaigneau, A., Peraltilla, S., Ledesma, J., Graco, M., Monetti, F., Chavez, F.P. (2011) Oxygen: A fundamental property regulating pelagic ecosystem structure in the coastal southeastern tropical Pacific. PLoS ONE **6:** e29558.

Brownell, C.L. (1983) Laboratory rearing of Cape anchovy *Engraulis capensis* and South African pilchard *Sardinops ocellata* through metamorphosis. S Afr J Mar Sci **1:** 181–188.

Catalán, I.A., Folkvord, A., Palomera, I., Quilez-Badia, G., Kallianoti, F., Tselepides, A., Kallianotis, A. (2010) Growth and feeding patterns of European anchovy (*Engraulis encrasicolus*) early life stages in the Aegean Sea (NE Mediterranean). Estuar Coast Shelf S **86:** 299–312.

Chiu, T.S., Chen, C.S. (2001) Growth and temporal variation of two japanese anchovy cohorts during their recruitment to the East China Sea. Fish Res **53:** 1–15.

Cole, J.F.T. (1999) Environmental conditions, satellite imagery, and clupeoid recruitment in the northern Benguela upwelling system. Fish Oceanogr **8:** 25–38.

Conway, D.V.P., Coombs, S.H., Smith, C. (1998) Feeding of anchovy *Engraulis encrasicolus* larvae in the northwestern Adriatic Sea in response to changing hydrobiological conditions. Mar Ecol Prog Ser **175:** 35–49.

Cram, D.L. (1977) Research and management in Southeast Atlantic pelagic fisheries. Cal Coop Ocean Fish **19:** 33–62.

Cury, P.M., Bakun, A., Crawford, R.J.M., Jarre, A., Quinones, R.A., Shannon, L.J., Verheye, H.M. (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES J Mar Sci **57:** 603–618.

Cury, P.M., Shannon, L.J. (2004) Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. Prog Oceanogr **60:** 223–243.

Cushing, D.H. (1996) Towards a science of recruitment in fish populations. Oldendorf/Luhe: Ecology Institute, 175pp.

Dalsgaard, J., St. John, M.A., Kattner, G., Muller-Navarra, D., Hagen, W. (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol **46:** 225–340.

Daskalov, G.M., Boyer, D.C., Roux, J.P. (2003) Relating sardine *Sardinops sagax* abundance to environmental indices in northern Benguela. Prog Oceanogr **59:** 257–274.

Duncombe Rae, C.M. (2005) A demonstration of the hydrographic partition of the Benguela upwelling ecosystem at 26°40'S. Afr J mar Sci **27(3):** 617-628.

Ekau, W., Verheye, H.M. (2005) Influence of oceanographic fronts and low oxygen on the distribution of ichthyoplankton in the Benguela and southern Angola currents. Afr J Mar Sci **27:** 629–639.

Folkvord, A., Mosegaard, H. (2002) Some uses of individual age data. A. Age and growth analysis. In: *Manual of fish sclerochronology.* J. Panfili, H. Troadec, H. dePontual, P.J.Wright (eds) Brest: Ifremer–IRD co-edition pp. 146–166.

Gaughan, D.J., Fletcher, W.J., White, K.V. (2001) Growth rate of larval *Sardinops sagax* from ecosystems with different levels of productivity. Mar Biol **139:** 831–837.

Grote, B., Hagen, W., Lipinski, M.R., Verheyem H.M., Stenevik, E.K., Ekau, W. (2011) Lipids and fatty acids as indicators of egg condition, larval feeding and maternal effects in cape hakes (*Merluccius paradoxus* and M. *capensis).* Mar Biol **158:** 1005–1017.

Grote, B., Ekau, W., Stenevik, E.K., Clemmesen, C., Verheye, H.M., Lipinski, M.R., Hagen, W. (2012) Characteristics of survivors: growth and nutritional condition of early stages of the hake species *Merluccius paradoxus* and *M. capensis* in the southern Benguela ecosystem. ICES J Mar Sci **69(4):** 553-562.

Håkanson, J.L. (1993) Nutritional condition and growth rate of anchovy larvae (*Engraulis mordax*) in the California Current: two contrasting years. Mar Biol **115:** 309-316.

Heincke, F. (1908) Bericht über die Untersuchungen der Biologischen Anstalt auf Helgoland zur Naturgeschichte der Nutzfische. Die Beteiligung Deutschlands an der Internationalen Meeresforschung **4:** 67–155.

Heymans, J.J., Shannon, L.J., Jarre, A. (2004) Changes in the northern Benguela ecosystem over three decades: 1970s, 1980s, and 1990s. Ecol Model **172:** 175–195.

Houde, E.D. (1987) Fish early life dynamics and recruitment variability. Am Fish S S **2:** 17–29.

Hutchings, J.A. (2000) Collapse and recovery of marine fishes. Nature **406:** 882–885.

Hutchings, J.A., Reynolds, J.D. (2004) Marine fish population collapses: consequences for recovery and extinction risk. BioScience **54:** 297–309.

Islam, M.S., Tanaka, M. (2009) Diet and prey selection in larval and juvenile japanese anchovy *Engraulis japonicus* in Ariake Bay, Japan. Aquat Ecol **43:** 549–558.

John, H.C., Mohrholz, V., Lutjeharms, J.R.E., Weeks, S.J., Cloete, R., Kreiner, A., daSilva Neto, D. (2004) Oceanographic and faunistic structures across an Angola Current intrusion into northern Namibian waters. J Marine Syst **46:** 1–22.

King, D.P.F., Robertson, A.A., Shelton, P.A. (1978) Laboratory observations of the early development of the anchovy *Engraulis capensis* from the Cape Peninsula. Fish Bull S Afr **10:** 37–45.

Kirchner, C.H., Bartholomae, C.H., Kreiner, A. (2009) Use of environmental parameters to explain the variability in spawner-recruitment relationships of Namibian sardine *Sardinops sagax*. Afr J Mar Sci **31**(2): 157-170.

Kreiner, A., Yemane, D., Stenevik, E.K., Moroff, N.E. (2011) The selection of spawning location of sardine (*Sardinops sagax*) in the northern Benguela after changes in stock structure and environmental conditions. Fish Oceanogr **20:** 560–569.

Lasker, R. (1978) The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. Int. Explor. Mer **173:** 212–230.

Malzahn, A.M., Boersma, M. (2009) Trophic flexibility in larvae of two fish species (lesser sandeel, *Ammodytes marinus* and dab, *Limanda limanda*). Sci Mar **73S1:** 131-139.

Masuda, R. (2003) The critical role of docosahexaenoic acid in marine and terrestrial ecosystems: from bacteria to human behavior. In: *The Big Fish Bang*. H.I. Browman, A.B. Skiftesvik (eds) Bergen: Inst. Mar Res, pp. 249–256.

Mohrholz, V., Bartholomae, C.H., van der Plas, A.K., Lass, H.U. (2008) The seasonal variability of the northern Benguela undercurrent and its relation to the oxygen budget on the shelf. Cont Shelf Res **28:** 424–441.

Mohrholz, V. (2012a-c) Hydrographic measurements in the Northern Benguela upwelling system during the cruise AFR 258 (a), D356 (b), MSM17/3 (c) . Leibniz-Institut für Ostseeforschung Warnemünde, unpublished datasets #784364 - 784366.

Morote, E., Olivar, M.P., Villate, F., Uriarte, I. (2008) Diet of round sardinella, *Sardinella aurita*, larvae in relation to plankton availability in the NW Mediterranean. J Plankton Res **30:** 807–816.

Morote, E., Olivar, M.P., Villate, F., Uriarte, I. (2010) A comparison of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) larvae feeding in the northwest Mediterranean: influence of prey availability and ontogeny. ICES J Mar Sci **67:** 897–908.

Muck, P., de Mendiola, B.R., Antonetti, E. (1989) Comparative studies on feeding in larval anchoveta (*Engraulis ringens*) and sardine (*Sardinops sagax*). In: *The Peruvian upwelling ecosystem: dynamics and interactions*. D. Pauly, P. Muck, J. Mendo (eds) Callao, Peru: Instituto del Mar Perú (IMARPE), pp. 86-96.

Mullon, C., Fréon, P., Parada, C., van der Lingen, C.D., Huggett, J.A. (2003) From particles to individuals: modelling the early stages of anchovy (*Engraulis capensis/encrasicolus*) in the southern Benguela. Fish Oceanogr **12:** 396–406.

Olivar, M.P., Fortuño, J.M. (1991) Guide to ichthyoplankton of the southeastAtlantic (Benguela Current region). Sci Mar **55:** 1–383.

Pearre, S.Jr (1982) Estimating prey preference by predators: uses of various indices, and a proposal of another based on χ2. Can J Fish Aquat Sci **39:** 914–923.

Peters, J., Renz, J., von Beusekom, J., Boersma, M., Hagen, W. (2006) Trophodynamics and seasonal cycle of the copepod *Pseudocalanus acuspes* in the central Baltic Sea (Bornholm Basin): evidence from lipid composition. Mar Biol **149:** 1417–1429.

Peterson, B.J., Fry, B. (1987) Stable isotopes in ecosystem studies. Ann Rev Ecol Syst **18:** 293–320.

Pikitch, E.K., Rountos, K.J., Essington, T.E., Santora, C., Pauly, D., Watson, R., Sumaila, U.R., Boersma, P.D., Boyd, I.L., o'Conover, D., Cury, P.M., Heppell, S.S., Houde, E.D., Mangel, M., Plagányi, É., Sainsbury, K., Steneck, R.S., Geers, T.M., Gownaris, N., Munch, S.B. (2012) The global contribution of forage fish to marine fisheries and ecosystems. Fish Fish: doi 10.1111/faf.12004.

Richardson, A.J., Mitchell-Innes, B.A., Fowler, J.L., Bloomer, S.F., Verheye, H.M., Field, J.G., Hutchings, L., Painting, S.J. (1998) The effect of sea temperature and food availability on the spawning success of cape anchovy *Engraulis capensis* in the southern Benguela. S Afr J Mar Sci **19:** 275–290.

Santos, A.M.P., Chícharo, M.A., dosSantos, A., Moita, T., Oliveira, P.B., Peliz, A., Ré, P. (2007) Physical–biological interactions in the life history of small pelagic fish in the western Iberia upwelling ecosystem. Prog Oceanogr **74:** 192–209.

Schickenberg, N. (2011) Stable isotope (13C & δ15N) signatures of 3 micro-copepod groups important for the horse mackerel diet. Project thesis, University of Bremen, 15pp.

Schukat A, Auel H, Teuber L, Lahajnar N, Hagen W (2013) Complex trophic interactions of calanoid copepods in the Benguela upwelling system. J Sea Res (in press). doi: 10.1016/j.seares.2013.04.01

Schwartzlose, R.A., Alheit, J., Bakun, A., Baumgartner, T.R., Cloete, R., Crawford, R.J.M., *et al.* (1999) Worldwide large-scale fluctuations of sardine and anchovy populations. S Afr J Mar Sci **21:** 289–348.

Schwinghammer, K. (2011) Zusammensetzung des Mikroplanktons im Südsommer vor Namibia. BSc thesis, University of Bremen, 36pp. (In German).

Shannon, L.J., Field, J.G., Moloney, C.L. (2004) Simulating anchovy–sardine regime shifts in the southern Benguela ecosystem. Ecol Model **172:** 269–281.

Shannon, L.V., Crawford, R.J.M., Brundrit, G.B., Underhill, L.G. (1988) Responses of fish populations in the Benguela ecosystem to environmental change. J Cons int Explor Mer **45:** 5-12.

St. John, M.A., Lund, T. (1996) Lipid biomarkers: Linking the utilization of frontal plankton biomass to enhanced condition of juvenile North Sea cod. Mar Ecol Prog Ser **131:** 75–85.

Takahashi, M., Checkley, D.M.Jr. (2008) Growth and survival of Pacific sardine (*Sardinops sagax*) in the California Current region. J Northwest Atl Fish Sci **41:** 129–136.

Takahashi, M., Checkley, D.M.Jr., Litz, M.N.C., Brodeur, R.D., Peterson, W.T. (2012) Responses in growth rate of larval northern anchovy (*Engraulis mordax*) to anomalous upwelling in the northern California Current. Fish Oceanogr **21(6):** 393–404.

Takasuka, A., Oozeki, Y., Kubota, H., Lluch-Cota, S.E. (2008) Contrasting spawning temperature optima: Why are anchovy and sardine regime shifts synchronous across the north Pacific? Prog Oceanogr **77:** 225–232.

Thomas, R.M. (1986) Growth of larval pelagic fish in the south-east Atlantic from daily otolith rings in 1982/83 and 1983/84. S Afr J Mar Sci **4:** 61–77.

Tjizoo, B.M. (2008) Characterizing and comparing the spawning habitats of sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) in the northern Benguela region. MSc Thesis, University of Cape Town, 115pp.

van der Lingen, C.D., Hutchings, L., Field, J.G. (2006) Comparative trophodynamics of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela: are species alternations between small pelagic fish trophodynamically mediated? Afr J Mar Sci **28:** 465–477.

van der Lingen, C.D., Bertrand, A., Bode, A., Brodeur, R.D., Cubillos, L.A., Espinoza, P., Friedland, K., Garrido, S., Irigoien, X., Miller, T., Möllmann, C., Rodriguez-Sanchez, R., Tanaka, H., Temming, A. (2009) Trophic dynamics. In: *Climate change and small pelagic fish*. D.M.Jr Checkley, J. Alheit, Y. Oozeki, C. Roy (eds) Cambridge: Cambridge University Press, pp. 112–157.

van der Zanden, M.J., Rasmussen, J.B. (2001) Variation in δ15N and δ13C trophic fractionation: implications for aquatic food web studies. Limnol Oceanogr **46:** 2061–2066.

Wu, J., Calvert, S.E., Wong, C.S. (1997) Nitrogen isotope variations in the subarctic northeast Pacific: relationships to nitrate utilization and trophic structure. Deep-Sea Res Pt I **44:** 287–314.

SUPPORTING INFORMATION

SuppInfo 1: Geographical position and bottom depth of sampling stations of the four research cruises with an indication of deployments of quantitative hauls (oblique MultiNet) and presence of clupeoid species

For SuppInfo 1 please refer to Annex I (pp. 152-156). This table has the similar content and additionally includes presence indications for *T. capensis*.

$$SL_c = u * OR_c{}^w$$

S.s.: u = 2.720 ± 0.132, w = 0.407 ± 0.034, n = 36, R^2 = 0.81

E.e.: u = 1.376 ± 0.163, w = 0.551 ± 0.040, n = 49, R^2 = 0.80

S.a.: u = 4.299 ± 0.206, w = 0.291 ± 0.051, n = 22, R^2 = 0.62

S.a.& S.s.: u = 2.924 ± 0.107, w = 0.388 ± 0.027, n = 58, R^2 = 0.78
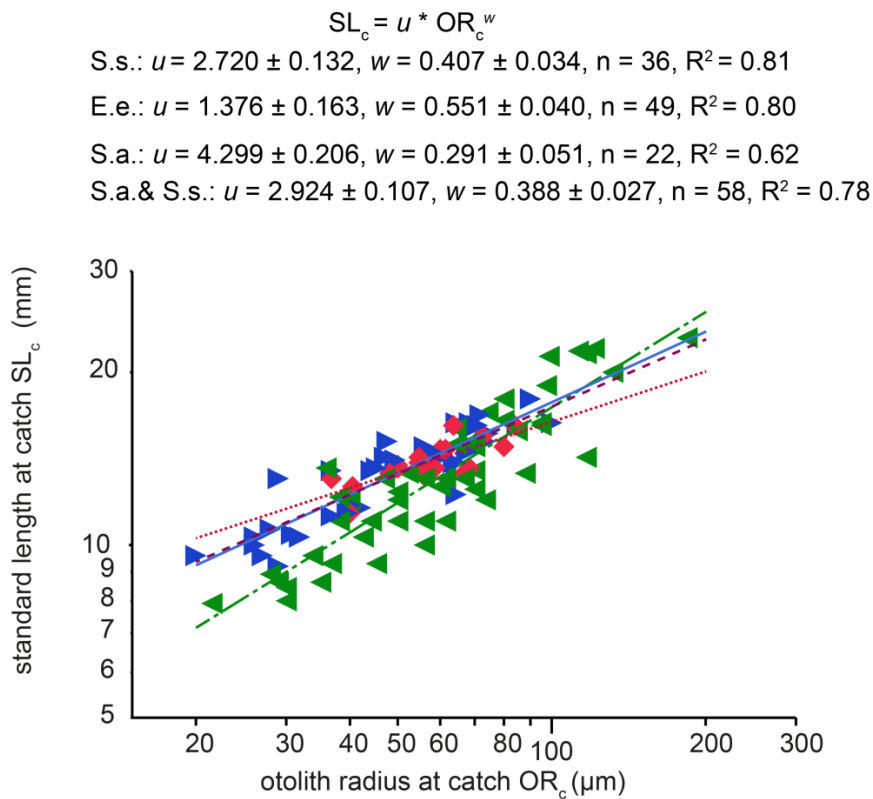
SuppInfo 2: Potential regressions of otolith radius and standard length at catch for *S.sagax* (S.s., blue), *E. encrasicolus* (E.e., green) and *S. aurita* (S.a., red). Due to the small size range of *S. aurita, w* of the combined fit of S.a. and S.s. (purple) was used for the *DGR*-back-calculation

106

SuppInfo 3: $\delta^{15}N$ values of potential prey components and larval sardine, anchovy and round sardinella larvae and trophic level estimations of larvae from four cruises during different seasons

Taxonomic group (post hoc results)	Year Month	Subgroup or size range (mm)	n	Mean±S.E.	Trophic level
A) Phytoplankton	08/2011	diatoms	10	-1.01±0.36	1
	09/2010	diatoms	3	1.87±0.14	1
	12/2009	diatoms ± water	4	1.15±0.32	1
B) Dinoflagellata	09/2010	*Noctiluca*	3	2.81 ± 0.14	1.3
C) Cyclopoida	10/2011	*Oncaea + Oithona*	4	5.75 ± 0.19	2
	02/2011	*Oncaea*	1	8.48	2
D) Harpacticoida	10/2011	*Microsetella*	4	7.09 ± 0.36	
E) Calanoida	09/2010	*Nannocalanus*	3	4.80 ± 0.21	1.9
	12/2009	*Aetideopsis*	4	6.03 ± 0.17	2.4
	12/2009	*Calanoides* C5	4	6.08 ± 0.13	2.3
	12/2009	*Calanoides* f.	3	8.17 ± 0.07	2.9
	03/2008	*Calanoides* C5	2	7.4 ± 0.2	2.3
Sardinops sagax (>A, B, C, E and c>d)	a) 09/2010	18.0 ± 20.9	2	8.95	3.1
	b) 12/2009	16	1	10.26	3.5
	c) 02/2011	10.0 - 22.0	24	10.83 ± 0.15	2.7
	d) 03/2008	13.9 - 15.9	8	9.79 ± 0.2	3.0
Engraulis encrasicolus (>A, E and c>a, b, d; d>a)	a) 09/2010	11.4 - 22.4	11	6.72 ± 0.14	2.4
	b) 12/2009	11.4 - 16.4	3	7.87 ± 0.06	2.8
	c) 02/2011	6.0-29.0	18	10.91 ± 0.14	2.7
	d) 03/2008	8.1 – 29.0	71	9.13 ± 1.01	2.8
Sardinella aurita (>A, C, D, E and c>d)	c) 02/2011	11.0-13.6	4	11.05 ± 0.58	2.8
	d) 03/2008	10.9-16.0	7	9.39 ± 0.28	2.9

Trophic levels estimated with $\delta^{15}N$-values of the organism group representing the lowest trophic level (phytoplankton or copepod) available in the respective year taken as baseline (BL, in bold): 09/2010, BL = 1 - phytoplankton; 12/2009, BL = 1 - median of phytoplankton at Stat.256 and Stat.257; 02/2011, BL = 2 – cyclopoida; 03/2008, BL = 2.3 - *Calanoides* C5. Taxonomic groups were significantly different ($\chi^2_{(7, 194)}$ = 111.05, P < 0.0001). Fish larvae signatures were also compared between cruises: *Engraulis*: $\chi^2_{(3, 103)}$ = 56.92, P < 0.0001; *Sardinella*: $\chi^2_{(1, 11)}$ = 7.00, P = 0.0082; *Sardinops*: $\chi^2_{(1, 32)}$ = 9.28, P = 0.0023. n = number of analysed samples can consist of multiple pooled individuals from the same site. Dunn's post hoc tests were calculated to discriminate significantly different groups

SuppInfo 4: Statistical results of Table 2 "Inter- and intra-specific comparisons of condition measures, trophic tracers and daily growth rates of sardine, anchovy and round sardinella larvae from the northern Benguela from two selected stations differing in their environmental parameters (see Tab.1), sampled during 02/2011. Only significant differences are shown. Non-parametric Wilcoxon tests were applied on lipid condition markers, condition factor, stable isotopes and daily growth rates original values. All single fatty acids and groups (% total fatty acids) were arcsin-square-root transformed before two-tailed t-tests (between stations) or 1-way ANOVAs (interspecific within stations) were performed

Station	Sardinops sagax 266	305	Engraulis encrasicolus 266	305	Sardinella aurita 266	305
Sample size	6	4	5	5	4	3
TFA (% DM)			305>266: χ^2 = 6.82, P = 0.009			
EPA (µg mg DM^{-1})	305>266: χ^2 = 6.12, P = 0.0133		305>266: χ^2 = 6.86, P = 0.0088			
DHA (µg mg DM^{-1})			305>266: χ^2 = 6.82, P = 0.009			
ΣMUFA			interspecific at S266: S. s.>E. e., χ^2 = 6.86, P = 0.0088	interspecific at S305: E. e.>S. s., S. a., F = 9.70, P = 0.0057		
18:0			interspecific at S266: S. s.> E. e., F = 4.28, P = 0.0395			
16:1ω7			305>266: t = 5.45, P = 0.0006			interspecific at S305: E. e.>S. s., F = 7.12, P = 0.0140
18:1ω9	interspecific at S266: E. e.>S. s., F = 4.21, P = 0.0411; interspecific at S305: E. e.>S. s., F = 4.51, P = 0.0347		266>305: t = -4.24, P = 0.0029			
20:5ω3 (EPA)	305>266: t = 3.00, P = 0.0168		305>266: t = 4.20, P = 0.0030; interspecific at S266: E. e.>S. s., F = 4.51, P = 0.0347			
22:6ω3 (DHA)			266>305: t = -2.37, P = 0.0455			
FATM diatoms			305>266: t = 5.67, P = 0.0005			
FATM heterotrophs			266>305: t = -4.09, P = 0.0035			
Sample size	10	6	6	4	0	3
$\delta^{13}C$			305>266: χ^2 = 6.56, P = 0.0105			
Sample size	26	7	7	8	17	6
mDGR at 4-7 mm SL_i (mm SL d^{-1})					interspecific at S266: S. a.>S. s., χ^2 = 6.65, P = 0.036	

Abbreviations and explanations: Lipid analysis: the given values are proportions (%) of total fatty acids (TFA), if not indicated specifically. EPA= eicosapentaenoic acid, DHA= docosahexaenoic acid, SFA= saturated fatty acids, MUFA= mono-unsaturated fatty acids, PUFA= poly-unsaturated fatty acids, AA= arachidonic acid. Nomenclature of single fatty acids: the No. before the colon= the number of carbon atoms, the No. after the colon= the number of double bonds, the No. after ω= position of first double bond. Trophic markers include the following fatty acids: diatoms=Σ(16:1ω7. 18:1ω7. 16:4 ω1), dinoflagellates=18:4 ω3, heterotrophs=Σ(18:1 ω9. 20:1ω9. 22:1ω11)

Chapter III

Early life history traits determine success of Cape horse mackerel,
Trachurus capensis Castelnau, 1861, in the degraded northern Benguela
upwelling ecosystem off Namibia

GEIST SJ[1], corresponding author

simon.geist@zmt-bremen.de

+49 421 238 00 -124 (phone), -30 (fax)

KUNZMANN A[1]

andreas.kunzmann@zmt-bremen.de

VERHEYE HM[2]

hverheye@environment.gov.za

EKAU W[1]

werner.ekau@zmt-bremen.de

[1] *Leibniz Center for Tropical Marine Biology, ZMT*

Fahrenheitstr. 6

D-28359 Bremen

[2] *Oceans and Coasts Research, Department of Environmental Affairs,*

and Marine Research Institute, University of Cape Town

- Cape Town, South Africa

ABSTRACT

Early life history (ELH) traits are key to understand variable recruitment success and hence the stock size of marine fish. One of the currently most puzzling marine ecosystems in this regard is the northern part of the Benguela Current upwelling system off Namibia. Here populations of the formerly dominant pelagic species, sardine and anchovy, failed to recover during the last three decades after a dramatic decline. In contrast, Cape horse mackerel, *T. capensis*, maintained a constant population size. Changes in the temperature and oxygen regime together with feedback loops within an altered food web are discussed to be responsible for this regime shift. In this study we address the question as to what enables *T. capensis* to act as a "pelagic performer" under the present environmental conditions. Therefore, we investigated seasonal variations of the geographical distribution, growth rate, feeding ecology and nutritional condition of their ELH stages and examined relationships with water temperature, dissolved oxygen concentration and microzooplankton composition. We found a wide spatial and seasonal distribution of *T. capensis*' early life stages, a preference for higher water temperatures (18-20°C) and presence over a wide range of dissolved oxygen concentrations (0.13-6.35 mL O_2 L^{-1}). Furthermore, they showed an opportunistic feeding behaviour and fed successfully on the most abundant microzooplankton (different groups of Copepoda), and as result displayed a higher daily growth rate in terms of biomass compared to larvae of clupeoid species. Altogether, these traits enhance this species' probability to encounter suitable environments for the survival of their early life stages, which is likely to lead to their high recruitment success in the northern Benguela ecosystem.

KEYWORDS

geographic distribution, seasonal, feeding ecology, gut content, stable isotopes, fatty acids, daily growth rate, nutritional condition

INTRODUCTION

Horse or jack mackerels of the genus *Trachurus* occupy an important trophic position in all eastern boundary current upwelling (Humboldt, Canary, California, Benguela and Iberian Peninsula) and many other large marine ecosystems worldwide (e.g. Japan, Black Sea, Mediterranean; Crawford, 1987; Fréon *et al.*, 2005; Abaunza *et al.*, 2003). *T. murphyi* from the Humboldt Current ranks among the global top ten species in terms of fisheries yield, although catches declined tremendously during the last decade (FAO, 2012). *T. trachurus* was a profiteer of a regime shift in the North Sea, which was related to rising sea temperatures (Alheit *et al.*, 2005). Cape horse mackerel, *T. capensis* Castelnau, 1861 from the Benguela Current is an important fisheries resource in the northern part of this coastal upwelling system, ~16°S to ~27°S off Namibia (van der Lingen *et al.*, 2006b).

The northern Benguela Current ecosystem (NBCE) is characterised by seasonality in upwelling activity with lower intensity during austral summer (Bartholomae and van der Plas, 2007). In the last 20 years, warm-water events during austral summer have frequently led to elevated temperatures (Bartholomae and van der Plas, 2007) likely contributing to the intensification of seasonal hypoxia (Mohrholz *et al.*, 2008; Monteiro *et al.*, 2008; Ekau *et al.*, 2010). Changes in the temperature and oxygen regime combined with overfishing are considered as main factors driving the regime shift that occurred in the 1970s (Cury and Shannon, 2004; Ekau *et al.*, 2010). This shift led to a severe and persistent loss of fisheries productivity caused by a decline in sardine and anchovy fish stocks (van der Lingen *et al.*, 2006b; Hutchings *et al.*, 2009). Therefore, the NBCE is perceived as a warning example for possible future developments of upwelling ecosystems (Bakun *et al.*, 2010). *T. capensis* is the only pelagic fish species in the NBCE, which maintained a relatively constant stock size during the last 30 years and presently is an important exploited resource (Cury *et al.*, 2005; Kirchner *et al.*, 2010). However, fisheries management of the species is based on limited knowledge of their ecology and uncertainties about recruitment processes (Kirchner *et al.*, 2010).

Although fishing impact can be an important factor controlling stock development, long-term trends are controlled by environmental factors (Houde, 1987; Lehodey *et al.*, 2006). The linkage of climate phenomena to pelagic fish population dynamics continues to largely elude us (Bakun, 2010). Recruitment stages are a bottleneck for the development of fish stock because early life stages are particularly vulnerable to environmental fluctuations (reviewed by Bakun, 2010; Drinkwater *et al.*, 2010). Consequently, temperature and dissolved oxygen are two important abiotic factors that structure ichthyoplankton distribution in the NBCE (e.g. Ekau and Verheye, 2005), both having the potential to influence the physiological performance

of the larvae (Drinkwater *et al.*, 2010; Pörtner, 2010). Combined with adequate food supply, these factors determine growth rate and condition (Cushing, 1996; Ekau *et al.*, 2010). These environmental factors can indeed affect larval mortality rate, either directly or indirectly by prolonging the duration of larval stages, characterised by high vulnerability to starvation or predation (Houde, 1987).

Knowledge of the biology of early life stages of *T. capensis* is scarce. Larvae from other *Trachurus* species were described as copepod feeders (Arthur, 1976; Young and Davis, 1992; Sassa and Tsukamoto, 2012), which are able to ingest larger prey compared to clupeoid larvae at similar body size, and usually have a high feeding success (Arthur, 1976). *Trachurus* larvae are perceived as robust larvae that quickly develop outer body walls (Arthur, 1976). Together with a fast burst swimming speed they are able to cope with the presence of competitors and/or predators like jellyfish from the post-flexion stage onwards (Masuda, 2009). Thus, similar traits in *T. capensis* would be beneficial in the NBCE, since jellyfish are an important ecosystem component at present (Flynn *et al.*, 2012).

The study on hand forms an integral part of GENUS (Geochemistry and Biology of the Namibian Upwelling System), a Germany-funded interdisciplinary research project focusing on the northern Benguela aiming to understand and quantify energy and matter fluxes in the NBCE. Within this context we focus on the early life history (ELH) traits of *T. capensis* larvae and early juveniles, the dominant small pelagic species in the system. We need to understand potential reasons for superior performance of *T. capensis* under the current environmental conditions compared to other small pelagic species, such as the formerly dominant sardines. Do *T. capensis* utilise different food sources or show a more efficient food conversion than clupeids? Is a higher environmental resilience against increased temperature or lowered oxygen level responsible for better performance?

We investigate (1) the spatial distribution of *T. capensis* early life stages during different seasons in relation to *in-situ* water temperature and oxygen concentration and (2) their feeding ecology by combining three methodological approaches operating at different time scales (gut content, stable isotopes and fatty acid trophic markers) and discuss the combined effect of (1) and (2) on larval condition and growth.

MATERIAL AND METHODS

Field sampling

T. capensis early life stages and data on prevailing environmental conditions were collected in the NBCE off Namibia (~16°S to ~27°S) during four research cruises at different times of year. Sampling was conducted during late summer in March/April 2008 and February/March 2011 (*FS Maria S. Merian*, cruises MSM 7-2/3 and 17-3), early summer in December 2009 (*FRS Africana,* cruise Afr258) and spring in September/October 2010 (*RRV Discovery*, cruise D356). Quantitative ichthyoplankton collections in the upper 200 m were made, both day and night, at 94 stations using a MultiNet type Midi (Hydrobios™, mouth area: 0.25 m^2, mesh size: 500 µm) equipped with five nets and hauled obliquely from one depth to the next at 1 m s^{-1}
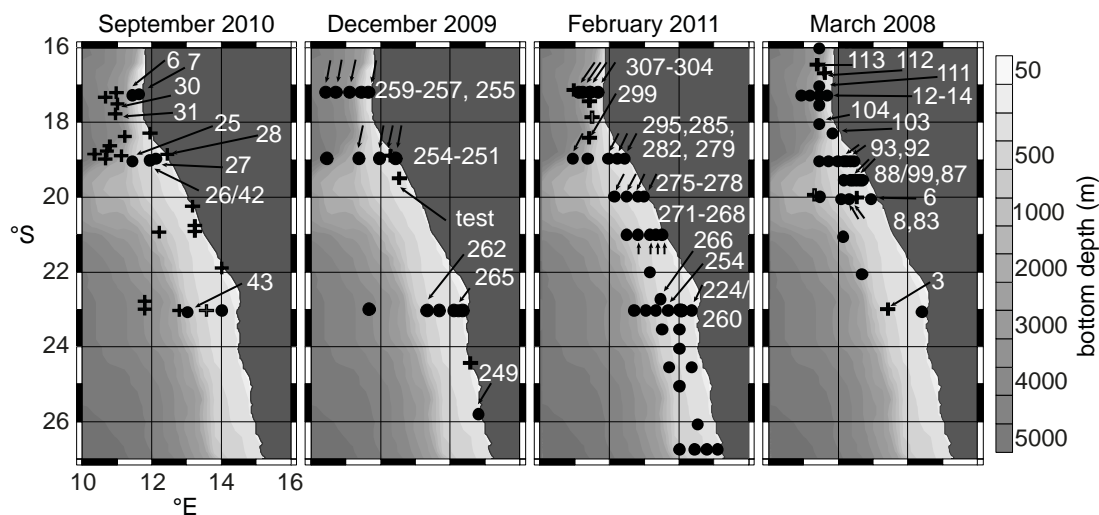
Fig. 1: Station grid of ichthyoplankton hauls during four research cruises ordered by season from austral spring to late-summer. Quantitative sampling with a MultiNet (black dots), and exclusively qualitative hauls (cross). Stations referred to in the text are indicated ('/' = similar latitude & longitude; ',' and '-' = similar latitude). Bathymetry as greyscale

ship speed from 200 m to the surface (Fig. 1). At each station the nets sampled in depth strata determined according to water column structure in terms of temperature and dissolved oxygen identified from preceding CTD-casts (Mohrholz, 2012 a-c and pers. comm.). Two of the nets were equipped with net-inlays (mouth diameter: 10 cm, mesh size: 55 µm) for simultaneous sampling of microzooplankton in the two uppermost depth strata, except in 03/2008. In order to augment the number of specimen used for stomach content, growth and biochemical analyses and to catch juveniles, additional hauls were made with a trawled or drifting ring net (mouth area: 2 m^2, mesh size: 1000 µm), a Tucker trawl (mouth area: 1 m^2, mesh size: 1000 µm) and a MOCNESS (mouth area: 1 and 2 m^2). Fish larvae were sorted on board and kept deep-frozen at -80°C immediately after catching until further analyses in the laboratory. After

removal of the larvae on board, the remaining catches of MultiNets were preserved in a 4% formalin-seawater-solution for community composition analyses of ichthyo-, zoo- and microzooplankton (net inlays catches). Samples for quantitative and qualitative phytoplankton analyses were taken from the mixed layer (usually upper 30 m) by means of a rosette sampler during the cruises in 2009-2011 (data courtesy of Wasmund, IOW).

Basic analyses and morphometric condition factor

Phytoplankton cells were counted according to the method of Uthermöhl (1958). Cell abundance was converted into bio-volume and –mass by means of their geometric shapes (Hillebrand *et al.*, 1999). The taxonomic composition of microzooplankton was identified according to Gibbons (1999) and Huggett and Bradford-Grieve (2007). Microzoo- and Zooplankton biomass was determined as drained wet mass after removal of all large gelatinous organisms (salps) and macrozooplankters (euphausiids and amphipods).

T. capensis were identified according to Olivar and Fortuño (1991) and Bianchi *et al.* (1999). Larval densities per station were calculated from the MultiNet catches for each single net (ind. 100 m^{-3}), and standardised per unit area (ind. 10 m^{-2}). Based on the observed depth distribution of the larvae, water temperature at 20 m was chosen to optimally compare the thermal regime between stations. Body length of larvae was measured as standard length (*SL*; notochord length in early larvae). In *Trachurus*, distinctive morphological developments occur at the following sizes (Arthur, 1976; Westhaus-Ekau, 1988; Olivar and Fortuño, 1991): 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. Accordingly, specimen were categorised into the following size classes: 3-4 mm = pre-flexion larva, 5-7 mm = flexion larva, 8-11 mm = post-flexion I larva, 12-15 mm = post-flexion II larva, 16-20 mm = transformation larva, and 21-40 mm juveniles.

Body mass was determined as dry mass (mg *DM*) using a high-precision balance after freeze-drying the larvae, which had their intestinal tract carefully removed. The morphometric condition factor (Heincke, 1908) adjusted for the species-specific length-weight relationship was calculated as:

$$k = GDM \, SL^{-b} \, 10^{-5} \tag{2}$$

where *GDM* is gutted dry mass (mg), *SL* is standard length (mm) and *b* is derived from species-specific potential length-weight regressions.

Daily growth rate

We used daily increments observed in otoliths to assess growth rates under different environmental conditions. Otoliths were removed from larvae and carefully cleaned, immersed in water using dissecting needles and subsequently dried. Otoliths from the smallest larvae (3-5 mm) were placed in a drop of Immersion Oil (Zeiss) on a cavity slide to increase contrast. Otoliths from larger individuals (6-16 mm) were mounted with epoxy resin, polished and ground with silicon carbide paper of respectively 2400 and 4000 granulation to reveal all growth increments. Daily increments have been validated in larvae of *Trachurus declivis* (Jordan, 1994), *T. trachurus* (Waldron and Kerstan, 2001) and *T. japonicus* (Xie *et al.,* 2005). We assumed *T. capensis* to behave similarly to its congeners. Daily growth rate (*DGR*) during the first month of life was estimated using back-calculations from growth increment readings of sagittal otoliths. Following the procedure described by Grote *et al.* (2012) the model of Folkvord and Mosegaard (2002) was applied:

$$SL_i = (OR_i \, OR_c^{-1})^w \, SL_c \qquad\qquad\qquad (3)$$

where SL_i is standard length (mm) at increment i, OR_i is the otolith radius (mm) at increment i, OR_c is the otolith radius (mm) at capture, *w* is the exponent of the potential regression between SL_c and OR_c (*w* = 0.55), and SL_c is the standard length (mm) at capture. For each specimen analysed, we calculated the mean *DGR* (*mDGR*) in two size classes (3-4 mm and 5-7 mm SL_i) from the respective individual *DGR*s. *DGR* was converted from length (mm) into biomass (g) using the length-weight regressions that were calculated for the species-specific condition factor *k*.

Trophic ecology

We used an integrated approach combining three methods to study the trophic ecology, namely analyses of gut contents, stable isotopes (*SI*) and fatty acids (*FA*).

Gut content analysis (intestinal tract) provides information about the ingested food items at the time of catch and allows for a high taxonomic resolution, but can be biased towards hard-structured, undigested items that are more easily identifiable. In the home laboratory, each frozen larva was thawed, its feeding incidence recorded, a stomach fullness index assigned (0 = empty to 5 = very full), the digestive tract carefully removed. Every food item was identified to the lowest possible taxonomic level under a dissecting microscope. Prey items were measured to the nearest 0.1 µm from digital images, using a Zeiss AxioCam Icc1 and Axiovision software. The bio-volume of each item was estimated according to its shape: the volume of a sphere for eggs and that of a cylinder for copepods and calyptopes larvae (prosome length and width) and for centric diatoms (height and diameter). The generalised

117

importance index (*%GII*; Assis, 1996) was calculated, using the relative values of abundance, bio-volume and the frequency of occurrence for each taxonomic group to compare the dietary composition of the different size classes. Prey selectivity index (*C*) of Pearre (1982) was calculated just for larvae collected in samples where concurrent microzooplankton data were obtained, and that contained ≥5 prey items. A positive or negative sign of the index indicates positive or negative selection respectively.

δ¹⁵N **stable isotope (SI) compositions** of *T. capensis*' muscle tissue and potential food organisms (phyto- and zooplankton) were analysed to obtain an intermediate to long-term record (>1 day) of metabolised food (Vander Zanden and Rasmussen, 2001). Sampling of phytoplankton is described and SI data of potential prey organisms already presented in Geist *et al.* (2013b). SI-data of Calanoida are taken from Schukat *et al.* (2013). All samples were rinsed in distilled water, freeze-dried and ground to a homogenous powder prior to transfer into tin capsules for elemental micro-analysis. If the individual body mass was too small to be measured, multiple specimens of similar size and from the same location were pooled. *SI*-compositions were analysed in a gas isotope ratio mass spectrometer (Thermo Finnigan, Delta Plus) after high-temperature combustion in an elemental analyser (Thermo Finnigan, Flash EA 1112) at ZMT Bremen with atmospheric air (*δ¹⁵N*) and PDB carbonate (*δ¹³C*) as reference standards.

Lipid analysis was applied as the third method for investigating trophic ecology. We used fatty acid trophic markers (*FATM*) as medium- to long-term record (>1 day) of metabolised food (Dalsgaard *et al.*, 2003) to reveal the relative importance of diatom- and autotroph-dinoflagellate-based prey in the diet of *T. capensis*' early stages. The fatty acids 16:1ω7, 18:1ω7 and 16:4ω1 were used as markers for diatoms, 18:4ω3 as dinoflagellate marker, and 18:1ω9, 20:1ω9 and 22:1ω11 as markers for heterotroph organisms indicating carnivory (Dalsgaard *et al.*, 2003). In addition to the *FATM* analysis, we used the contribution of total fatty acids, *TFA,* (% tissue dry mass) as a lipid-based condition measure (Dalsgaard *et al.*, 2003). *TFA*-content was analysed in muscle tissue of 102 and FA-composition of 121 individuals. Lipid extraction, fatty acid methyl ester preparation and FA-measurements were done according to Kattner and Fricke (1986) and as described in Peters *et al.* (2006). The internal standard, tricosanic acid (23:0), was added at the beginning of the extraction process to determine absolute amounts of *FA*. Gas chromatography measurements were conducted in the BreMarE laboratories, University of Bremen with settings described in Schukat *et al.* (2013).

Data analyses

Sample sizes (the number of larvae and juveniles) used in this study per cruise and for each analytical method are summarised in Table 1. Plots of depth-integrated larval abundance superimposed on water temperature at 20 m depth at sampling stations were constructed using Ocean Data View 4.5.0 software (30‰-DIVA-gridding). All statistical tests were performed using JMPpro 10.0.0 software. Categorical groups were tested either by Student's t-tests and Welch-ANOVAs or their non-parametric analogues of Wilcoxon tests (Mann-Whitney and Kruskal-Wallis-type), depending on whether preconditions were met. *TFA*-proportions were arcsin-square-root-transformed for all analyses, which require a normal distribution. Data averages are given as mean ± standard deviation, if not indicated otherwise. Statistical results are given in the form: "Value of test statistic$_{\text{(degrees of freedom, sample size)}}$ = X.XX". The relationships between condition factor and major environmental factors were analysed by cubic spline plots for four different size classes. The environmental factors shown were selected based on Principal Component Analysis and Generalised Linear Models (assuming Poisson distribution and log-link functions; not shown). Graphs were post-processed using Adobe Illustrator CS 5.1 software.

Table 1: Summary of sample sizes: number of *T. capensis* larvae used for each of the analyses of growth, diet, stable isotopes, lipids and condition per cruise. Due to inherent methodological constraints, it was not always possible to apply all analyses to each individual larva collected. The complete set of analyses within a method was only conducted on a subsample of the larvae

method	analysis	09/2010	12/2009	02/2011	03/2008	total
Abundance in MultiNets		134	115	750	596	1595
Growth	*DGR* 3-4 mm *SL*$_i$	8	13	21	16	57
	DGR 5-7 mm *SL*$_i$	5	10	12	13	40
diet	Gut fullness	52	34	123	119	328
	prey size	16	36	55	14	121
	voracity	16	40	60	26	142
	gut composition	16	40	62	29	147
	Prey selectivity	11	12	50	0	73
Stable Isotopes		4	31	27	70	132
lipid	*FA*-composition/*FATM*	19	13	45	44	121
	TFA content	19	11	43	29	102
Nutritional condition		55	76	87	191	409

Abbreviations: *DGR* = daily growth rate, *SL* = standard length, *FA* = fatty acid, *FATM* = fatty acid trophic markers, *TFA* = total fatty acid

RESULTS

Seasonal and geographical variations of water temperature, salinity and oxygen concentration

Water temperatures at 20 m depth (T_{20m}) during the four research cruises ranged from 10.5 to 28.9°C, and were on average lower during 09/2010 and 12/2009 than during 02/2011 and 03/2008 (Fig. 2). Temperatures usually increased with distance from the coast (Fig. 2). At stations on the shelf (<500 m depth) in the area between 24°S and 17°S, average T_{20m} was higher during 03/2008 and 02/2011 than during 12/2009 and 09/2010 (Table 2). Surface salinities were significantly higher during 03/2008 than during 12/2009 and 09/2010, but not 02/2011 (Table 2). The depth of the 2.5 mL O_2 L^{-1} isopleth was significantly shallower during 03/2008 than during 09/2010 and 02/2011 (Table 2). Warm sea surface temperatures (*SST*, >19°C) extended further southward during 02/2011 (19.1°C at 23.5°S) and 03/2008 (21.4°C at 22°S) than during 12/2009 (19.4°C at 19°S). At 23°S, the 14°C isotherm at inshore stations (65-250 m) was shallower during 09/2010 (at 0% and 25% of total depth) and 12/2009 (n = 3, 14-31% of total depth) compared to 03/2008 (n = 4, 29-56% of total depth) and 02/2011 (n = 7, 30-100% of total depth).

Table 2: Average water temperature at 20 m (*T20m*), surface salinity and depth of the 2.5 mL O_2 L^{-1} isopleth (mean ± standard deviation) at stations over the shelf (<500 m depths) in the main spawning area of *T. capensis* (17°S – 24°S) during the four research cruises. Cruises were compared using Wilcoxon tests. Data source: Mohrholz (2012 a-c and unpublished data)

	09/2010	12/2009	02/2011	03/2008	χ^2	p-value
n	8	10	28	28		
T_{20m} (°C)	14.97 ± 0.87	16.03 ± 1.92	18.54 ± 2.17	18.33 ± 1.50	24.61	< 0.0001
Salinity at surface	35.32 ± 0.24	35.24 ± 0.17	35.46 ± 0.27	35.58 ± 0.16	18.09	0.0004
Depth of 2.5 mL O_2 L^{-1} (m)	84.0 ± 37.8	55.5 ± 46.5	69.9 ± 59.5	30.7 ± 18.0	16.35	0.0010

Spatial distribution of T. capensis larvae in relation to temperature and dissolved oxygen

During the four research cruises 1595 larvae of *T. capensis* were caught in quantitative MultiNet hauls at 57 of a total of 101 stations sampled. In addition, larvae occurred at another 20 stations, which were sampled only qualitatively (Fig. 2). During the late summer cruises (02/2011 and 03/2008) larvae were more abundant than during the spring and early summer cruises (09/2010 and 12/2009, Fig. 2). During all four cruises, the principal area of larval distribution was located between 17°S and 20°S, and only in 02/2011 high abundances also occurred around Walvis Bay (~23°S, Fig. 2). Most of the larvae were caught within the upper 50 m of the water column (Fig. 3) and at *in-situ* temperatures (at net closing depth) between 15

and 20°C (n = 113 nets, median = 18°C), with a thermal range of occurrence between 12.8 and 25.7°C (Fig. 3). *T. capensis* larvae occurred at a wide range of dissolved oxygen levels between 0.13 and 6.35 mL O_2 L^{-1} (n = 107 nets, median = 4.28 mL O_2 L^{-1}; Fig. 3).
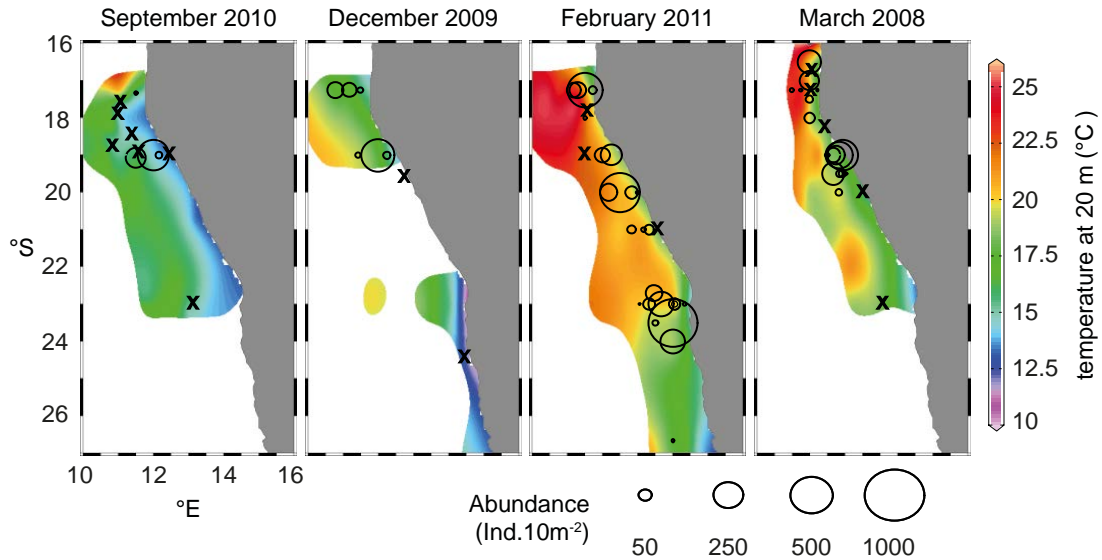
Fig. 2: Spatio-temporal distribution of *T. capensis* larvae and temperature at 20 m depth in sequence of season from different years. Circles indicate larval abundance (Ind. 10m^{-2}); crosses indicate the presence of larvae in qualitative catches when no parallel positive catch was made in quantitative hauls. Temperature data is taken from CTD-casts (Mohrholz 2012 a, b, c, unpublished data) extrapolated with 30‰-DIVA-gridding (ODV version 4.5)
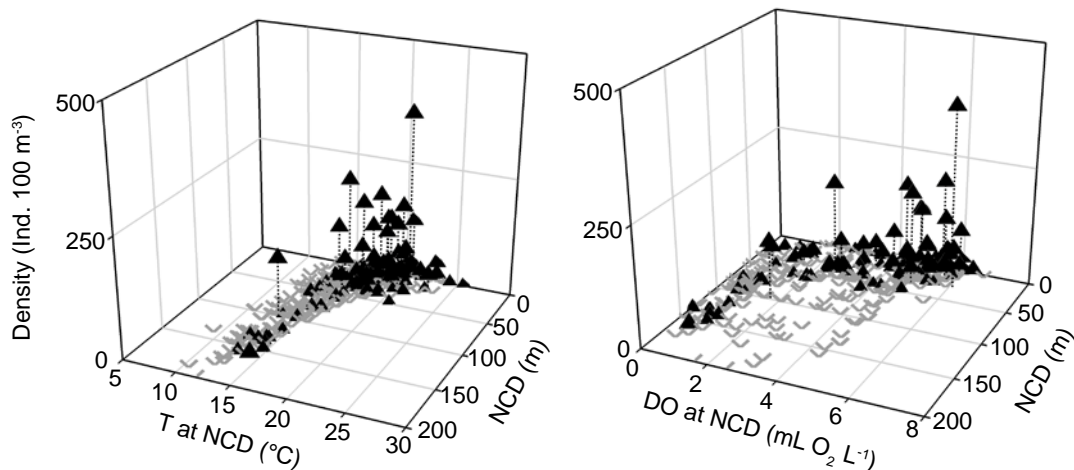
Fig. 3: Densities of *T. capensis* larvae (black triangles) for each net from quantitative MultiNet hauls in relation to water temperature and dissolved oxygen concentration (DO) at closing depth of the respective net (NCD). Grey crosses indicate empty nets. Temperature and oxygen data taken from CTD casts (Mohrholz, 2012 a,b,c, unpublished data)

Back-calculated mean daily growth rate (mDGR) in pre- and early post-flexion stage

mDGR, (mm *SL* d^{-1}) back-calculated from daily otolith increments ranged from 0.14 to 0.40 in the pre-flexion stage (3-4 mm SL_i, n = 57) with an average of 0.24 ± 0.06 (mean ± standard deviation) and from 0.13 to 0.47 in the post-flexion I stage (5-7 mm SL_i, n = 40) with an average of 0.28 ± 0.09. This is equivalent to an average daily increase in body mass of 0.094 ± 0.005 mg *DM* d^{-1} at a size of 3.5 mm SL_i and of 0.49 ± 0.02 mg *DM* d^{-1} at a size of 6 mm SL_i. When comparing between seasons, m*DGR* was lower during 09/2010 than during 02/2011 and 03/08 in both size classes (Fig. 4, $\chi^2_{(3, 57)}$ = 22.20, p < 0.0001 and $\chi^2_{(3, 40)}$ = 13.71, p = 0.0033, respectively). *mDGR* at single stations (only stations with ≥ 3 individuals considered) generally followed the seasonal trends, with the exception that at 3-4 mm SL_i *DGR* at Stat.276 (02/2011) was low (Fig. 4, $\chi^2_{(11, 46)}$ = 3.33, p = 0.0034). At a size of 5-7 mm SL_i, *mDGR* at Stat.26 (09/2010) was significantly lower than at Stat.275 (02/2011) while *mDGR* of larvae at Stat.305 were higher compared to the other stations (Fig. 4, $\chi^2_{(8, 30)}$ = 16.97, p = 0.0305). *mDGR* in the pre-flexion stage was linearly correlated with T_{20m} (n = 56, R^2 = 0.30, a = -0.032 ± 0.058, b = 0.0149 ± 0.003, p<0.0001) within a temperature range of 14.3-21.4°C. In contrast, *mDGR* in the post-flexion I stage did not show a correlation with temperature (15.7-21.4°C).
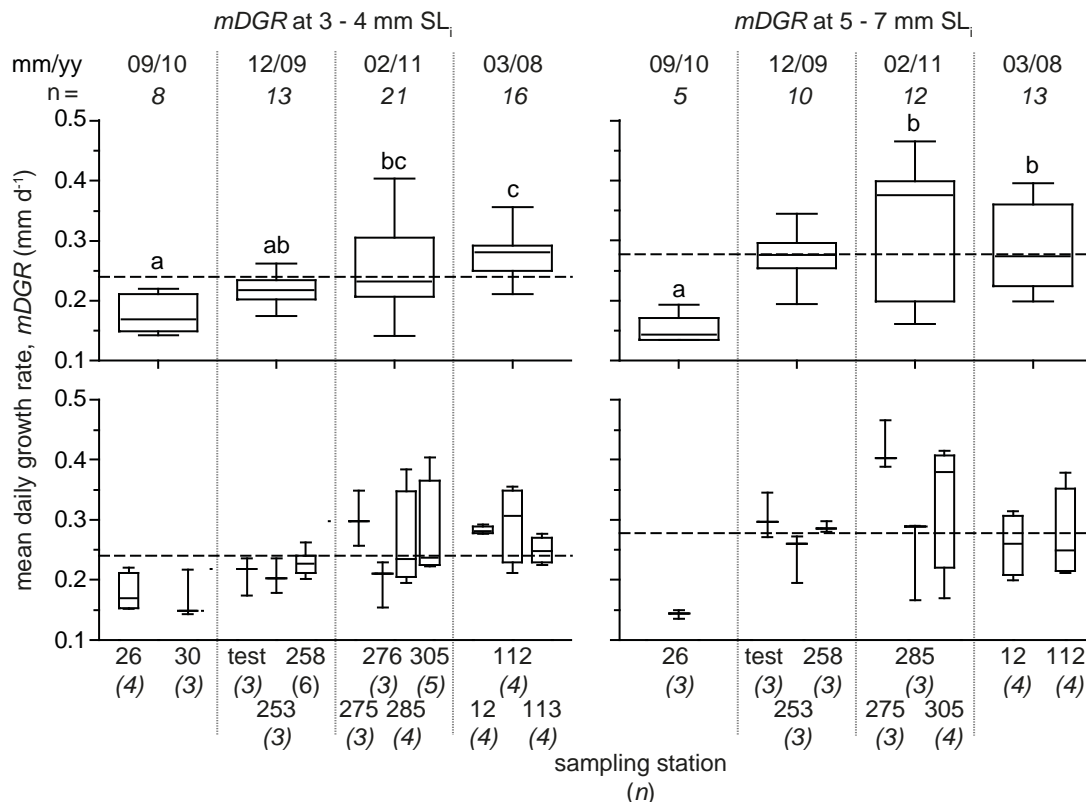
Fig. 4: Variation of mean daily growth rates (*mDGR*) at two different size classes derived from back-calculated data (*SL$_i$*, standard length back-calculated) between seasons (top), and stations if n≥3 (bottom), ordered by season, and within season from north to south). Shown as box-whisker-plots with mid-line, box and whiskers (median, 1st and 3rd quartiles, and range) in sequence of season from austral spring to late summer. X-axis labels show station numbers and respective number of specimen examined (in parentheses)

Trophic ecology of T. capensis early stages and microzooplankton composition
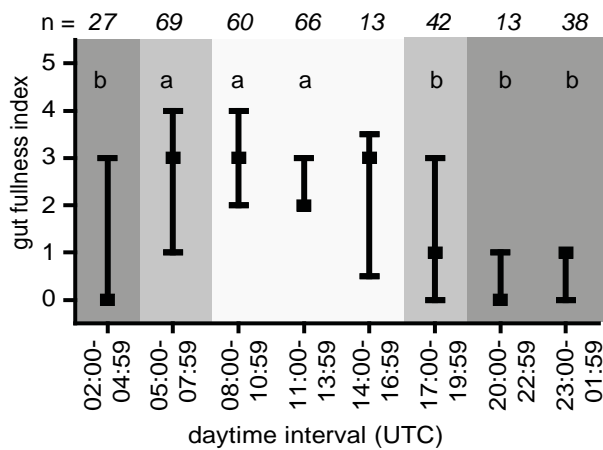
Fig. 5: Diel variation of mean gut fullness index (from 0 = empty to 5 = very full) in 3 h – intervals (median and interquartile range), a and b indicate two significantly different groups of daytime intervals (Wilcoxon test, $\chi^2_{(7,\ 328)}$ = 70.70, p<0.0001 followed by Dunn's post hoc test)

T. capensis larvae showed a feeding incidence of >75%, with 250 of 328 individuals examined containing food items in their digestive tracts (stomach and gut). A significant diel variation in feeding incidence was observed, with highest gut fullness during the period 05:00 a.m. - 16:59 p.m. UTC (Fig. 5, $\chi^2_{(7,\ 328)}$ = 70.70, p<0.0001).

The development of prey characteristics with body size was analysed in 121 larvae with full guts over the size range 3-20 mm *SL*. The upper range of individual prey width and prey volume increased with larval body size (Fig. 6 a, b). The number of prey items per gut, voracity, also increased with larval size and showed a clear step-up around 8 mm (Fig. 6 d). In contrast, the trophic niche breadth (after Pearre, 1986) remained fairly constant throughout the investigated size range (Fig. 6 c).
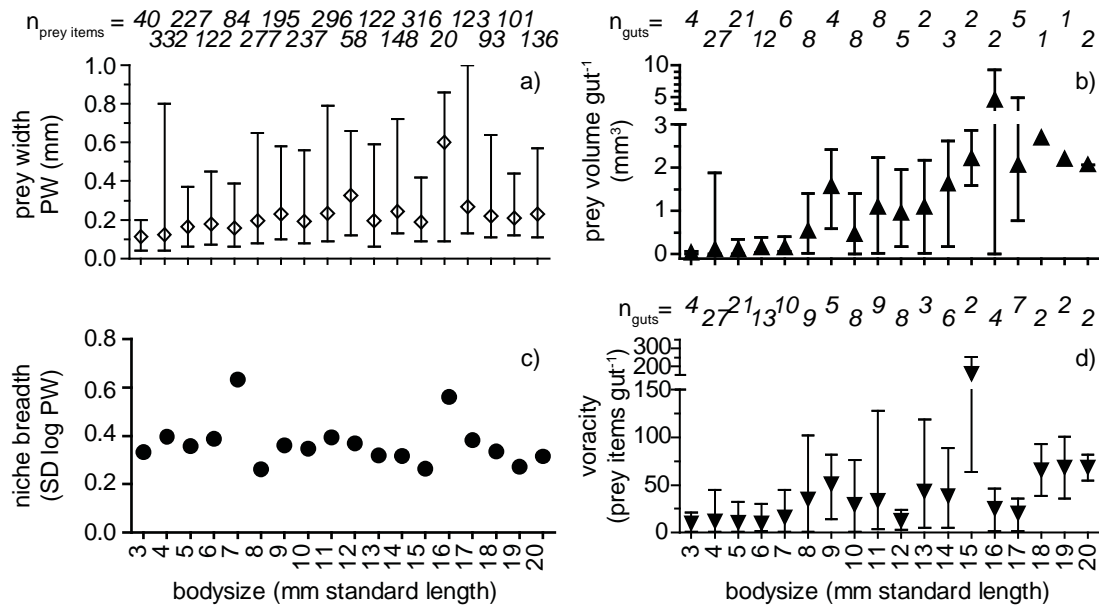
Fig. 6: Development of prey characteristics of *T. capensis* larvae over a size range of 3-20 mm standard length: a) prey width; b) total prey volume per gut; c) trophic niche breadth (Pearre, 1986), and d) voracity. Data are shown as mean and range, except in (c). The number of analysed guts and prey items therein are the same in (a), (b) and (c), and the number of analysed guts is different in (d), as shown above the respective graphs

Different size- and taxonomic groups of Copepoda dominated the ***gut content composition*** throughout the investigated size range of larvae and juveniles (3-40 mm *SL*, n= 147; Fig. 7). Copepod eggs (n = 120, diameter = 0.20 ± 0.20), nauplii (n = 126, prosome width (PW) = 0.12 ± 0.08, prosome length (PL) = 0.23 ± 0.15; mean ± standard deviation) and Harpacticoida (n = 146, PW = 0.10 ± 0.02, PL = 0.35 ± 0.09) were important in pre-flexion larvae (3-4 mm). *Oncaea* sp. (n = 500, PW = 0.17 ± 0.05, PL = 0.31 ± 0.08) and *Oithona* sp. (n = 1610, PW = 0.18 ± 0.03, PL = 0.35 ± 0.05) made up similar proportions in the different size classes from 5-20 mm *SL*. Both the relative importance and the mean prosome length of Calanoida present in the gut contents increased from larval to juvenile size classes (Table 3).
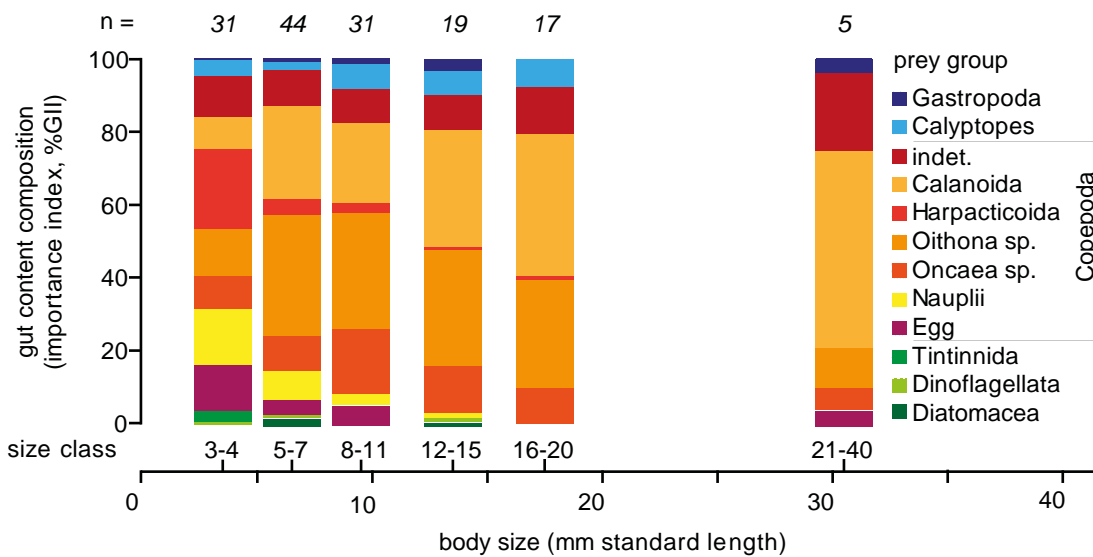
Fig. 7: Gut content composition of *T. capensis* larvae divided into six size classes according to morphological developmental stages, expressed as "general importance index, %GII" incorporating relative abundance, bio-volume and frequency of occurrence of prey items. Sample size (n) refers to the number of guts analysed per size class

Table 3: Prosome length and width (both in mm, mean ± standard deviation) of calanoid copepods found in guts of *T. capensis* larvae of six different size classes (SL, in mm)

Larval size (SL)	3-4	5-7	8-11	12-15	16-20	21-40
n Calanoida	84	101	128	142	174	23
Prosome length	0.22 ± 0.13	0.48 ± 0.25	0.69 ± 0.28	0.72 ± 0.26	0.82 ± 0.26	1.22 ± 0.44
Prosome width	0.10 ± 0.05	0.21 ± 0.10	0.31 ± 0.10	0.32 ± 0.11	0.35 ± 0.13	0.44 ± 0.12

Different copepod groups also dominated the microzooplankton community (Fig. 8). Two or three groups usually made up for >50% of total abundance with differences between the cruises. Copepod nauplii dominated in 12/2009 and copepod eggs and Harpacticoida in 02/2011. In 09/2010, the community structure was more variable between sampling stations (Fig. 8).

Fig. 8: Taxonomic composition of micro-zooplankton caught with a 55μm inlay net in the uppermost stratum of MultiNet catches (ca.20-0 m depth) during 09/2010, 12/2009 and 02/2011 (not sampled during 03/2008)
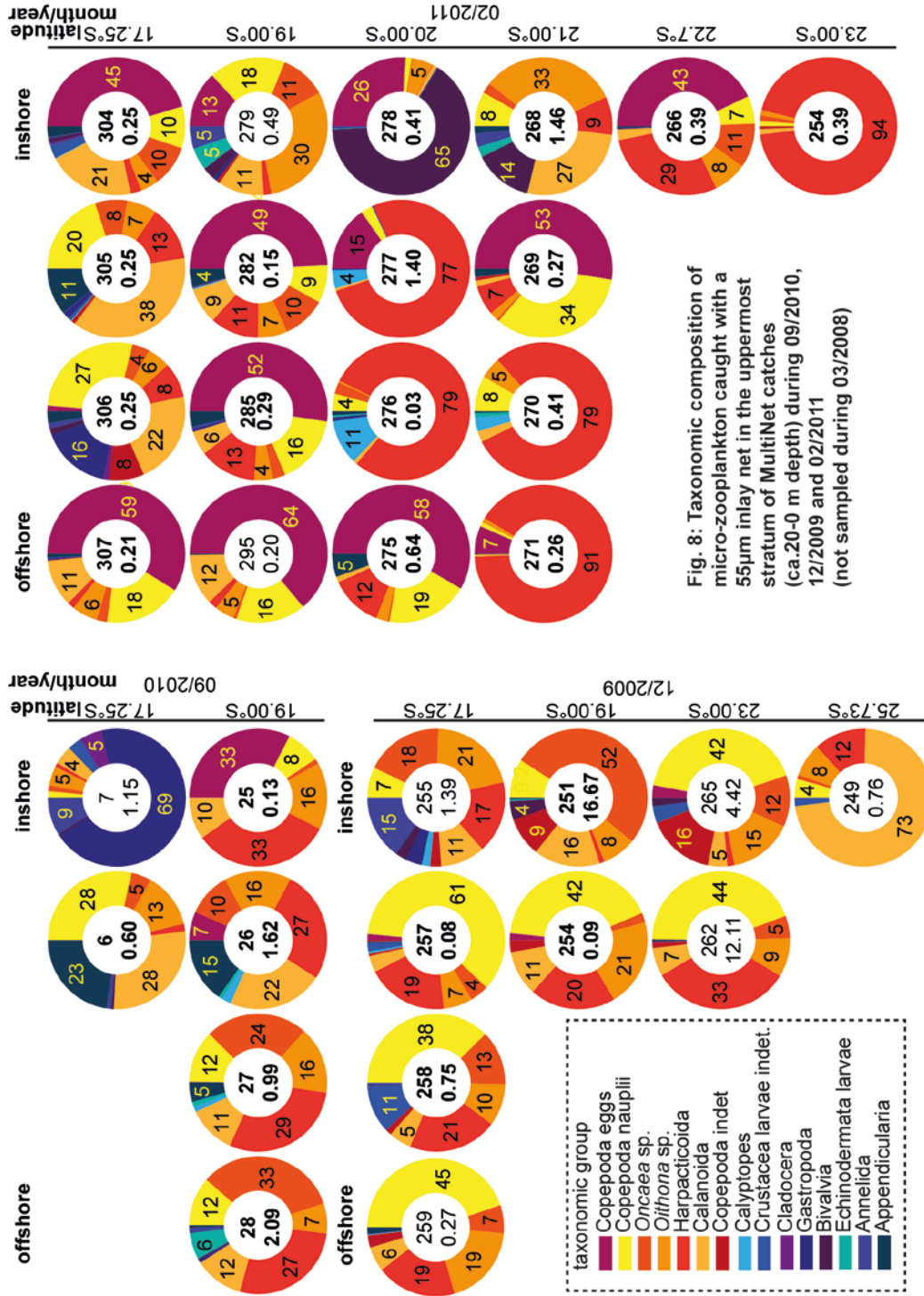
Within each year stations are ordered by latitude and by their relative position to the coastline. The different Copepoda groups are shown in shades of yellow-orange-red. Proportions of major groups are given as %. The numbers inside the rings indicate sampling station number (top) and biomass in g wet mass per 100 m towing distance (bottom), bold typing if *T. capensis* larvae were present

125

The six most important prey groups (copepod eggs, copepod nauplii, Harpacticoida, *Oncaea* sp., *Oithona* sp. Calanoida) were differently selected by *T. capensis* larvae depending on larval size class (Fig. 9). In some cases similarly sized larvae also showed seasonal differences, e.g. larvae in the size class 8-11 mm selected Harpacticoida and *Oncaea* sp. positively during 02/2011 but negatively during 09/2010 (Fig. 9). Copepod eggs and nauplii were mostly negatively selected from 5 mm *SL* onward. Selection of Poecilostomatoida and Cyclopoida (*Oncaea* and *Oithona*) was highly variable. Harpacticoida were negatively selected in most cases, in line with their low importance for gut content composition. Calanoida were selected positively at larger body size (Fig. 9).
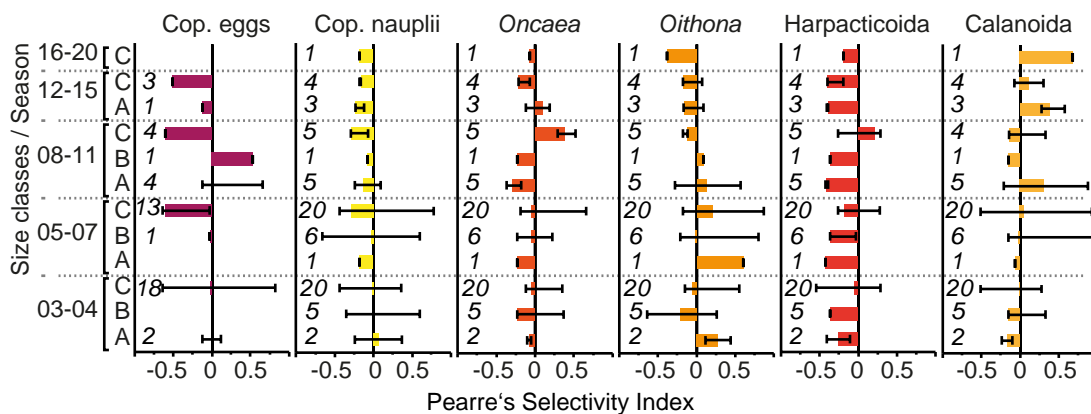
Fig. 9: Selection by five size classes of *T. capensis* larvae of the six most important prey groups derived from gut content composition analysis, calculated using the relative abundance of major zooplankton groups in the guts and *in situ*. Selectivity is shown as median and range per season/cruise, size group calculated with respective individual selectivity (respective n are indicated at the left of prey group graphs). Values >0 indicate positive selection, those <0 negative selection. The label columns on the y-axis refer to larval size class and cruise ordered by season (A = 09/2010, B = 12/2009, C = 02/2011)

In addition to gut content, δ^{15}***N-ratios*** of muscle tissue were analysed from 132 individuals, categorised into the same size classes caught during all four cruises to obtain information about metabolised prey. Median δ^{15}*N-ratios* of *T. capensis* tissue were in the same range as those of sardine, *S. sagax*, and anchovy, *E. encrasicolus* with the exception of 09/2010 (Fig. 10). *T. capensis* δ^{15}*N*-signatures were always higher than phytoplankton and copepod signatures, except for the large calanoid species *Rhincalanus* sp. (Fig. 10). At three stations, from where a broad size range of *T. capensis* early stages was analysed, a significant linear correlation was found between body size and δ^{15}N-signatures (02/2011 Stat.224, n = 7, size range = 15-49 mm, b = 0.027, R^2 = 0.84, p = 0.0036; 12/2009 Stat.test, n = 25, size range = 7-16 mm, b = 0.136, R^2 = 0.29, p = 0.0054; 03/2008 Stat.13, n = 11, size range = 10-45 mm, b = 0.075, R^2 = 0.83, p < 0.0001). This was in agreement with the general trend that was observed in samples from different stations in respective cruises (Fig. 10).
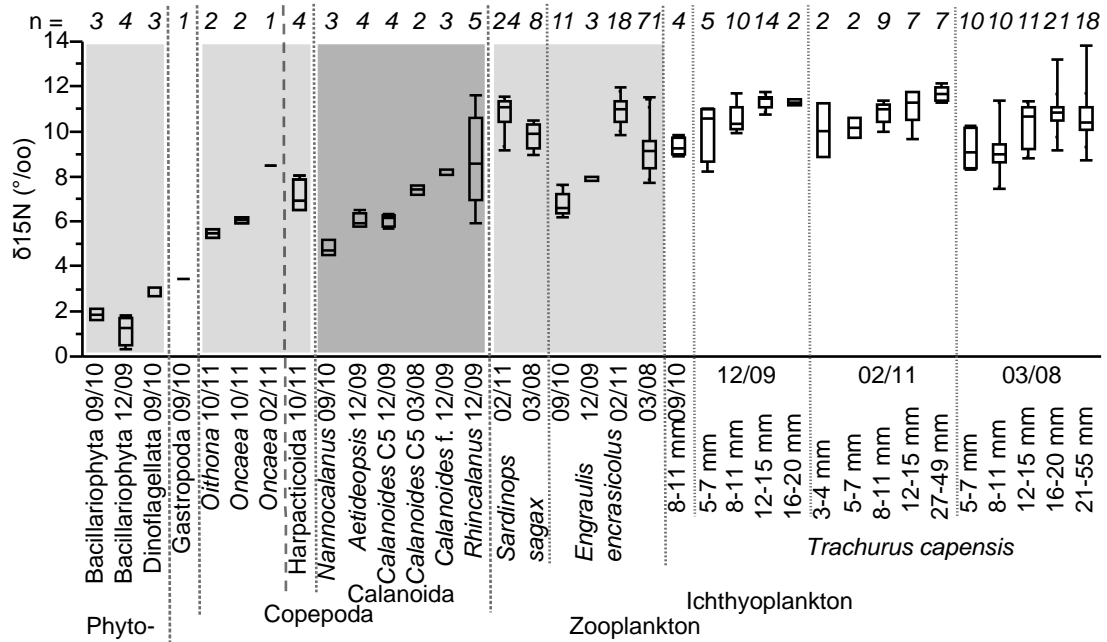
Fig. 10: δ¹⁵N signatures of larvae and juveniles of *T. capensis* (divided into size classes) and clupeoid (*S. sagax*, *E. encrasicolus*) and potential prey items. Each group calculated separately for cruises and ordered in sequence of season from austral winter to summer. Phytoplankton samples were mixed samples dominated by *Coscinodiscus walesii* ("Bacillariophyta", diatoms) or *Noctiluca* scintillans ("Dinoflagellata"). "Gastropoda" is *Limacina* sp. and "Harpacticoida" is *Microsetella* sp. Mid-line, box and whiskers represent median, 1ˢᵗ and 3ʳᵈ quartile and range. Labels on the x-axis show taxonomic levels, size classes in mm *SL* (*T. capensis* only) and time of year (mm/yy). Data already presented in other publications and shown here for comparative purpose are highlighted with different shades of grey: Calanoid data (dark grey) taken from Schukat *et al.* (2013) and clupeoid and prey item data (light grey) from Geist *et al.* (2013b)

The ***fatty acid (FA) composition*** of muscle tissue was analysed in 119 early-stage *T. capensis* in the size range 3-55 mm *SL* and in 102 of these individuals, measuring 4-49 mm *SL*, the total *FA* (*TFA*) content was also measured. Average *TFA* content was $3.78 \pm 0.97\%$ *DM* and did not change significantly with body size. No seasonal difference was detected. Spatially, *TFA* content was significantly higher in larvae from Stat.269 (n = 4, 6.6 ± 2.2) compared to Stat.224 (n = 7, 3.2 ± 0.6), which were both sampled during 02/2011 ($\chi^2_{(16, 75)} = 33.71$, p = 0.0059). Over the entire size range examined, five FAs contributed proportions >5% of *TFA*: the saturated *FA*s, palmitic (16:0) and stearic (18:0) acid; the monounsaturated oleic acid (18:1) and the polyunsaturated *FA*s eicosapentaenoic (*EPA*, 20:5ω3) and docosahexaenoic acid (*DHA*, 22:6ω3; Supplementary online material). Fatty acid trophic markers (*FATM*) for diatoms ($4.88 \pm 1.18\%$ *TFA*, mean ± S.D.) and dinoflagellates ($0.92 \pm 0.46\%$ *TFA*) were not correlated with body size. The proportions of *FATM* for dinoflagellates were significantly different between seasons, with 03/2008>09/2010 and 02/2011 (ANOVA on seasons, $F_{(3,119)} = 10.90$, p<0.0001). In contrast to phytoplankton markers, *FATM* for heterotroph organisms ($7.01\% \pm 1.97\%$ *TFA*) were linearly correlated with body size (a = 5.48 ± 0.27, b = 0.13 ±

0.02, $R^2 = 0.37$, p < 0.0001). Similar to the dinoflagellate *FATM*, a seasonal difference was detected, with 03/2008 and 02/2011>09/2010>12/2009 (ANOVA on seasons with body size as continuous cofactor, $F_{(4, 119)} = 16.39$, p<0.0001).

Nutritional condition

The nutritional condition factor k was calculated with a species-specific length exponent b derived from a power fit between body length and mass (n = 316, R^2 = 0.95, a = 0.0014 ± 0.0919, b = 3.178 ± 0.040, as mean ± standard error). When compared seasonally, k was significantly lower during 12/2009 than during 02/2011 and 03/2008 (Fig. 11, $\chi^2_{(3, 409)} = 44.97$, p<0.0001). During 02/2011, a geographic trend in larval condition with an increase towards the north was observed (Fig. 11).

Relationships between condition factor k and major environmental factors were analysed using cubic spline plots for the larval size classes (Fig. 12). In relation to T_{20m}, smaller larvae (3-7 mm *SL*) showed a Gaussian preference window with highest k values at T_{20m} of around 19-20°C. The optimal depth of the

Fig. 11: Variation of condition factor k between seasons (top) and stations if n≥3 (bottom, ordered by season, and within season from north to south). Shown as box-whisker-plots with mid-line, box and whiskers (median, 1st and 3rd quartiles, and range) in sequence of season from austral spring to late summer. X-axis labels show station numbers and respective number of specimen examined (in parentheses). k calculated with gutted dry mass (*GDM*) and standard length (*SL*)

17°C isotherm was shallower for smaller larvae (3-7 mm SL) compared to post-flexion I larvae. k of post-flexion II larvae was not affected. In relation to the depth of the 2.5 mL $O_2 L^{-1}$ isopleth, k decreased from 30 to 100 m depth in all size classes. With the exception of post-flexion I larvae, a negative relationship over the entire depth range was observed for the 1.0 mL $O_2 L^{-1}$ isopleth. At shallower stations k of larvae <12 mm was higher. Diatom biomass did not affect k when levels were below ca. 300 mg m^{-3}, but above this limit k of flexion and post-flexion I larvae started to decrease. In relation to autotroph dinoflagellate biomass, pre- and

post-flexion I larvae showed an inverse response, with pre-flexion larvae responding positively to elevated dinoflagellate biomass, whereas post-flexion II larvae did not respond at all. The condition factor *k* of pre-flexion larvae increased with increasing bulk zooplankton biomass. Larvae of 5-11 mm showed a declining *k* between ca. 10 and 100 g zooplankton biomass m^{-2} and an increase in nutritional condition at zooplankton concentrations >100g m^{-2} (Fig. 12).
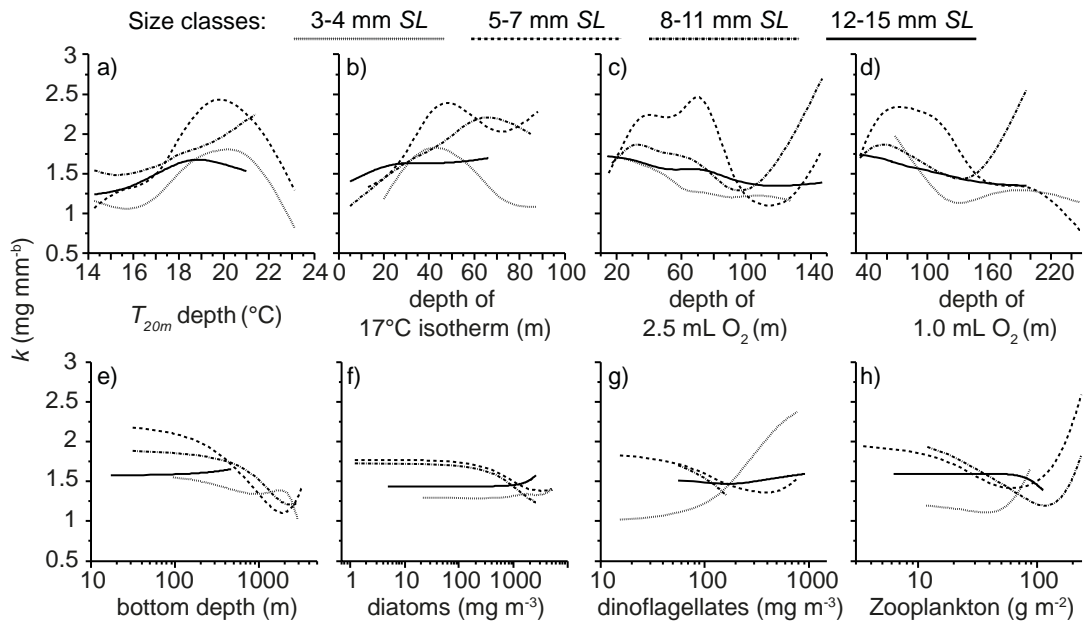
Fig. 12: Relation of condition factors of *T. capensis* larval size classes to major environmental factors shown by cubic spline plots. Plots constructed with: a) λ = 10, n per size class (in sequence of size classes) = 40, 125, 105, 55. b) λ = 10 000, n = 30, 105, 68, 22. c) λ = 10 000, n = 40, 103, 78, 40. d) λ = 100 000, n = 36, 100, 68, 25. e) λ = 1 E +9, n = 42, 132, 90, 47. f) λ= 1 E +10, n = 34, 56, 24, 10. g) λ = 10 000 000, n = 34, 56, 24, 10. h) λ = 100 000, n = 31, 64, 38, 18

DISCUSSION

An array of ELH traits of the dominant pelagic fish species in the NBCE, *T .capensis,* was investigated with focus on their spatial distribution, feeding ecology, nutritional condition and growth rate in relation to ambient conditions (e.g. water temperature, dissolved oxygen concentration and zooplankton composition) and with regard to seasonal variations. In the following, we particularly highlight differences to larval stages of formerly dominant clupeoid species caught during the same cruises (Geist *et al.*, 2013b), that potentially favour *T. capensis,* and that can explain their comparatively high recruitment success under changed environmental conditions in the degraded NBCE (van der Lingen *et al.*, 2006b, Hutchings *et al,.* 2009, Bakun *et al.*, 2010, Ekau *et al.*, 2010).

T. capensis larvae occurred mainly over the shelf where a high condition factor *k* indicated favourable feeding conditions. Their vertical distribution was similar to that of anchovy and sardine larvae that were usually caught within the upper 50 m of the water column (Geist *et al.*, 2013b). *T. capensis* larvae occurred along the entire latitudinal range of the NBCE, but were most abundant in the region north of 20°S, in contrast to sardine larvae that were mainly found around 23°S (Geist *et al.*, 2013b). Based on this distribution pattern, *T. capensis* larvae show less overlap with areas of high jellyfish concentrations and have a lower risk for food competition and predation through the latter (Flynn *et al.*, 2012). Moreover, larvae of *T. japonicus* have been shown to be less affected by jellyfish predation than anchovy larvae (*E. japonicus*) and can even use them as a refuge and prey collector (Masuda, 2009).

T. capensis larvae were present during all seasons covered by the four research cruises, however higher abundances and a better nutritional condition infer better recruitment during late summer. Indeed, their overall higher abundance compared to clupeoid species, and their relatively evenly distributed densities over a larger area enhance the chances of *T. capensis* larvae to encounter favourable environmental conditions necessary for successful recruitment.

T. capensis larvae occurred at water temperatures up to T_{20m} = 25.7°C, their nutritional condition factor *k* was highest at a T_{20m} of 18-22°C and for small larvae (<8 mm) at a shallow 17°C isotherm depths. These traits are indicative of a preference for warmer water and quiescent upwelling conditions especially during the early larval stages. These results are in agreement with a previous report (albeit based on one sampling station only, O'Toole, 1977) and support the general hypothesis that *T. capensis* is favoured by warmer conditions (Shannon *et al.*, 1988), which similarly applies to anchovy but differs from sardine larvae (Geist *et al.*, 2013b). The occurrence of horse mackerel and anchovy larvae over a wider temperature range and at higher temperatures than sardines has also been reported from the north-east Atlantic (Ibaibarriaga *et al.*, 2007). Compared to anchovy (8-22 mm SL), horse

mackerel (4-18 mm SL) larvae had significantly higher total fatty acid content in their dorsal muscle tissue during all seasons investigated. This indicates perennially better feeding and, hence, better nutritional condition of *T. capensis* ($\chi^2_{(2, 130)}$ = 19.51, p<0.0001, with data of sardine and anchovy from Geist *et al.*, 2013b). In 02/2011, *TFA*-levels as well as nutritional condition factor *k* were lower at stations around Walvis Bay (e.g. Stat.224, 266) where total ichthyoplankton density was high. This observation indicates that high larval density may lead to food competition and subsequently causes low nutritional condition and in consequence affects recruitment success. Similarly, low nutritional conditions were found in clupeoid larvae at the same stations (Geist *et al.*, 2013b).

With regard to dissolved oxygen, *T. capensis* larvae were still present at concentrations as low as 0.12 mL O_2 L^{-1}. This is in agreement with a parallel respirometry study of juvenile *T. capensis* that revealed a physiological adaptation to cope with low oxygen conditions and indicated that this adaptation is already present in the larval stages (Geist *et al.*, 2013a). The extension of low oxygen concentrations to the upper water layers is increasingly observed in the NBCE (Ekau *et al.*, 2010). A tolerance of lower oxygen concentrations could favour *T. capensis* larval survival as it allows them to undertake vertical migrations into deeper, onshore currents thus ensuring retention, according to the vertical migration/retention model of Stenevik and Sundby (Kjesbu, 2009).

Mean daily growth rate of *T. capensis* during the pre- and post-flexion stages were within the range of *T. declivis* from eastern Tasmania (Jordan, 1994), but lower than those of *T. lathami* from tropical south-eastern Brazil (Katsuragawa and Ekau, 2003), and higher than in *T. symmetricus* from the California Current (Hewitt *et al.*, 1985). Growth rates in fish larvae depend on water temperature (e.g. Wootton, 2011) and ingestion rates (Checkley, 1984); hence the observed difference is likely attributable to better feeding conditions and slightly higher temperatures compared to the Californian upwelling system. In the pre-flexion stage, a relationship between daily growth rate and water temperature was found, which follows the general relation of higher metabolic activity with increasing temperatures within the natural thermal window of a species. This could also suggest better feeding conditions under quiescent upwelling conditions. The lack of a correlation during the post-flexion I stage suggests an increased influence of feeding success on the growth rate due to an increase in foraging potential after flexion, which might mask the temperature effect. Successful feeding is crucial for good recruitment success, as demonstrated by the identification of starvation as a major factor influencing the mortality of *T. symmetricus* larvae (Hewitt *et al.*, 1985).

The general features of *T. capensis* larval feeding ecology with different copepod stages and groups forming the main prey and daytime feeding are comparable with observations of larvae

of *T. symmetricus* (Arthur, 1976), *T. declivis* (Young and Davis, 1992) or *T. japonicus* from the East China Sea (Sassa and Tsukamoto, 2012). Daytime feeding and ingestion of copepods as main food source are also characteristic of juvenile and adult *T. capensis* (Pillar and Barange, 1998). The observed dietary shift during the early ontogeny of *T. capensis* towards a higher relative importance of larger prey items together with an increase in trophic level in older stages indicates a change in their position in the planktonic food web. The smaller copepod groups (nauplii, Cyclopoida and Harpacticoida) feed on small prey items and/or on sinking detrital aggregates (Richardson and Verheye, 1999; Kattner *et al.*, 2003; Maar *et al.*, 2006). Likewise, our observation that pre-flexion larvae were in higher nutritional condition at higher ambient dinoflagellate biomass and dinoflagellates were absent in their guts, infers mediation via feeding on small zooplankton. The ability of larvae to obtain significant portions of their energy demand from cyclopoid and poecilostomatoid copepods until the post-larvae stage (16-20 mm) could be another advantage of *T. capensis* over clupeoid species, since they were far less abundant in the guts of sardine and anchovy larvae (Geist *et al.*, 2013b). These small copepods are believed to proliferate during periods of quiescent upwelling and stable conditions (van der Lingen *et al.*, 2006a) This is a typical situation during "warm-water events", which have been increasingly observed for the last 20 years, especially during summer (Bartholomae and van der Plas, 2007). Parallel, *Oithona* increased in abundance during the last ten years in the NBCE (Verheye and Kreiner, 2013). High water temperatures and salinities over the shelf during 02/2011 and 03/2008 are indicative of such warm water intrusions.

However, the constantly high proportions of diatom *FATM* throughout the ontogenetic development of *T. capensis* emphasize the importance of diatom-derived food; probably the dominant calanoid copepod in the NBCE, *Calanoides carinatus* is acting as an important link (Verheye *et al.*, 2005; Schukat *et al.*, 2013). The larger sized Calanoida occupy higher trophic levels in the NBCE (Schukat *et al.*, 2013). Thus, the correlation of larval size with a higher proportion of heterotrophy *FATM* is likely caused by the increasing average size of calanoid prey paralleled by an increasing degree of carnivory by these copepods.

In a comparison of daily growth rate at the size of 6 mm, with growth expressed in terms of biomass rather than body size, larvae of *T. capensis* grow faster (65.5 µg d^{-1}) than anchovy (25.0 µg d^{-1}) and sardine larvae (9.0 µg d^{-1}; with data from Geist *et al.*, 2013b). This reflects the more substantial body shape (stout vs. slender) and higher robustness of *Trachurus* compared to clupeoid species (Arthur, 1976). It is also an indication of a higher feeding success of *T. capensis* larvae in the NBCE compared to clupeoid larvae. This is likely a result of higher feeding incidence and voracity probably afforded by their proportionally larger mouth (Arthur, 1976), accessibility of a higher diversity of prey and high plasticity in prey

selectivity. The gut of *Trachurus* larvae is looped and readily developed at ~12 mm (Westhaus-Ekau, 1988). Assuming that early onset and quick development of gut differentiation are reflected by a higher digestive effectiveness, the earlier gut differentiation of *Trachurus* compared to clupeoid larvae is another advantage allowing for a high biomass growth rate. A higher digestive effectiveness with increasing body size during *T. capensis* ontogeny may be an important stage-specific feature representing the end of a critical period and might explain the weak/neutral response of the condition factor *k* to environmental factors in post-flexion II larvae (12-15 mm).

Another important factor in this regard is the development of better swimming capabilities with increasing body size, since foraging range and, as consequence, availability of food sources increase. Indeed, increasing burst swimming capacities with size have been demonstrated in larvae of the congener *T. japonicus* (Masuda, 2009). These capacities were better than in *Engraulis japonicus* larvae, moreover allowing for a more effective anti-predator performance against jellyfish (Masuda, 2009, 2011).

Shoaling of the oxygen minimum zone can compress the habitat of vertical migrating species (Seibel, 2010), probably affecting vertical distribution of copepod species in the NBCE (Auel and Verheye, 2007). Thus, the shallower depth of hypoxic waters during 03/2008 compared to 02/2011 might have caused higher zooplankton densities in the upper water layers. Higher plankton densities increase encounter rates with predators and the agile *T. capensis* larvae, following a strategy of active predator avoidance, are more likely to survive under these conditions in comparison to clupeoid larvae, which exhibit a passive strategy expressed by a more transparent, less conspicuous appearance. In consequence, the resulting lower total densities of fish larvae together with high prey densities represent better feeding conditions for *T. capensis* larvae and can explain their higher nutritional condition during late summer 2008 compared to late summer 2011.

In conclusion, we found evidence that ELH traits of *T. capensis* permit successful recruitment under the prevailing hydro- and trophodynamic conditions in the NBCE. Their wide thermal window and trophic plasticity, as demonstrated by successful feeding upon a wide spectrum of prey organisms, suggests that *T. capensis* is favoured by longer periods of quiescent upwelling, as observed in recent years especially during summer (Hutchings *et al.*, 2009). Furthermore, they are tolerant of the associated phenomenon of low oxygen concentrations. Successful feeding results in fast growth associated with a quick development of swimming behaviour, which in turn increases foraging and predator avoidance potential.

ACKNOWLEDGEMENTS

REFERENCES

Abaunza, P., Gordo, L., Karlou-Riga, C., Murta, A., Eltink, A. T. G. W., García Santamaría, M. T., Zimmermann, C., *et al.* 2003. Growth and reproduction of horse mackerel, *Trachurus trachurus* (Carangidae). Reviews in Fish Biology and Fisheries, 13: 27–61.

Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V. and Wasmund, N. 2005. Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. ICES Journal of Marine Science, 62: 1205-1215.

Arthur, D.K. 1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fishery Bulletin, 74 (3): 517–530.

Assis, C.A. 1996. A generalised index for stomach contents analysis in fish. Scientia Marina, 60 (2-3): 385–389.

Auel, H. and Verheye, H. M. 2007. Hypoxia tolerance in the copepod *Calanoides carinatus* and the effect of an intermediate oxygen minimum layer on copepod vertical distribution in the northern Benguela Current upwelling system and the Angola-Benguela Front. Journal of Experimental Marine Biology and Ecology, 352: 234–243.

Bakun, A. 2010. Linking climate to population variability in marine ecosystems characterized by non-simple dynamics: conceptual templates and schematic constructs. Journal of Marine Systems, 79: 361–373.

Bakun, A., Babcock, E. A., Lluch-Cota, S. E., Santora, C. and Salvadeo, C. J. 2010. Issues of ecosystem-based management of forage fisheries in "open" non-stationary ecosystems: the example of the sardine fishery in the Gulf of California. Reviews in Fish Biology and Fisheries, 20 (1): 9–29.

Bartholomae, C. H. and van der Plas, A. K. 2007. Towards the development of environmental indices for the Namibian shelf, with particular reference to fisheries management. African Journal of Marine Science, 29 (1): 25–35.

Bianchi, G., Carpenter, K., Roux, J.-P., Molloy, F., Boyer, D. and Boyer, H. J. 1999. Field guide to the living marine resources of Namibia. FAO, Rome. 265 pp.

Checkley, D. M. Jr. 1984. Relation of growth to ingestion for larvae of Atlantic herring Clupea harengus and other fish*. Marine Ecology Progress Series, 18: 215–224.

Crawford, R. J. M. 1987. Food and population variability in five regions supporting large stocks of anchovy, sardine and horse mackerel. South African Journal of Marine Science, 5: 735–757.

Cury, P. M. and Shannon, L. J. 2004. Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. Progress in Oceanography, 60: 223–243.

Cury, P. M., Shannon, L. J., Roux, J.-P., Daskalov, G. M., Jarre, A., Moloney, C. L. and Pauly, D. 2005. Trophodynamic indicators for an ecosystem approach to fisheries. ICES Journal of Marine Science, 62: 430-442.

Cushing, D.H. 1996. Towards a science of recruitment in fish populations. Ecology Institute, Oldendorf/Luhe. 175pp.

Dalsgaard, J., St. John, M., Kattner, G., Müller-Navarra, D. and Hagen, W. 2003. Fatty acid trophic markers in the pelagic marine environment. Advances in Marine Biology, 46: 225–340.

Drinkwater, K. F., Beaugrand, G., Kaeriyama, M., Kim, S., Ottersen, G., Perry, R. I., Pörtner, H.-O., Polovina, J. J. and Takasuka, A. 2010. On the processes linking climate to ecosystem changes. Journal of Marine Systems, 79: 374-388.

Ekau, W., Verheye, H.M. 2005. Influence of oceanographic fronts and low oxygen on the distribution of ichthyoplankton in the Benguela and southern Angola currents. African Journal of Marine Science, 27: 629–639.

Ekau, W., Auel, H., Pörtner, H.-O. and Gilbert D. 2010. Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). Biogeosciences, 7: 1669–1699.

FAO, 2012. The state of world fisheries and aquaculture - 2012. FAO, Rome. 230 pp.

Folkvord, A. and Mosegaard, H. 2002. Some uses of individual age data. A. Age and growth analysis. In: Manual of fish sclerochronology, pp. 146–166. Ed. by J. Panfili, H. Troadec, H. de Pontual and P.J.Wright. Ifremer, Brest. 463 pp.

Flynn, B. A., Richardson, A. J., Brierley, A. S., Boyer, D. C., Axelsen, B. E., Scott, L., Moroff, N. E. *et al.* 2012. Temporal and spatial patterns in the abundance of jellyfish in the northern Benguela upwelling ecosystem and their link to thwarted pelagic fishery recovery. African Journal of Marine Science, 34: 131–146.

Fréon, P., Cury, P. M., Shannon, L., and Roy, C. 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. Bulletin of Marine Science, 76: 385–462.

Geist, S. J., Ekau, W. and Kunzmann, A. 2013a. Energy demand of larval and juvenile Cape horse mackerels, *Trachurus capensis*, and indications for hypoxia tolerance as an advantage in a changing environment. Marine Biology (accepted)

Geist, S. J., Kunzmann, A., Verheye, H. M. and Ekau, W. 2013b. Larval feeding ecology of clupeoid fish in the degraded northern Benguela Current upwelling system and its implications for stock recruitment processes. Fisheries Oceanography (under review)

Gibbons, M. 1997. An introduction to the zooplankton of the Benguela Current region. Zoology Department, University of Western Cape, Belville. 51 pp.

Grote, B., Ekau, W., Stenevik, E. K., Clemmesen, C., Verheye, H. M., Lipinski, M. R. and Hagen, W. 2012. Characteristics of survivors: growth and nutritional condition of early stages of the hake species *Merluccius paradoxus* and *M. capensis* in the southern Benguela ecosystem. ICES Journal of Marine Science, 69(4): 553-562.

Heincke, F. 1908. Bericht über die Untersuchungen der Biologischen Anstalt auf Helgoland zur Naturgeschichte der Nutzfische. Die Beteiligung Deutschlands an der Internationalen Meeresforschung, 4: 67–155.

Hewitt, R. P., Theilacker, G. H. and Lo, N. C. H. 1985. Causes of mortality in young jack mackerel. Marine Ecology Progress Series, 26: 1-10.

Hillebrand, H., Durselen, C. D., Kirschtel, D., Pollingher, U. and Zohary, T. 1999. Biovolume calculation for pelagic and benthic microalgae. Journal of Phycology, 35: 403–424.

Houde, E. D. 1987. Fish early life dynamics and recruitment variability. American Fisheries Society Symposium, 2: 17–29.

Huggett, J. A., Bradford-Grieve, J. 2007. Guide to some common copepods in the Benguela Current LME. Zooplankton Workshop BCLME, Swakopmund. 44 pp.

Hutchings, L., van der Lingen, C. D., Shannon, L. J., Crawford, R. J. M., Verheye, H. M., Bartholomae, C. H., van der Plas, A. K. *et al.* 2009. The Benguela Current: an ecosystem of four components. Progress in Oceanography, 83: 15–32.

Ibaibarriaga, L., Irigoien, X., Santos, M., Motos, L., Fives, J. M., Franco, C., Lago de Lanzós, A., et al. 2007. Egg and larval distributions of seven fish species in north-east Atlantic waters. Fisheries Oceanography, 16: 284–293.

Jordan, A. R. 1994. Age, growth and back-calculated birth-date distributions of larval jack mackerel, *Trachurus declivis* (Pisces, Carangidae), from eastern Tasmanian coastal waters. Australian Journal of Marine and Freshwater Research, 45: 19-33.

136

Katsuragawa, M. and Ekau, W. 2003. Distribution, growth and mortality of young rough scad, *Trachurus lathami*, in the south-eastern Brazilian Bight. Journal of Applied Ichthyology, 19: 21–28.

Kattner, G. and Fricke, H. S. G. 1986. Simple gas–liquid chromatography method for simultaneous determination of fatty acids and alcohols in wax esters of marine organisms. Journal of Chromatography, 361: 263– 268.

Kattner, G., Albers, C., Graeve, M. and Schnack-Schiel, S. B. 2003. Fatty acid and alcohol composition of the small polar copepods, *Oithona* and *Oncaea*: indication on feeding modes. Polar Biology, 26: 666–671.

Kirchner, C., Bauleth-D'Almeida, G. and Wilhelm, M. R. 2010. Assessment and management of Cape horse mackerel *Trachurus capensis* off Namibia based on a fleet-disaggregated age-structured production model. African Journal of Marine Science, 32: 525–541.

Kjesbu, O. 2009. Applied fish reproductive biology: contribution of individual reproductive potential to recruitment and fisheries management. In: Jakobsen T, Fogarty MJ, Megrey B, Moksness E (eds) Fish reproductive biology - implications for assessment and managment, 1st edn. Wiley-Blackwell, Oxford, p 429

Lehodey, P., Alheit, J., Barangé, M., Baumgartner, T. Beaugrand, G., Drinkwater, K., Fromentin, J.-M., Hare, S. R., Ottersen, G., Perry, R. I., Roy, C., van der Lingen, C. and Werner, F. 2006. Climate variability, fish, and fisheries. Journal of Climate, 19: 5009–5030.

Maar, M., Visser, A. W., Nielsen, T. G., Stips, A., and Saito, H. 2006. Turbulence and feeding behaviour affect the vertical distributions of *Oithona similis* and *Microsetella norwegica*. Marine Ecology Progress Series, 313: 157–172.

Masuda, R. 2009. Behavioral ontogeny of marine pelagic fishes with the implications for the sustainable management of fisheries resources. Aqua-BioScience Monographs, 2 (2): 1–56.

Masuda, R. 2011. Ontogeny of swimming speed, schooling behaviour and jellyfish avoidance by Japanese anchovy *Engraulis japonicus*. Journal of Fish Biology, 78:1323–1335.

Mohrholz, V., Bartholomae, C. H., van der Plas, A. K. and Lass, H. U. 2008. The seasonal variability of the northern Benguela undercurrent and its relation to the oxygen budget on the shelf. Continental Shelf Research, 28: 424-441.

Mohrholz, V. 2012a-c. Hydrographic measurements in the Northern Benguela upwelling system during the cruise AFR 258 (a), D356 (b), MSM17/3 (c). Leibniz-Institut für Ostseeforschung Warnemünde, unpublished datasets #784364 – 784366.

Monteiro, P. M. S., van der Plas, A. K., Melice, J. L., and Florenchie, P. 2008. Interannual hypoxia variability in a coastal upwelling system: Ocean-shelf exchange, climate and ecosystem-state implications. Deep-Sea Research Part I, 55: 435-450.

Olivar, M.-P. and Fortuño, J.-M. 1991. Guide to ichthyoplankton of the southeast Atlantic (Benguela Current region). Scientia Marina 55: 1–383.

O'Toole, M. 1977. Influence of some hydrological factors on the depth distribution of maasbanker (*Trachurus trachurus*) larvae off South-West Africa. Fisheries Bulletin of South Africa, 9: 46–47.

Pearre Jr., S. 1982. Estimating prey preference by predators: uses of various indices, and a proposal of another based on $\chi 2$. Canadian Journal of Fisheries and Aquatic Sciences, 39 (6): 914–923.

Pearre Jr, S. 1986. Ratio-based trophic niche breadths of fish, the Sheldon spectrum, and the size-efficiency hypothesis. Marine ecology progress series. 27: 299-314.

Peters, J., Renz, J., von Beusekom, J., Boersma, M. and Hagen, W. 2006. Trophodynamics and seasonal cycle of the copepod *Pseudocalanus acuspes* in the central Baltic Sea (Bornholm Basin): evidence from lipid composition. Marine Biology, 149: 1417–1429.

Pillar, S. C. and Barange, M. 1998. Feeding habits, daily ration and vertical migration of the cape horse mackerel off South Africa. South African Journal of Marine Science, 19: 263–274.

Pörtner, H.-O. 2010. Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. The Journal of Experimental Biology, 213: 881–893.

Richardson, A. J. and Verheye, H. M. 1999. Growth rates of copepods in the southern Benguela upwelling system: the interplay between body size and food. Limnology and Oceanography, 44: 382–392.

Sassa, C. and Tsukamoto, Y. 2012. Inter-annual comparison of diet and daily ration of larval jack mackerel *Trachurus japonicus* in the southern East China Sea. Journal of Plankton Research, 34 (2): 173–187.

Schukat A, Auel H, Teuber L, Lahajnar N, Hagen W (2013a) Complex trophic interactions of calanoid copepods in the Benguela upwelling system. J Sea Res (in press). doi: 10.1016/j.seares.2013.04.01

Seibel, B. A. 2010. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. Journal of Experimental Biology, 214: 326–336.

Shannon, L. V., Crawford, R. J. M., Brundrit, G. B. and Underhill, L. G. 1988. Responses of fish populations in the Benguela ecosystem to environmental change. ICES Journal of Marine Science, 45: 5-12.

Uthermöhl, H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. Internationale Vereinigung fuer theoretische und angewandte Limnologie, Mitteilungen, 9: 1-39.

van der Lingen, C. D., Hutchings, L. and Field, J. G. 2006a. Comparative trophodynamics of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela: are species alternations between small pelagic fish trophodynamically mediated? African Journal of Marine Science, 28: 465–477.

van der Lingen, C. D., Shannon, L. J., Cury, P., Kreiner, A., Moloney, C. L., Roux, J. P., and Vaz-Velho, F. 2006b. Resource and ecosystem variability, including regime shifts, in the Benguela Current system. In: Large Marine Ecosystems, Vol.14, Benguela: Predicting a large marine ecosystem, pp. 147-184. Ed. by V. Shannon, G. Hempel, P. Malanotte-Rizzoli, C. L. Moloney and J. Woods. Elsevier, Amsterdam. 410 pp.

Vander Zanden, M. J. and Rasmussen, J. B. 2001. Variation in δ^{15}N and δ^{13}C trophic fractionation: implications for aquatic food web studies. Limnology and Oceanography, 46 (8): 2061–2066.

Verheye, H. M., Hagen, W., Auel, H., Ekau, W., Loick, N., Rheenen, I., Wencke, P., and Jones, S. 2005. Life strategies, energetics and growth characteristics of *Calanoides carinatus* (Copepoda) in the Angola-Benguela frontal region. African Journal of Marine Science, 27: 641–651.

Verheye, H. M. and Kreiner, A. 2013. SCOR-WG125, Zooplankton abundance and biomass of the Northern Benguela Current, Walvis Bay 23S. http://www.st.nmfs.noaa.gov/nauplius/media/time-series/site__satl-walvis-bay-23s/, accessed: 20.4.2013.

Waldron, M. E. and Kerstan, M. 2001. Age validation in horse mackerel (*Trachurus trachurus*) otoliths. ICES Journal of Marine Science, 58: 806-813.

Westhaus-Ekau, P. 1988. Verbreitung und Nahrungsökologie der Fischbrut vor Nord-West-Afrika unter besonderer Berücksichtigung der kleinräumigen Variabilität. PhD-thesis, Universität Hamburg. 143pp. (in german)

Wootton, R. J. 2011. Growth: Environmental Effects. In: encyclopedia in fish physiology, From genome to environment, 1st edition, pp. 1629-1635. Ed. by A. P. Farrell Academic Press, London. 2163 pp.

Xie, S., Watanabe, Y., Saruwatari, T., Masuda, R., Yamashita, Y., Sassa, C. and Konishi, Y. 2005. Growth and morphological development of sagittal otoliths of larval and early juvenile *Trachurus japonicus*. Journal of Fish Biology, 66: 1704–1719.

Young, J. W. and Davis, T. L. O. 1992. Feeding ecology and interannual variations in diet of larval jack mackerel, *Trachurus declivis* (Pisces: Carangidae), from coastal waters of eastern Tasmania. Marine Biology, 113: 11–20.

SUPPLEMENTARY ONLINE MATERIAL

Extended results of lipid analyses of caudal muscle tissue of T. capensis larvae grouped into size classes. The upper part gives the relative amounts of main groups of fatty acids, important single fatty acids and the three trophic markers groups as proportions of TFA. The lower part gives the relative amount of fatty acids in relation to dry mass. All data as mean ± standard error

size class (SL)	3-4mm	5-7mm	8-11mm	12-15mm	16-20mm	21-30mm	31-40mm	41-55mm
	mean±SEM	mean±SEM	mean±SEM	mean±SEM	mean±SEM	mean±SEM	mean±SEM	mean±SEM
n	14	43	18	15	11	5	10	5
SFA	32.27±0.51	32.42±0.21	33.90±0.56	32.10±0.35	33.19±0.60	32.95±0.70	32.73±0.56	33.06±1.77
MUFA	11.89±0.26ᵃ	12.03±0.28ᵃ	13.86±0.61ᵃ	13.95±0.50ᵃ	12.44±0.60ᵃ	12.74±0.42ᵃ	17.03±1.16ᵇ	19.52±2.32ᵇ
PUFA	55.83±0.62ᵃ	55.55±0.39ᵃ	52.24±1.03ᵇᶜ	53.95±0.36ᵃᵇ	54.38±0.59ᵃᵇ	54.32±0.69ᵃᵇᶜ	50.25±1.43ᶜᵈ	47.41±1.81ᵈ
14:0	1.05±0.12ᵃ	1.21±0.11ᵃ	2.25±0.30ᵇ	1.79±0.16	1.40±0.14	1.42±0.15	1.79±0.19	2.81±0.60ᵇ
16:0	18.70±0.50ᵃ	19.85±0.29ᵃᵇ	21.65±0.43ᶜ	20.48±0.40	21.34±0.36ᵇᶜ	21.50±0.64	21.12±0.45ᵇᶜ	20.98±1.36
18:0	10.00±0.46ᵃ	8.96±0.23ᵃᵇ	7.71±0.32ᶜ	7.97±0.32ᵇᶜ	8.19±0.21ᵇᶜ	8.11±0.18	7.83±0.33ᵇᶜ	7.11±0.52ᵇᶜ
16:1ω7	2.08±0.12ᵃᵇ	2.16±0.11ᵃ	2.97±0.33ᵇᶜ	2.55±0.18	2.25±0.19ᵃᵇ	2.46±0.21	2.56±0.16	3.90±0.60ᶜ
18:1ω7	2.23±0.10	2.27±0.08	2.50±0.11	2.16±0.20	2.28±0.15	2.09±0.04	2.11±0.08	2.04±0.18
18:1ω9	5.93±0.27	5.80±0.18	6.28±0.35	6.68±0.44	5.69±0.22	5.76±0.27	5.93±0.23	6.40±0.17
16:2ω4	4.60±0.59ᵃ	2.88±0.23ᵇ	1.77±0.20ᶜ	1.14±0.07ᶜᵈ	0.90±0.05ᶜᵈ	1.19±0.32ᶜᵈ	0.63±0.08ᵈ	0.93±0.10ᶜᵈ
18:4ω3	0.79±0.07ᵃ	0.94±0.07	0.80±0.10	0.72±0.14ᵃ	1.26±0.13ᵃ	1.10±0.21	1.02±0.10	1.18±0.25
20:4ω6	1.07±0.09	0.95±0.05	1.01±0.12	1.22±0.16	0.81±0.07	1.10±0.25	0.70±0.04	0.85±0.15
20:5ω3 (EPA)	10.89±0.61	11.64±0.37	12.39±0.71	13.62±1.02ᵃ	11.06±0.70	11.11±0.73	9.33±0.37ᵇ	9.94±0.97
22:5ω3	1.40±0.12	1.46±0.10	1.48±0.14	2.07±0.17	1.51±0.07	1.84±0.21	1.43±0.07	1.63±0.14
22:6ω3 (DHA)	32.18±0.79	32.83±0.52	30.15±1.07	30.40±1.02	34.07±0.88ᵃ	33.23±1.23	32.87±1.16	27.95±1.51ᵇ
n	14	43	15	14	10	3	1	2
diatom	4.46±0.17ᵃ	4.63±0.17ᵃ	5.73±0.36ᵇ	4.95±0.29	4.68±0.32	4.79±0.29	4.77±0.18	6.29±0.62ᵇ
dinoflagellata	0.79±0.07	0.94±0.07	0.80±0.10	0.72±0.14ᵃ	1.26±0.13ᵇ	1.10±0.21	1.02±0.10	1.18±0.25
heterotrophy	6.14±0.28ᵃᵇ	6.23±0.20ᵃ	6.96±0.40ᵃᵇ	8.00±0.59ᵇ	6.37±0.40ᵃᵇ	6.89±0.20ᵃᵇ	10.83±0.98ᶜ	11.95±2.26ᶜ
n	14	43	15	14	10	3	1	2
TFA (% DM)	3.82±0.41	3.99±0.15	3.93±0.13	3.33±0.16	3.41±0.19	3.57±0.21	3.07	3.61
EPA (µg mg DM⁻¹)	0.413±0.045	0.466±0.022	0.494±0.039	0.469±0.058	0.783±0.419	0.410±0.046	0.270	0.390
DHA (µg mg DM⁻¹)	1.200±0.138	1.280±0.055ᵃ	1.191±0.049	0.971±0.039ᵇ	2.561±1.444	1.083±0.019	1.170	1.010

Abbreviations: SFA = saturated fatty acids, MUFA = mono-unsaturated fatty acids, PUFA = poly-unsaturated fatty acids, EPA = eicosapentaenoic acid, DHA = docosahexaenoic acid, TFA = total fatty acids, DM = dry body mass. Nomenclature of single fatty acids: No. before the colon = number of carbon atoms, No. after the colon = number of double bonds, No. after ω = position of first double bond. Fatty acid trophic markers (FATM) include the following fatty acids: diatoms = Σ(16:1ω7, 18:1ω7, 16:4 ω1), dinoflagellates = 18:4 ω3, heterotrophs = Σ(18:1 ω9, 20:1ω9, 22:1ω11)

Additional scientific output within the scope of the thesis

Geist, S. J., Schukat, A., and Werner, T. 2012. Environmental changes in the pelagic: consequences and acclimatization strategies:From plankton to fish. In: Conference Book Youmares 3.0, 3rd Young Marine Research network meeting 2012 „Recent Impulses to Marine Science and Engineering: Between Space and Seafloor: Aqua vita est!", Lübeck 12. – 14.9 2012, pp. 28-32. Ed. by J. Wiedling and M. Einsporn. German Society for Marine Research, Hamburg, 87 pp.

Contribution of authors: All authors contributed equally to this review article and chaired a similar entitled session at the Youmares 3.0 conference.

Michalek, K., Geist, S., Saborowski, R., and Kunzmann, A. Enzyme metabolism of larval and juvenile Cape horse mackerels, *Trachurus capensis* from the Northern Benguela Upwelling System. (in preparation)

Contribution of authors: Kati Michalek, Simon Geist and Andreas Kunzmann developed the study concept. Kati Michalek did the lab analyses and wrote the manuscript. Simon Geist, Reinhard Saborowski and Andreas Kunzmann advised the practical work and data analyses and assisted in conceptual design and writing of the manuscript.

Co-supervision/tutoring of MSc and BSc students

Michalek, K. 2012. Activity of metabolic key enzymes in early life stages of cape horse mackerels, *Trachurus trachurus capensis* from the northern Benguela Current upwelling system. MSc thesis, Faculty of Biology and Chemistry, University Bremen, 56 pp.

Michalowski, K. 2010. Wachstum und trophische Stellung der subtropischen Grundel Sufflogobius bibarbatus im Nahrungsgefüge des nördlichen Benguela-Auftriebssystems. Diplomarbeit, Faculty of Biology and Chemistry, University Bremen, 66 pp.

Schwinghammer, K. 2011. Zusammensetzung des Mikroplanktons im Südsommer vor Namibia. BSc thesis, Faculty of Biology and Chemistry, University Bremen, 36 pp.

Schickenberg, N. 2011. Stable isotope (δ^{13}C & δ^{15}N) signatures of 3 micro-copepod groups important for the Horse Mackerel diet". Project thesis, Faculty of Biology and Chemistry, University Bremen, 15 pp.

Presentations at international conferences

Geist, S. J. 2011. Food sources of early life stages of horse mackerel (*Trachurus trachurus capensis*) and anchovy (*Engraulis capensis*) from the Northern Benguela System revealed by stomach content, stable isotope and lipid analysis. 14th SAMSS / 49th ECSA International Conference, Grahamstown, South Africa, 3.4. 2011 – 7.4. 2011.

Other presentations

Geist, S. J. 2012. Trophic ecology and metabolic demands of early life stages of cape horse mackerel, *Trachurus capensis (Castelnau, 1861)* in the Northern Benguela Current Upwelling System. Ecology Department, ZMT, Bremen, 27.4.2012, oral presentation

Geist, S. J. 2011. Routine metabolism of early life stages of cape horse mackerel (*Trachurus capensis*). ZMT Kolloquium, Bremen, 16.11.2011, oral presentation

Geist, S. J. 2011. AP Produktion/ Konsum: Physiologische Raten. GENUS phase I final conference, Hamburg, 5.9.2011, oral presentation

Geist, S. J. 2011. Trophic ecology and metabolism of early life stages of main pelagic fisheries resources in the Northern Benguela, GENUS Meeting, Hamburg, 7.7.2011, oral presentation

Geist, S. J. 2010. Trophic ecology of pelagic fish larvae in the Northern Benguela Current: First results. ZMT Kolloquium, Bremen, 23.6.2010 , oral presentation

Geist, S. J., Ekau, W., Kunzmann, A., Tjizoo, B. M., Moroff, N., Verheye, H., Kreiner, A., Michalowski, K., Schwinghammer, K., Francechinis, L. and Seguin, F. 2011. The impact of environmental variations on key fish stocks in the Northern Benguela Ecosystem. GENUS phase I final conference, Hamburg, 5.9.2011, poster presentation

Geist, S., Ekau, W., Kunzmann, A., Tjizoo, B., Michalowski, K., Michalek, K., Verheye, H., Kreiner, A., Schwinghammer, K., and Schickenberg, N. 2012. Fish in a changing ocean: The northern Benguela Current. ZMT International Scientific Advisory Board Meeting, Bremen, 16.10.2012, poster presentation

Geist, S., Ekau, W., Kunzmann, A., Tjizoo, B., Michalowski, K., Michalek, K., Verheye, H., Kreiner, A., Schwinghammer, K., and Schickenberg, N. 2013. Early life history traits of the old and new dominant pelagic fish species in the degraded northern Benguela ecosystem. ZMT Leibniz Society Evaluation, Bremen, 2.5.2013, poster presentation

Additional scientific output beyond the scope of the thesis

Geist, S. J., Nordhaus, I., and Hinrichs, S. 2012 Occurrence of species-rich crab fauna in a human-impacted mangrove forest questions the application of community analysis as an environmental assessment tool. Estuarine Coastal and Shelf Science, 96: 69-80.

Personal contribution: Raw data are from the diplom thesis from Simon Geist and Saskia Hinrichs. During 2009 and 2011 Simon Geist jointly analysed the datasets and wrote the manuscript.

Diele, K., Ngoc, D. M. T., Geist, S. J., Meyer, F. W., Pham, Q. H., Saint-Paul, U., Tran, T., and Berger, U. (2012) Impact of typhoon disturbance on the diversity of key ecosystem engineers in a monoculture mangrove forest plantation, Can Gio Biosphere Reserve, Vietnam. Global and Planetary Change. doi:10.1016/j.gloplacha.2012.09.003

Personal contributions: Simon Geist assisted in developing sampling scheme and method, conducted field work and lead crab identification in 2008. Multivariate statistical analyses and co-working on the different stages of the manuscript 2009-2012.

Nordhaus, I., Dsikowitzky, L., Geist, S., Hinrichs, S., and Jennerjahn, T. 2009. Ecological status of a mangrove-fringed lagoon in SE Asia affected by human activities. Galapagos Science Symposium, Puerto Ayora, Galapagos, 21 July 2009

Nordhaus, I., Geist, S., Hinrichs, S., and Dsikowitzky, L. 2010. Human impacts on a mangrove-fringed lagoon in Java: Consequences for tree and macrobenthic biodiversity. International Conference of the Association for Tropical Biology and Conservation, Sanur, Bali, Indonesia, 22 July 2010

Diele, K., Tran Ngoc, D. M., Tran, T., Saint-Paul, U., Pham, H. Q., Geist, S. J., Meyer, F. W., and Berger, U. 2012. Impact of Typhoon Disturbance on Key Macrobenthos in a Monoculture Mangrove Forest Plantation, Can Gio Biosphere Reserve, Vietnam. *et al.*3rd Meeting on Mangrove Ecology, Functioning and Management (MMM3), Galle, Sri Lanka, 2-6 July 2012

Nordhaus, I., Dsikowitzky, L., Geist, S., Jennerjahn, T., Schwarzbauer, J. 2012. Human-induced environmental change affecting macrobenthic communities in the Segara Anakan Lagoon, Indonesia. 3rd Meeting on Mangrove Ecology, Functioning and Management (MMM3), Galle, Sri Lanka, 2-6 July 2012

Field work and expeditions

07/2009	AWI Helgoland hosted by A. Malzahn: hands-on introduction on pelagic fish larvae
11/2009	Seapoint Aquarium, DEA, Cape Town, SA hosted by Hans Verheye
12/2009	research cruise Afr258 on board RV Africana
09-10/2010	research cruise D356 on board RRV Discovery
02-03/2011	research cruise MSM17-3 on board FS Maria S. Merian

Acknowledgements

"Das Gras wächst nicht schneller, wenn man daran zieht!", aber düngen hilft….

According to this motto, I would like to thank a great number of people who have contributed in one way or the other to the success of this thesis:

I am very grateful to my supervisors Werner Ekau and Andreas Kunzmann for their continuous support, guidance and advice and the fruitful discussions from the beginning to the end of my project.

Ulrich Saint-Paul for accepting me as his doctoral student and especially his patience and engagement towards the end of the thesis.

The examination board members Wilhelm Hagen, Tom Brey, Lena Teuber and Stephanie Simon for being available and their courteous support to find a date for my thesis defense.

Wilhelm Hagen for offering his lab facilities to conduct fatty acid analysis.

Hans Verheye, for being a good teacher on board, a great supporter of my work and his valuable comments on my manuscripts.

Anna Schukat, Anita Flohr, Lena Teuber and Thorsten Werner, thanks for everything! It was great to have such good friends as PhD-student colleagues in the GENUS project.

Alexander Wolf, Andreas Kubicek, Christian Jessen, Pia Kegler, Gerti Spörl, Hauke Schwieder and all other friends among the ZMT-PhD students for your support and for the good time we had!

Britta Grote, my predecessor in the working group and long-standing friend.

Philipp Kanstinger, old friend from Hamburg and expert in fish larvae rearing.

Stephanie Bröhl, Conny von Waldthausen, Epiphane Yeyi, Doro Dasbach, Matthias Birkicht, Dieter Peterke, Petra Käpnick and Gaby Böhme are thanked for their countless and superb technical support in Bremen and during the research cruises.

Kim Hünerlage, Kati Michalek, Katharina Michalowski, Katharina Schwinghammer and Nina Schickenberg: your assistance concerning the lab work was really great!!!

Special thanks go to my colleagues and friends at DEA and DAFF in South Africa for their really great support, advise, and hospitality and for lots of fun at sea and on land: Susan Jones, who is particularly thanked for her help with zooplankton analysis and identification, Marc Goodman, who hosted me at Seapoint, Marco Worship, Keshnee Pillay, Carl van der Lingen, Herman, Kanakana, Alistair and in memoriam, Never give up! Charly.

Not to forget the Namibian fraction: Beau Tjizoo, Nadine Moroff, Chris Bartholomae and Anja Kreiner, who were always supportive, especially in regard to my numerous questions on the state of the northern Benguela. Beau, thanks for the great evenings during your visits to Bremen talking about life in Africa, Europe and beyond…

Greatest thanks go also to all my german colleagues from GENUS, that have not been mentioned yet. Without your support, many things would not have been possible! It's a pleasure to work in such a great environment: Kai-Christian Emeis, Niko Lahajnar, Volker Mohrholz, Friedrich Buchholz, Holger Auel, Petra Wencke, Rolf Koppelmann, Thoralf Heene, Annethea Müller, Bettina Martin, Anja Hansen, Norbert Wasmund, Karo Bohata, Anja Eggert, Martin Schmidt, Cornelia Buchholz, Markus Ankele, Andreas Neumann and Frauke Langenberg.

The captains and crew members of RV Africana, RRV Discovery and FS Maria S. Merian to keep the ships and my work running at sea!

Many more important ZMT colleagues to thank for support: V. Ittekot, H. Westphal, U. Selent, C. Wild, I. Sanz-Jannke, U. Pint, K. Schrader, C. Fromm, C. Lutz, my former colleagues of ZMT's works council, and many more…

Karen Diele, Jose Paula, Martin Skov, who inspired me in my earlier steps becoming biologist.

Nils Krück, Alex Wolf, Thorsten Werner, Anna Schukat, Britta Grote and Elisabeth Mai for proof reading.

Alexander Gürten, for his wonderful cover drawing.

My friends from/in Bremen, Wiesbaden, Köln, Portugal, Spain, Switzerland, Austria, Australia, New Zealand, Argentina, Costa Rica, Indonesia, Vietnam and other beautiful parts of the world for being my friends and making me feel connected to the world during the many days in front of the PC.

Last but not least, my beloved family for always having faith in me: Elke and Martin; David, Hannah and Alma; Manuel and Getsi; my family in München, Franken and Bremen and in memoriam to my grandparents Irmi, Babett, Reas and Hans. And I also want to mention Ena and Hans-Jürgen Overbeck, whose big footsteps I try to follow..

Annex

List of content

Annex I Stationlist and respective presence of study species larvae (indicated by x)

date	cruise leg	station number	Longitude (° East)	Latitude (°North]	Bottom Depth (m)	MultiNet (quantitive)	S. sagax	E. encrasicolus	S. aurita	T. capensis
11/03/08	MSM07-2b	3	13.52	-23.00	220					x
13/03/08	MSM07-2b	6	12.95	-20.00	60			x		x
13/03/08	MSM07-2b	7	12.64	-20.00	127			x		
13/03/08	MSM07-2b	8	12.27	-19.99	238					x
13/03/08	MSM07-2b	9	11.32	-20.00	967			x		
16/03/08	MSM07-2b	12	11.06	-17.27	1607					x
17/03/08	MSM07-2b	13	11.29	-17.26	469			x		x
17/03/08	MSM07-2b	14	11.47	-17.27	165					x
23/03/08	MSM07-3	79	14.33	-23.00	73	x				
24/03/08	MSM07-3	80	12.67	-22.00	512	x				
24/03/08	MSM07-3	81	12.15	-21.00	808	x				
25/03/08	MSM07-3	82	11.50	-20.00	777	x		x		
25/03/08	MSM07-3	83	12.33	-20.00	213	x				x
25/03/08	MSM07-3	84	12.93	-20.00	68	x				
25/03/08	MSM07-3	85	12.70	-19.50	62	x				
26/03/08	MSM07-3	86	12.61	-19.50	89	x				
26/03/08	MSM07-3	87	12.52	-19.50	117	x				x
26/03/08	MSM07-3	88	12.43	-19.50	134	x			x	x
26/03/08	MSM07-3	89	12.35	-19.50	143	x		x		x
26/03/08	MSM07-3	90	12.17	-19.50	234	x		x		x
26/03/08	MSM07-3	91	12.45	-19.00	39	x		x		x
27/03/08	MSM07-3	92	12.35	-19.00	92	x		x	x	x
27/03/08	MSM07-3	93	12.25	-19.00	111	x		x	x	x
27/03/08	MSM07-3	94	12.17	-19.00	125	x		x		x
27/03/08	MSM07-3	95	12.00	-19.00	211	x		x		x
27/03/08	MSM07-3	96	11.75	-19.00	302	x				

date	cruise leg	station number	Longitude (° East)	Latitude (°North]	Bottom Depth (m)	MultiNet (quantitive)	S. sagax	E. encrasicolus	S. aurita	T. capensis
27/03/08	MSM07-3	97	11.50	-19.00	297	x				
28/03/08	MSM07-3	98	12.17	-19.50	240	x		x		
28/03/08	MSM07-3	99	12.43	-19.50	135	x				x
28/03/08	MSM07-3	100	12.53	-19.50	117	x				x
31/03/08	MSM07-3	103	11.87	-18.26	42	x	x	x	x	x
31/03/08	MSM07-3	104	11.50	-18.00	242	x			x	x
31/03/08	MSM07-3	105	11.50	-17.50	163	x			x	x
31/03/08	MSM07-3	106	11.72	-17.25	39	x			x	x
31/03/08	MSM07-3	107	11.50	-17.25	140	x				
01/04/08	MSM07-3	108	11.25	-17.25	597	x				x
01/04/08	MSM07-3	109	11.00	-17.25	2117	x				x
02/04/08	MSM07-3	111	11.50	-17.00	106	x	x	x	x	x
03/04/08	MSM07-3	112	11.50	-16.75	100		x	x	x	x
03/04/08	MSM07-3	113	11.50	-16.50	103	x		x	x	x
03/04/08	MSM07-3	114	11.50	-16.00	1246	x				x
06/12/09	Afr258	30249	14.77	-25.73	57	x				
06/12/09	Afr258	30250	14.48	-24.45	40					x
08/12/09	Afr258	30251	12.45	-19.00	32	x				
08/12/09	Afr258	30252	12.25	-19.00	103	x	x			x
08/12/09	Afr258	30253	12.00	-19.00	194	x	x	x	x	x
08/12/09	Afr258	test	12.68	-19.60						x
09/12/09	Afr258	30254	11.43	-19.00	418	x				x
09/12/09	Afr258	30255	11.70	-17.25	42	x				
09/12/09	Afr258	30256	11.50	-17.25	132	x				x
10/12/09	Afr258	30257	11.18	-17.25	820	x		x		x
10/12/09	Afr258	30258	10.78	-17.25	2900	x		x	x	x
10/12/09	Afr258	30259	10.50	-17.25	3240	x		x	x	
11/12/09	Afr258	30260a	10.53	-19.00	2070	x				

date	cruise leg	station number	Longitude (° East)	Latitude (°North]	Bottom Depth (m)	MultiNet (quantitive)	*S. sagax*	*E. encrasicolus*	*S. aurita*	*T. capensis*
12/12/09	Afr258	30261	11.72	-22.97	3094	x				
13/12/09	Afr258	30262	13.33	-23.00	357	x				
13/12/09	Afr258	30263	13.68	-23.00	146	x	x	x		
13/12/09	Afr258	30264	14.08	-23.00	122	x			x	
14/12/09	Afr258	30265	14.33	-23.00	65	x				
15/12/09	Afr258	30266	14.51	-26.81	298	x				
13/09/10	D356	6	11.50	-17.33	159	x	x			x
13/09/10	D356	7	11.68	-17.30	66	x				
15/09/10	D356	10	11.33	-18.46						x
20/09/10	D356	15	13.03	-23.05	468	x				
21/09/10	D356	17	13.50	-23.00	228	x				
22/09/10	D356	18	13.99	-23.00	130	x				
28/09/10	D356	24	11.08	-19.03	1094	x				
28/09/10	D356	25	11.51	-18.94	277	x		x		x
29/09/10	D356	26	12.00	-18.99	200	x	x			x
29/09/10	D356	27	12.16	-19.00	123	x				x
30/09/10	D356	28	12.38	-19.00	63	x				x
01/10/10	D356	30	11.00	-17.61	2257		x	x		x
02/10/10	D356	31	10.92	-17.92	2579			x		x
03/10/10	D356	33	10.77	-18.77	3017		x	x		x
06/10/10	D356	42	12.00	-19.00	250					x
08/10/10	D356	43	13.06	-23.00	395					x
31/01/11	MSM17-3	222	14.05	-23.00	134		x			
31/01/11	MSM17-3	224	14.05	-23.00	139	x	x	x	x	x
31/01/11	MSM17-3	225	14.00	-23.50	169	x	x	x	x	x
31/01/11	MSM17-3	226	13.50	-23.50	231	x	x	x		x
01/02/11	MSM17-3	228	14.00	-24.00	219	x	x		x	x
01/02/11	MSM17-3	229	14.33	-24.50	126	x				

date	cruise leg	station number	Longitude (° East)	Latitude (°North]	Bottom Depth (m)	MultiNet (quantitive)	*S. sagax*	*E. encrasicolus*	*S. aurita*	*T. capensis*
01/02/11	MSM17-3	230	14.00	-25.00	180	x				
02/02/11	MSM17-3	231	14.50	-26.00	194	x		x		
02/02/11	MSM17-3	232	15.06	-26.67	40	x				
02/02/11	MSM17-3	233	14.76	-26.67	193	x				
02/02/11	MSM17-3	234	14.42	-26.67	330	x				
03/02/11	MSM17-3	235	14.00	-26.67	422	x				x
04/02/11	MSM17-3	239	13.70	-24.49	358	x		x		
07/02/11	MSM17-3	243	12.80	-23.00	1400	x				
07/02/11	MSM17-3	246	13.05	-23.00	413	x				x
08/02/11	MSM17-3	250	13.33	-23.00	354	x	x	x		x
08/02/11	MSM17-3	254	13.67	-23.00	155	x	x	x	x	x
09/02/11	MSM17-3	260	14.05	-23.00	139	x	x	x	x	x
09/02/11	MSM17-3	264	14.33	-23.00	68	x	x			x
10/02/11	MSM17-3	266	13.46	-22.70	251	x	x	x	x	x
11/02/11	MSM17-3	267	13.17	-22.00	211	x	x	x		
11/02/11	MSM17-3	268	13.50	-21.01	17	x	x			x
11/02/11	MSM17-3	269	13.33	-21.00	95	x		x		x
11/02/11	MSM17-3	270	13.17	-21.00	128	x	x	x	x	x
11/02/11	MSM17-3	271	12.83	-21.00	300					x
12/02/11	MSM17-3	272	12.50	-21.00	434	x				
13/02/11	MSM17-3	275	12.17	-20.00	285	x		x		x
13/02/11	MSM17-3	276	12.50	-20.00	154	x		x		x
13/02/11	MSM17-3	277	12.83	-20.00	103	x		x		x
13/02/11	MSM17-3	278	13.00	-20.00	32	x		x		x
14/02/11	MSM17-3	279	12.45	-19.00	39	x		x		
14/02/11	MSM17-3	282	12.25	-18.99	113	x	x	x		x
14/02/11	MSM17-3	285	12.00	-19.00	211	x		x		x
15/02/11	MSM17-3	292	11.43	-19.00	420	x		x		

date	cruise leg	station number	Longitude (° East)	Latitude (°North]	Bottom Depth (m)	MultiNet (quantitive)	S. sagax	E. encrasicolus	S. aurita	T. capensis
16/02/11	MSM17-3	295	11.00	-19.00	1308	x	x		x	
16/02/11	MSM17-3	299	11.42	-19.00	443				x	x
16/02/11	MSM17-3	300	11.50	-18.00	241	x				x
19/02/11	MSM17-3	304	11.72	-17.25	40	x	x	x	x	x
19/02/11	MSM17-3	305	11.50	-17.83	149	x	x	x	x	x
19/02/11	MSM17-3	306	11.29	-17.25	498	x		x		x
20/02/11	MSM17-3	307	11.18	-17.25	924	x		x		x
20/02/11	MSM17-3	313	11.50	-17.25	150		x	x		x

Annex II Selection of available information on life history traits for higher taxonomic groups of the four study species. Literature sources are indicated by uppercase numbers and listed below the table. Full references are given, if not listen in the references section of the thesis

Order	Clupeiformes	Clupeiformes	Perciformes
Family	**Clupeidae**	**Engraulidae**	**Carangidae**
schooling	yes	yes	yes
Skin thickness / Mech. Protection against jellystings	low[1,2]	low[2]	Higher (earlier squamation and stronger scales)[3]
Life span	short (5-10 yrs)[2,4]	short (5-10 yrs)[2,4]	longer (max. 40 yrs)[5]
Recruit age	1-3 yrs[2,4]	1-3 yrs[2,4]	
Length of first spawning	10-20 cm[4]	10-20 cm[4]	
growth	rapid[2]	rapid[2]	rapid in first 3 yrs[5]
LH strategy	Early maturity at small size relative to adult size[6]		
Compensation in reproduction for high adult mortality	no[6]	no[6]	yes[6]
recruitment depends on	environment[6]	environment[6]	environment[2]
Spawning strategy	serial batch[4,7]	serial batch[4,7]	multiple batch[5]
Absolute fecundity (eggs per individual)	High[8]	High[8]	High[2]
Relative fecundity (eggs g body weight[-1])	400 (*S. melanostictus*)[9] 150-250 (*S. sagax*)[4]	600 (*E. japonicus*)[9] 200-350 (*E. capensis*)[4]	100 (*T. japonicus*)[9]
Parental investment[4] oder olivar1991	Low, oviparous, planktonic eggs and larvae	Low, oviparous, planktonic eggs and larvae	Low, oviparous, planktonic eggs and larvae
Genus	***Sardinops***	***Engraulis***	***Trachurus***
Development type			Smooth and gradual[14]
First erythrocytes		4.5-6 mm(7 d)[10] abundant at 12 mm (22d)[10] (*E. mordax*)	
Functional gills		16-17mm (32d)[10] (*E. mordax*)	
Looped gut			3-4 mm[11] (*T. trachurus*)
Differentiation of stomach start			12 mm[11] (*T. trachurus*)
Differentiation of stomach complete		20 mm[10]	17 mm[11] (*T. trachurus*)
Upper and lower jaws become mobile		30 mm[10]	
Ossification steps			3.0-4.5: premaxilla formed, maxilla ossified[14] 10: full tail ossified[14]
Ray formation at mm standard length	Pectoral Fin rays complete: 28[15]		5.8-6.6: median fin rays around 6: urostyl flexion 6.5: full primary caudal rays 9.0-10: dorsal spines complete

			11-12: dorsal and anal fins fully ossified >20: pectoral ossified lateral line complete: 18-19[14]
Onset of Squamation			19-21 mm[13]
Squamation complete	34 mm[15]		35 mm[13]
Metamorphosis at:	35 mm[16] 35 mm[17] 40 mm[12,15] 55 mm[15] 34mm[15]	32 mm[18] 37 mm[19] 35-40 mm[12, 20] 35-40 mm[4,12] 31mm[21]	
Onset of filter feeding	80-100 mm[4]	80-100 mm[4]	

1 Rombough, 1988

2 Freon *et al.,* 2005

3 Masuda, 2009

4 Blaxter and Hunter, 1982

5 Abaunza, P., Gordo, L., Karlou-Riga, C., Murta, A., Eltink, A., García Santamaría, M. T., Santamaría, M. G., et al. 2003. Growth and reproduction of horse mackerel, *Trachurus trachurus* (Carangidae). Reviews in Fish Biology and Fisheries, 13: 27-61.

6 Rochet, 2000

7 Bakun and Weeks, 2006

8 Boyer, D.,Cole, J., and Bartholomae, C. 2000. Southwestern Africa: Northern Benguela Current Region. Marine Pollution Bulletin, 41(1-6): 123-140.

9 as cited in Masuda, 2009

10 O'Connell, C. P. 1981. Development of organ systems in the Northern anchovy, *Engraulis mordax,* and other teleosts[1].American Zoologist, 21: 429-446.

11 Westhaus-Ekau, P. 1988. Verbreitung und Nahrungsökologie der Fischbrut vor Nord-West-Afrika unter besonderer Berücksichtigung der kleinräumigen Variabilität. PhD-thesis, Universität Hamburg. 143pp. (in german)

12 Santos, A. M. P., Chícharo, M. A., *et al.* 2007. Physical–biological interactions in the life history of small pelagic fish in the western Iberia upwelling ecosystem. Progress in Oceanography, 74: 192–209.

13 Ahlstrom, E. H., and Ball, O. P. 1954. Description of eggs and larvae of Jack Mackerel (*Trachurus symmetricus*) and distribution and abundance of larvae in 1950 and 1951. Fishery Bulletin, NOAA, 56: 209-245.

14 Haigh, 1972

15 Matsuoka (1997), and refernces therein

16 Butler, J. L. 1991. Mortality and recruitment of Pacific Sardine, *Sardinops sagax caerulea*, larvae in the California Current. Canadian Journal of Fisheries and Aquatic Sciences, 48: 1713–1723.

17 Takahashi, M., and Checkley, D. M., Jr. 2008. Growth and survival of Pacific sardine (Sardinops sagax) in the California Current region. J Northwest Atl Fish Sci, 41: 129–136.

18 Đurovic, M., Pesic, A., Regner, S., Joksimovic, A., Mandic, M., Kasalica, O., Ikica, Z., and Krpo-Cetkovic, J. 2012. Daily otolith increments and growth rate of juvenile anchovy, *Engraulis encrasicolus* (Linnaeus, 1758), in the south-eastern Adriatic Sea. Acta Adriatica, 53(3): 331–340.

19 Dulčić, J. 1997. Growth of anchovy, Engraulis encrasicolus (L.), larvae in the Northern Adriatic Sea. Fisheries Research, 31: 189–195.

20 La Mesa, M., Donato, F., Giannetti, G., and Arneri, E. 2009. Growth and mortality rates of European anchovy (*Engraulis encrasicolus*) in the Adriatic Sea during the transition from larval to juvenile stages. Fisheries Research, 96: 275–280.

21 Costalago *et al.,* 2011

Annex III Collection of life history traits of the four study species. Literature sources are indicated by uppercase capital letters and listed below the table. Full references are given, if not listen in the references section of the thesis

NBCE species	*Sardinops sagax*	*Engraulis encrasicolus*	*Sardinella aurita*	*Trachurus capensis*
Habitat[7]	epipelagic	epipelagic	epipelagic	epipelagic (juveniles) mesopelagic (adults)
Biomass estimate (t) 02-2009 / 02-2010	150 000 / 142 000[A]	37 000 / 135 000[A]		597 000 / 769 000[A]
Length of 50% maturity	before 1974: 22.0-23.7 cm[B] 1980s: 19.95 cm[B] 2000s: 16.46cm[B]			1970s: 27 cm[C] 1980s: ~25 cm[C] 1999-2004: < 20 cm[C] 2010: 20.1 cm[D]
Modal length at catch /common length	1952-1957: 25.5, 17-31 cm 1997-2008: 21.3, 15-26 cm	13.5 cm[E]	25 cm[E]	1970s: 28 cm[M] 2007: 20 cm[F] 2009-2012: 25 cm[F] 2012: 16 cm (pelagic)[F]
Max. length	29.5cm (1950ies); 39.5 cm[E]	20.0 cm[E]	31 cm[E]	35 cm; 40cm at 9 yrs[F] 60 cm at >10 yrs[E]
Age of maturity	≤ 2 yr[F]			3 years (97%)[F]
Max. age possible	before collapse: 11yrs[B] after collapse: 6 yrs[F,T] 25 yrs[E]	4 yrs[E] 3 yrs[W]	7 yrs[E]	10 yrs[F]
Max weight	486 g[E]		229 g[E]	
Adult feeding mode diet	Filter feeder small Calanoida Cyclopoida <1 200 µm[G]	Particulate feeder Calanoida Euphausiacea > 1 000 µm[G]	Zooplankton[E]	Zooplanktivorous[H,Q] Euphausiacea[I,Q] Amphipoda[Q] fish larvae[Q]
Fishery[C,F]	Purse-seine[F]	Purse seine	Purse seine, midwater trawl	Midwater trawling (adults, 85-90% TAC); Purse seine (juvenile, <17cm, 10-15%TAC)
MSY[F]				280 000 – 300 000 t
TAC 2012[F]	31 000 t			320 000 t
CPUE (t hr-1)[F]				~6 (1990-2007), >20 (2009-2012)
State of stock[F]	critical			Good condition
Resulting advice on Fishing pressure	Too high			Too high
Absolutefecundity: eggs per individual (size range)				4000-260000 (22-38 cm)[J]
Spawning depth	beneath Ekman layer[K]			Beneath Ekman layer, deeper than clupeoids, 50-150 m[K,P]
Daily growth after first feeding[L]	17°C: 0.6 mm d^{-1} 20°C: 0.8 mm d^{-1}	17°C: 0.5 mm d^{-1} 20°C: 0.6 mm d^{-1}		
O2 avoidance limit vertical distribution	2.5 mL L^{-1} [N], 2.0 mL L^{-1} [O]	2.0 mL L^{-1} [O]		2.5 mL L^{-1} [N]

larvae				
O2 limit vertical distribution adults				0.7 mL L^{-1} [P]
Spawning season	Peaks in September and February[U]	Peak in February[U]		September – May, peak December-March[T]
T preferences spawning	Peak egg production coincided with warm water peak at 18-20°S during January-March 1982[V]			Warmer water [V]

Abbreviations: MSY = maximum sustainable yield, TAC = total allowable catch, CPUE = catch per unit effort

A N. Moroff, NatMIRC, Swakopmund, pers. comm.

B Kreiner *et al.*, 2011

C van der Lingen *et al.*, 2006b and references therein

D Kirchner, 2011

E www.fishbase.de, data not necessarily from NBCE

F Kirchner, 2012

G van der Lingen *et al.*, 2006a

H Fréon *et al.,* 2005

I Crawford, 1987

J Macer, C. T. 1974. The reproductive biology of the horse mackerel *Trachurus trachurs* (L.) in the North Sea and English Channel. Journal of Fish Biology, 6: 415–438. (and references therein)

K Stenevik et al., 2003, and 2007 and refernces therein

L King, 1977 and Thomas, 1986 for sardine; Brownell, 1983, King *et al.*, 1978, and Thomas (1986) for E. encrasicolus: all cited in John *et al.*, 2004

M Bauleth-D'Almeida, G. 2007. An overview of the biology and state of the Cape horse mackerel *Trachurus capensis* stock of the northern Benguela current ecosystem. *In* Northern Benguela Transboundary small pelagic and mid-water resources research planning workshop, A synthesis of the scientific input, discussions and output from the workshop, pp.13-14. Ed by by D. C. Boyer and I. Hampton. Windhoek, Namibia.

N Ekau and Verheye, 2005

O Kreiner *et al.,* 2009

P Axelsen *et al.,* 2004

Q Haigh, 1972

R Andronov, V. N., 1983. Feeding of Cape horse mackerel (*Trachurus trachurus capensis*) and Cape Hake (Merluccius capensis) off Namibia 1982. ICSEAF Collection of Scientific Papers, 10, part I:1-6.

S Thomas, R., M. 1983. Catch, age and stock assessment of South West African pilchard Sardinops ocellata in divisions 1.3, 1.4, and 1.5 in 1982. ICSEAF Collection of Scientific Papers, 10, part I: 193-201.

T Olivar, M. P., and Rubiés, P. 1983. Distribution and abundance of Cape horse mackerel (*Trachurus trachurus capensis*) eggs and larvae caught during the Benguela III Cruise (March-April 1981). ICSEAF Collection of Scientific Papers, 10, part II: 161-172.

U Le Clus, F. 1983. Observations of the egg production of pilchard and anchovy off South West Africa in 1981/82. ICSEAF Collection of Scientific Papers, 10, part II: 139-146.
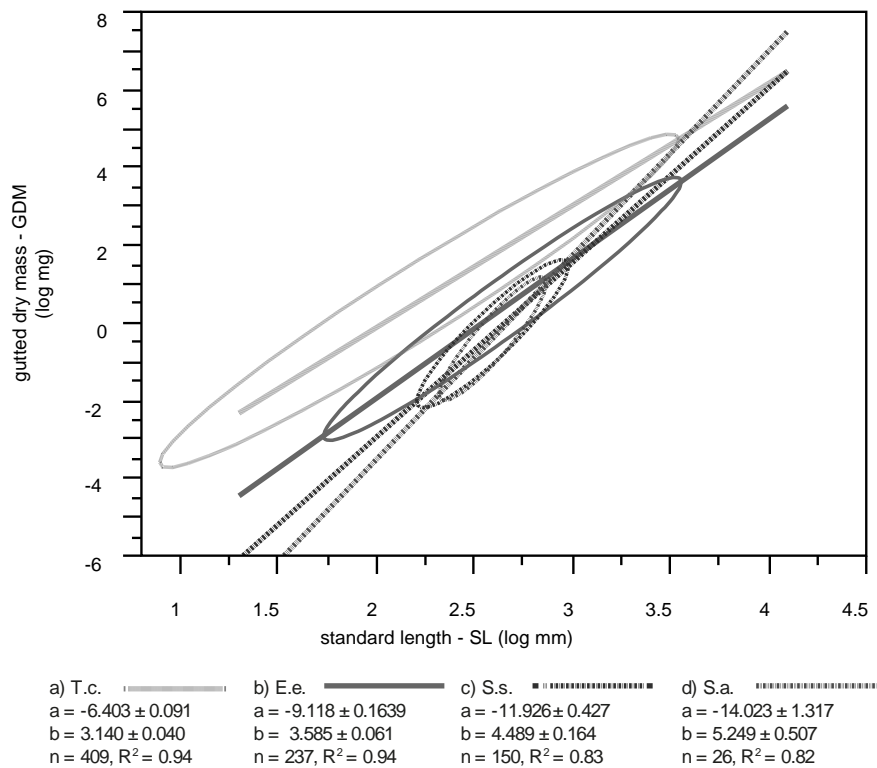
V Boyd *et al.,* 1985

W Melo, Y. C. 1985. Age composition of the South West African anchovy in 1984. ICSEAF Collection of Scientific Papers, 12: 63-68.

Annex IV Weight - length relationships

GDM = 0.1898 GWM, GWM = 5.2281 GDM, n = 240
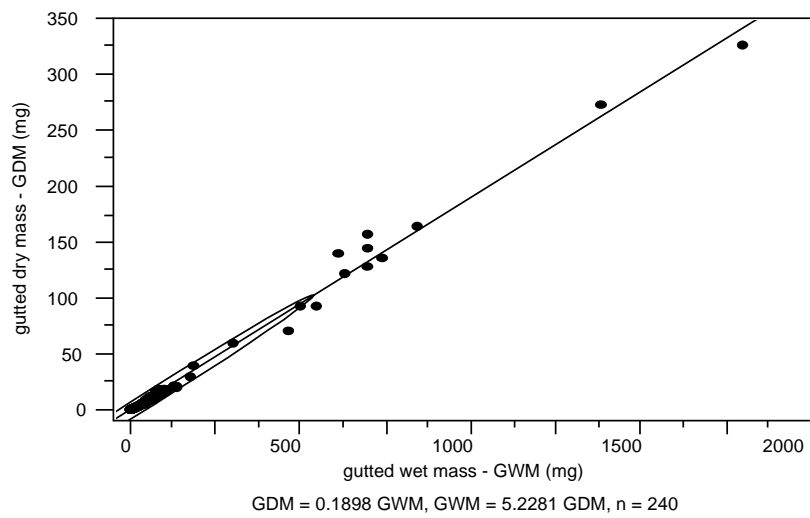
IVa Dry to wet mass relationship with pooled data from all four study species

a) T.c.	b) E.e.	c) S.s.	d) S.a.
a = -6.403 ± 0.091	a = -9.118 ± 0.1639	a = -11.926± 0.427	a = -14.023 ± 1.317
b = 3.140 ± 0.040	b = 3.585 ± 0.061	b = 4.489 ± 0.164	b = 5.249 ± 0.507
n = 409, R^2 = 0.94	n = 237, R^2 = 0.94	n = 150, R^2 = 0.83	n = 26, R^2 = 0.82

Length-weight relationships of early live stages of the four study species
T.c. = *T. capensis*, E.e. = *E. encrasicolus*, S.s. = *S. sagax*, S. a. = *S. aurita*

Plates

Plate I Impressions from field and lab work – photos by S. Geist, A. Flohr, W. Ekau, A. Neumann, and M. Steinmetz (29)

1 RV Africana, 2 RRV Discovery; 3-4 FS Maria S. Merian; 5 on board dissection of fish during Afr 258; 6-8 pelagic trawl haul full of jellyfish during Afr 258; 9 MultiNet; 10 microzooplankton Inlaynet; 11 Ring trawl; 12 Tucker trawl; 13-20 operation of plankton nets and subsequent sorting of catch; 21 net catch; 22-23 identification and length measurement; 24 on-board keeping of fish larvae at controlled temperatures; 25 wild caught *T. capensis* larvae; 26 on-board keeping of juveniles at controlled temperatures; 27 inside the temperature controlled lab-container for on-board respiration experiments; 28-29 respirometer setups; 30 example for the development of oxygen concentrations during hypoxia element with juvenile *T. capensis*

Plate II *Sardinops sagax* larval morphology 4-20 mm length – photos by S. Geist

Plate III *Engraulis encrasicolus* larval morphology 2-12 mm length – photos by S. Geist

Plate IV *Engraulis encrasicolus* larval morphology 13-21 mm length – photos by S. Geist

Plate V *Engraulis encrasicolus* larval morphology 22-38 mm length – photos by S. Geist
Plate VI *Trachurus capensis* larval morphology 3-11 mm length – photos by S. Geist

Plate VII *Trachurus capensis* larval morphology 13-38 mm length – photos by S. Geist

Plate VIII Prey items discovered in larval guts (exept No.4) – photos by S. Geist

1-2 *Ceratium* sp. – dinoflagellate; 3 flagellates; 4 *Noctiluca scintilans* – dinoflagellate; 5 Coscinodiscus sp. – diatom; 6-8 Gastropoda; 9-10 copepod eggs; 11-13 copeod nauplii; 14-17 *Oithona* sp., Cyclopoida, Copepoda; 18-20 *Oncaea* sp., Poecilostomatoida, Copepoda; 21 Oithona sp. and Oncaea sp.; 22-23 *Microsetella* sp., Harpacticoida, Copepoda; 24-28 Calanoida, Copeoda; 29-30 Calyptopes larvae, Euphausiacea

PLATE I
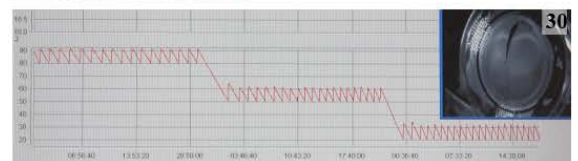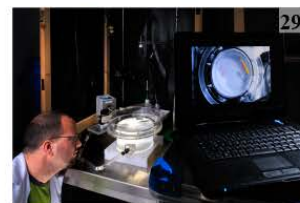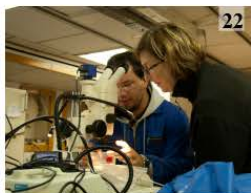
PLATE II

PLATE III

mm

2

6

8

9

10

11

12

mm

PLATE IV

13

14

15

16

17

19

20

21

mm

22

23

25

PLATE V

26

27

28

29

32

38

PLATE VI

mm

3

4

5

6

7

8

9

10

11

169

mm

12

13

14

15

16

17

18

20

21

PLATE VII

22

30

33

38
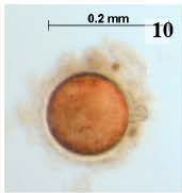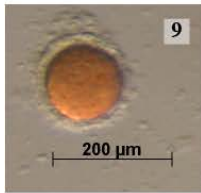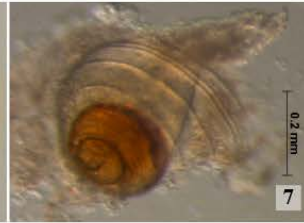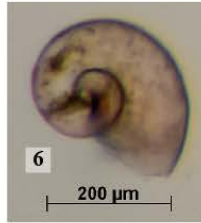
PLATE VIII

173
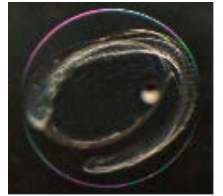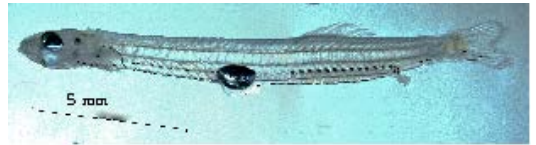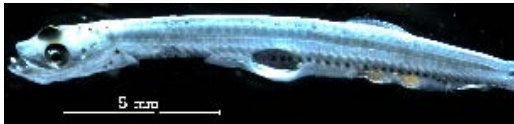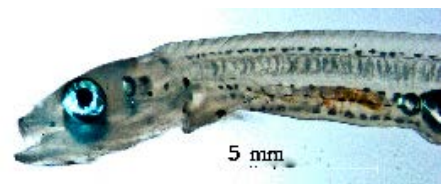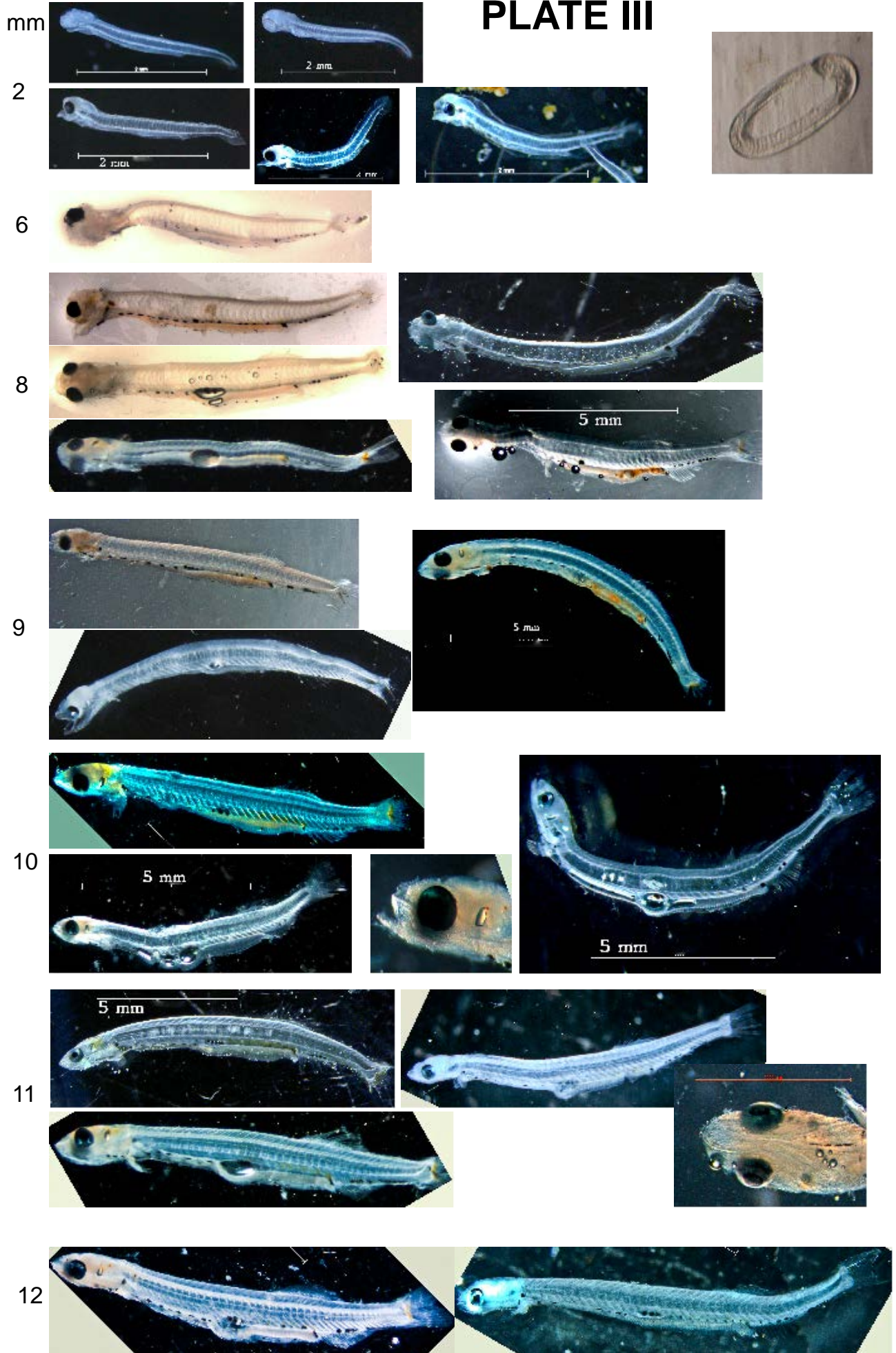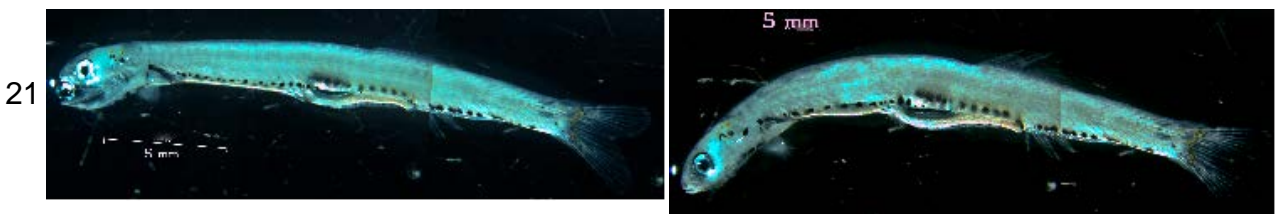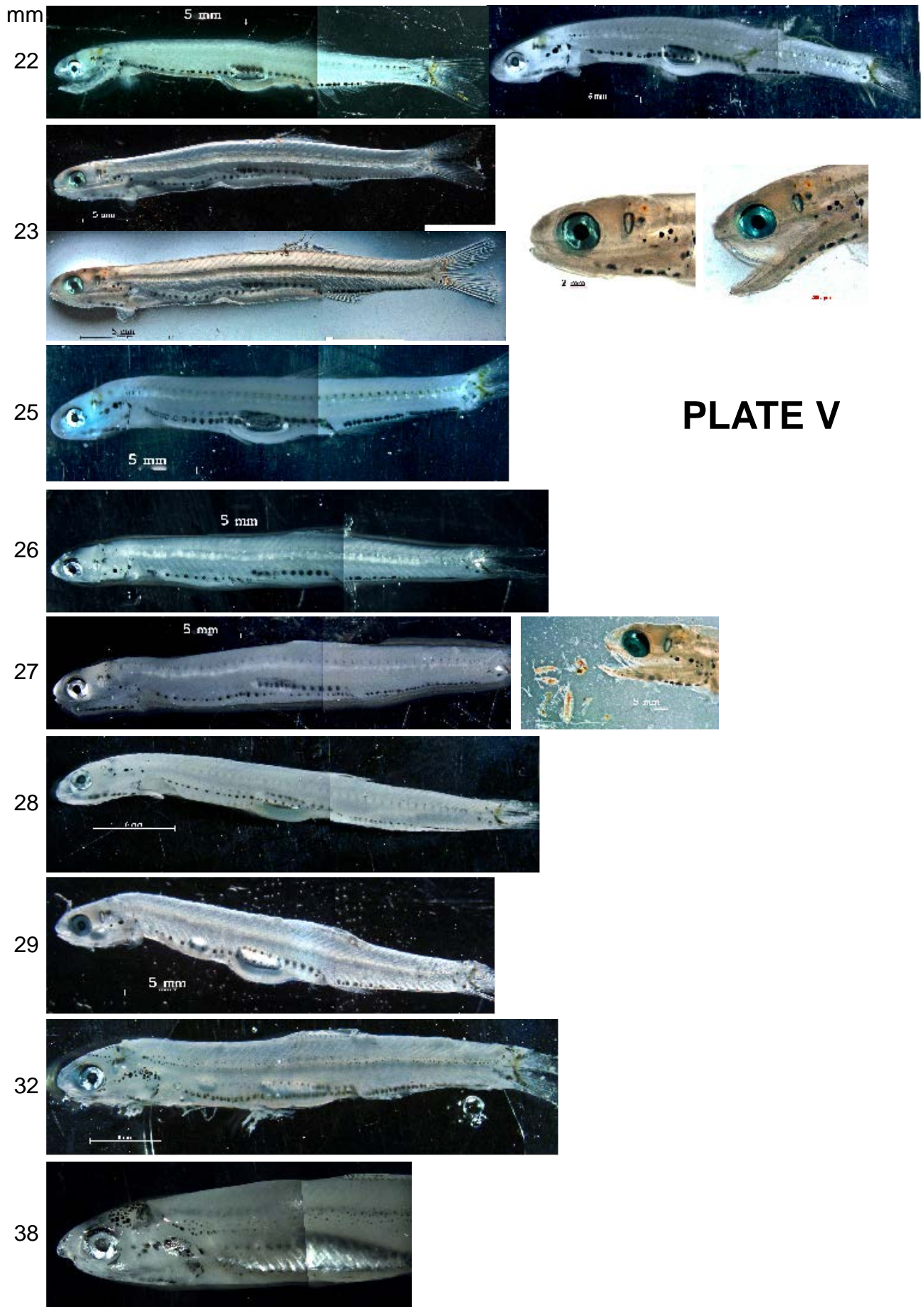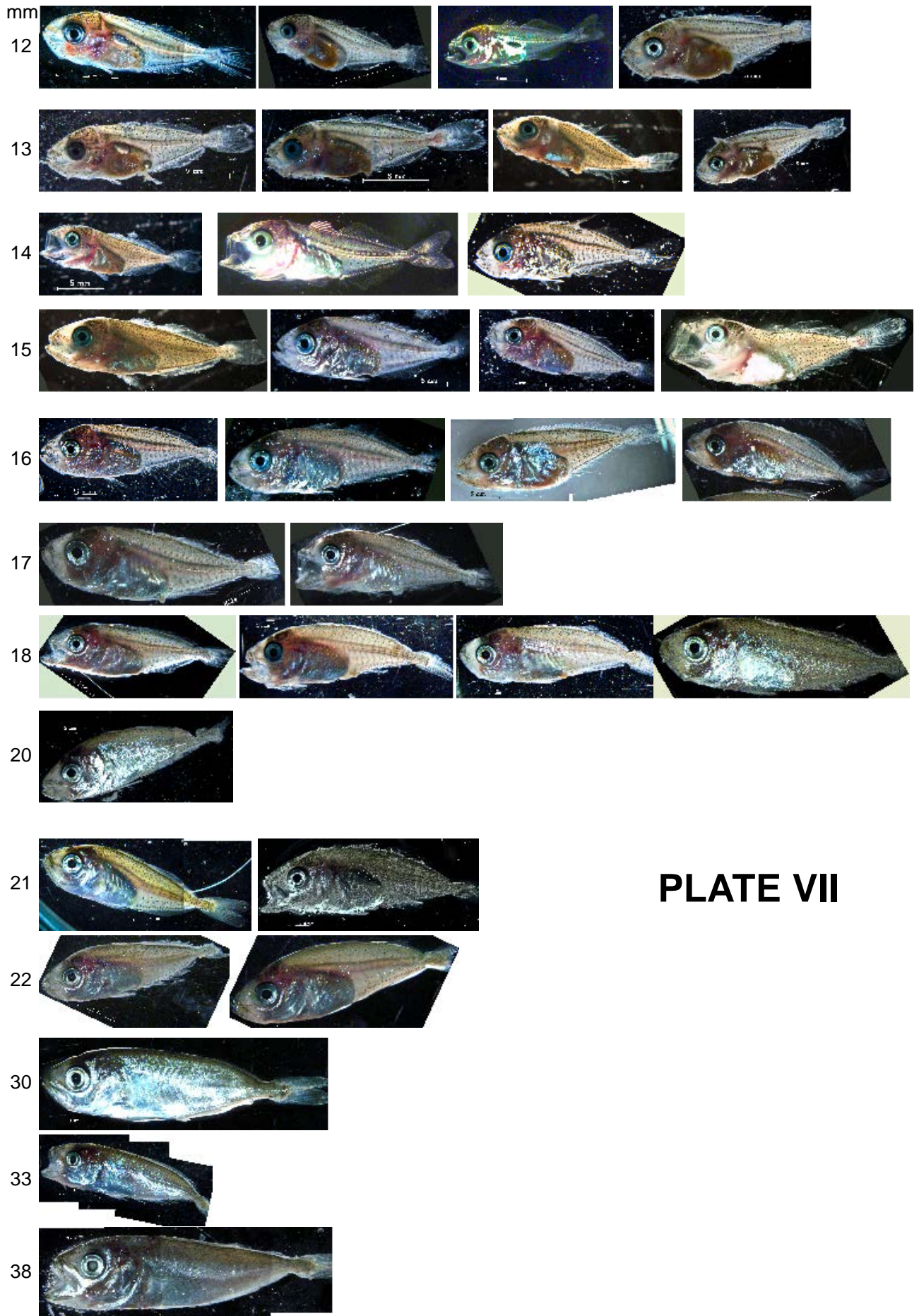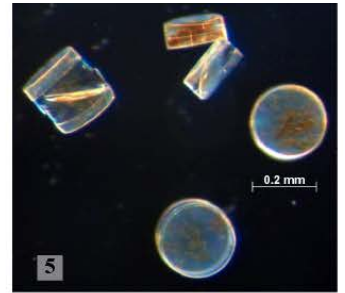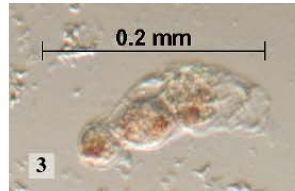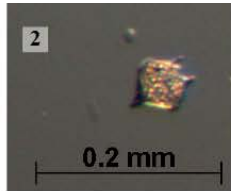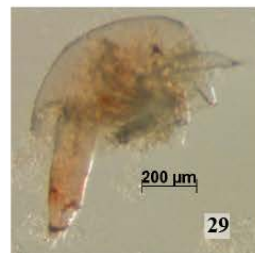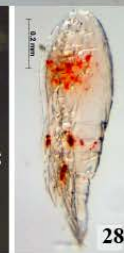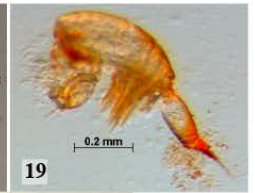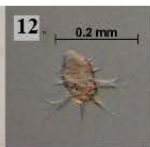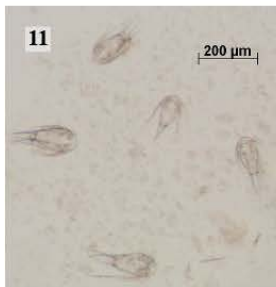
Eidesstattliche Erklärung

Eidesstattliche Erklärung

(Gem. § 6(5) Nr. 1-3 PromO)

Hiermit versichere ich, dass ich die vorliegende Arbeit mit dem Titel „Early life history traits of coastal pelagic fish in the northern Benguela Current upwelling ecosystem off Namibia":

1. ohne unerlaubte, fremde Hilfe angefertigt habe,

2. keine anderen, als die von mir im Text angegebenen Quellen und Hilfsmittel benutzt habe,

3. die den benutzten Werken wortlich oder inhaltlich entnommenen Stellen alssolche kenntlich gemacht habe.

Ebenfalls erkläre ich hiermit, dass es sich bei den von mir abgegebenen Arbeiten um drei identische Exemplare handelt.

Bremen, August 2013

Simon Geist