TO EAT, TO BE EATEN, AND A LOT OF QUESTIONS:

UNDERSTANDING THE TROPHIC ECOLOGY OF SMALL PELAGIC FISH

Susana Garrido

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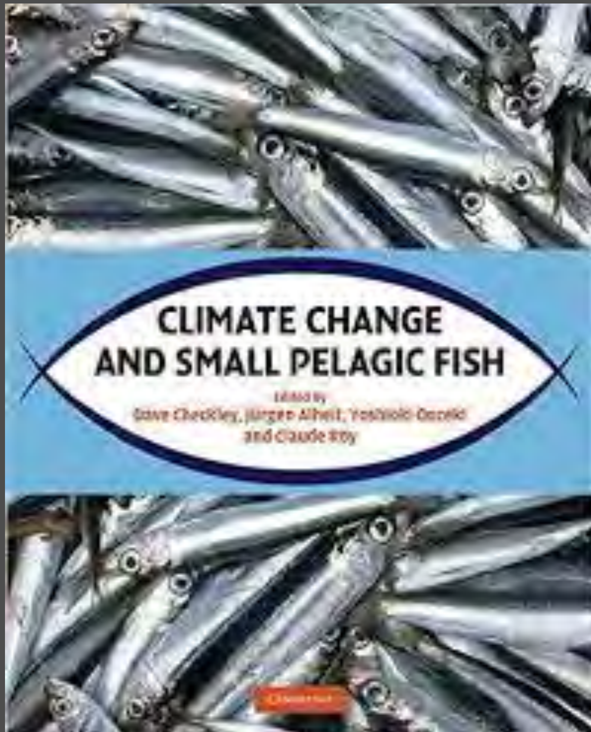
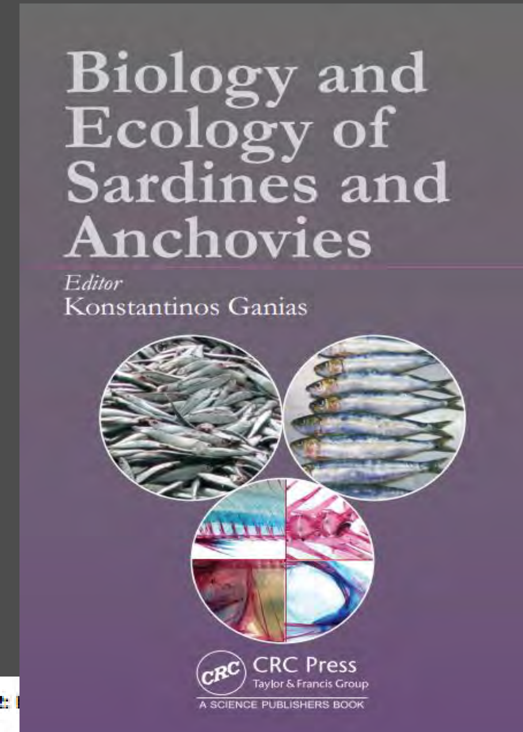
instituto português do mar e da atmosfera


CLIMATE CHANGE
AND SMALL PELAGIC FISH
Edited by
Dave Checkley, Jürgen Alheit, Yoshioki Oozeki
and Claude Roy

2009


Biology and Ecology of Sardines and Anchovies
Editor
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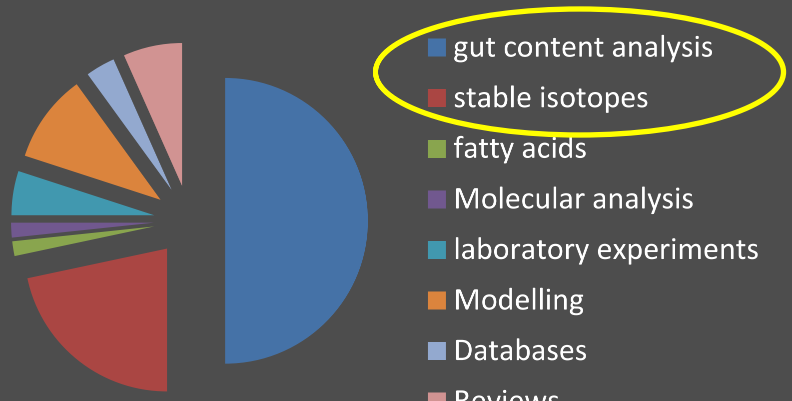
A SCIENCE PUBLISHERS BOOK

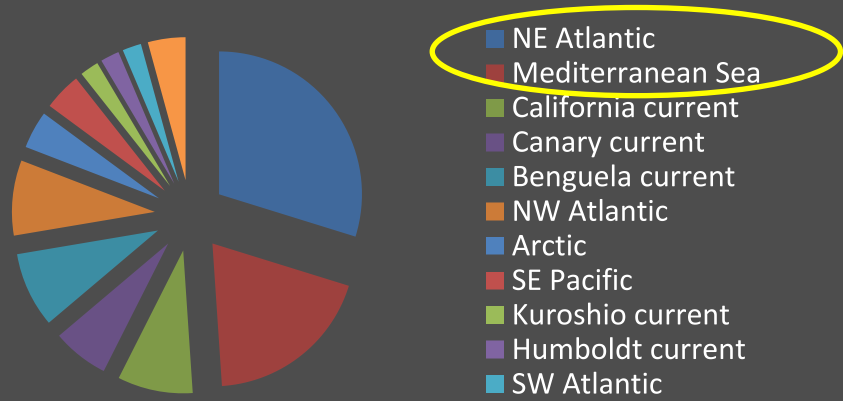
2014

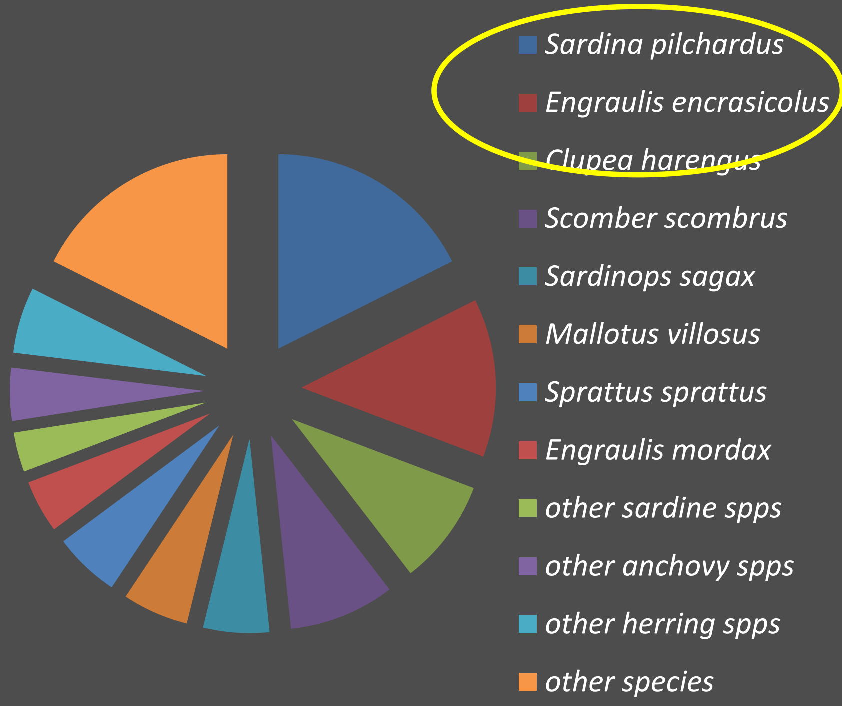
TO EAT

2014-2016

Small pelagics as predators





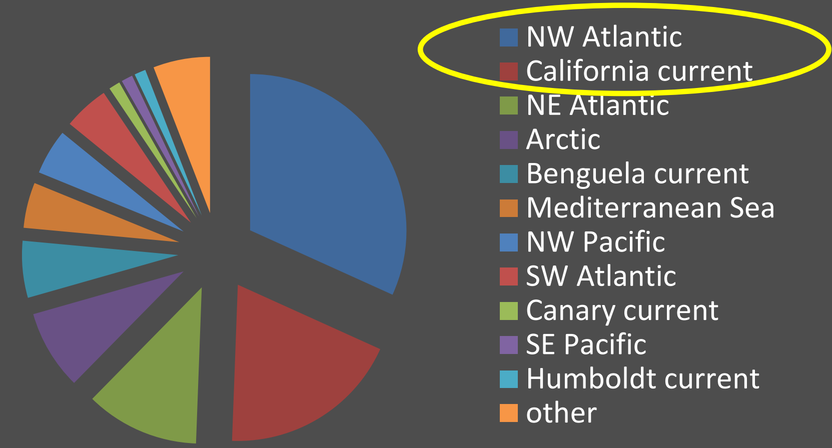


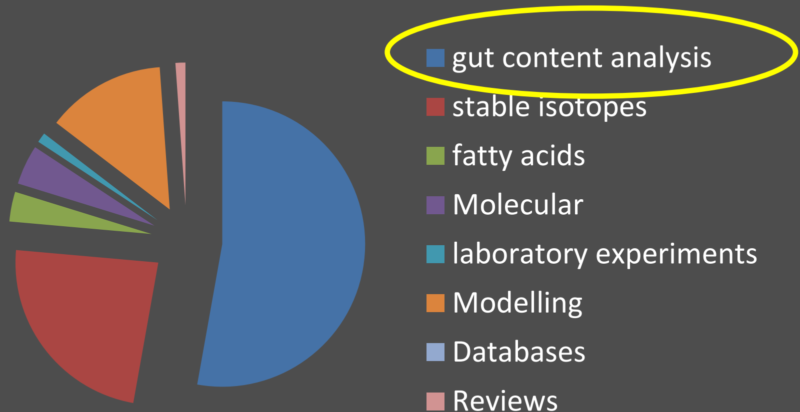
2014 to 2016

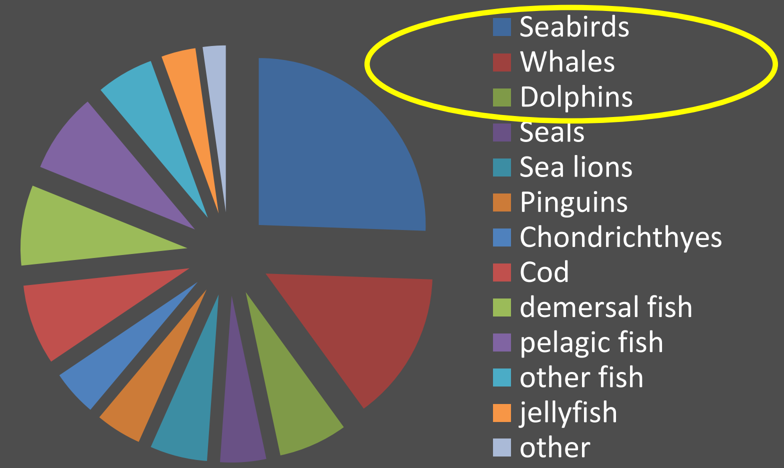
TO BE EATEN

2014-2016

Small pelagics as prey







OUTLINE

(w/ lots of questions)

1 - General considerations on the feeding ecology of small pelagics

1.1 – Morphology of the feeding apparatus

1.2 - Diet composition

1.3 – Feeding behaviour

2 – Trophodynamically-mediated processes that influence small pelagics

2.1 – Food availability and larval survival

2.2 – Competition and resource partitioning

2.3 – Cannibalism and intraguild predation

3 – Conclusions and future perspectives

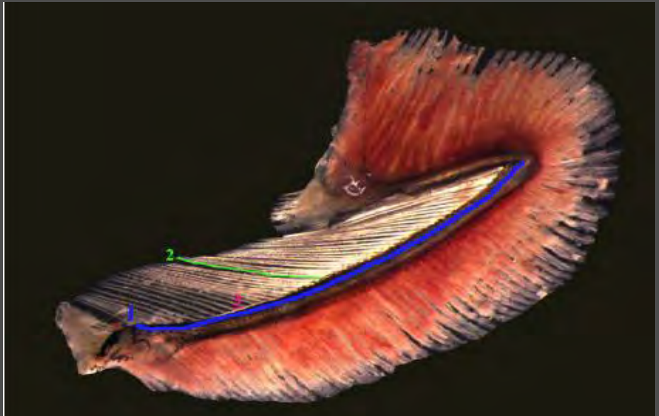
Morphology of the feeding apparatus

GENERAL CONSIDERATIONS

MORPHOLOGY OF FEEDING

Feeding apparatus is composed of several pairs of branchial arches.
Each supports a series of gill-rakers covered with denticles.

The morphology of the feeding apparatus will determine the minimum size of prey the fish is able to retain.



Costalago et al. 2014. Left branchial arch of *S. pilchardus*

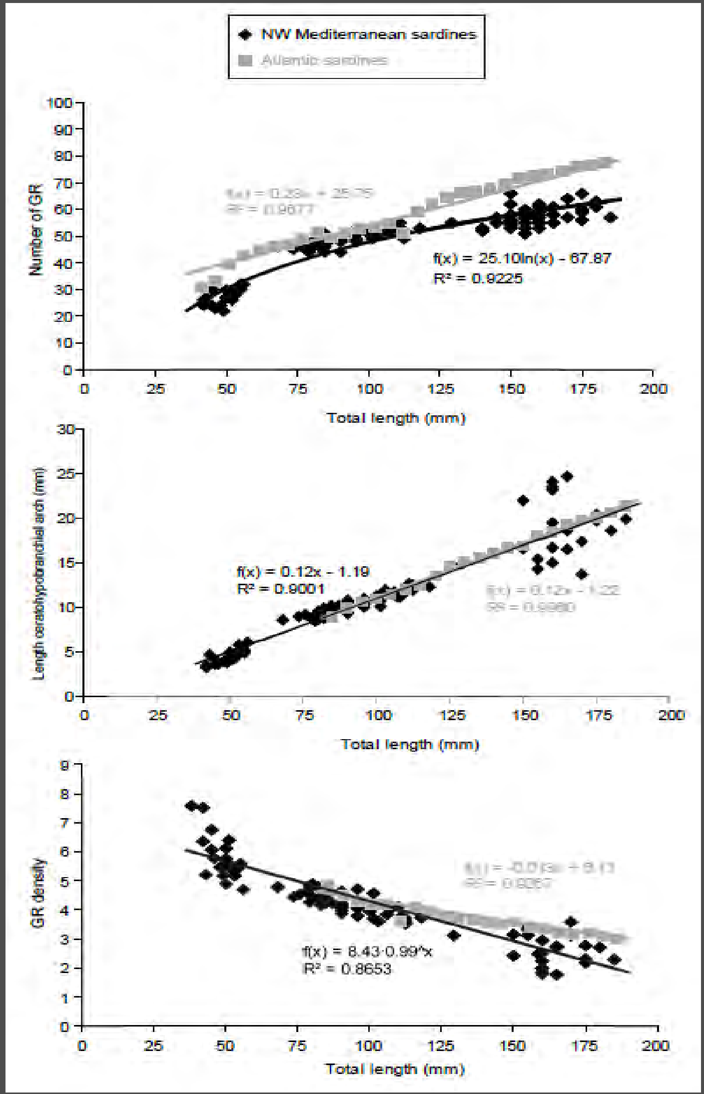
Co-occurring sardines and anchovies typically show significant differences in their feeding apparatus:
sardines: finer filtering system;
Feeding apparatus of anchovies is generally fully formed during the juvenile phase. That of sardines continues to develop throughout the adult phase.

References in Garrido and van der Lingen 2014 and van der Lingen et al. 2009

Intraspecific variability of the feeding apparatus

European sardine *Sardina pilchardus*

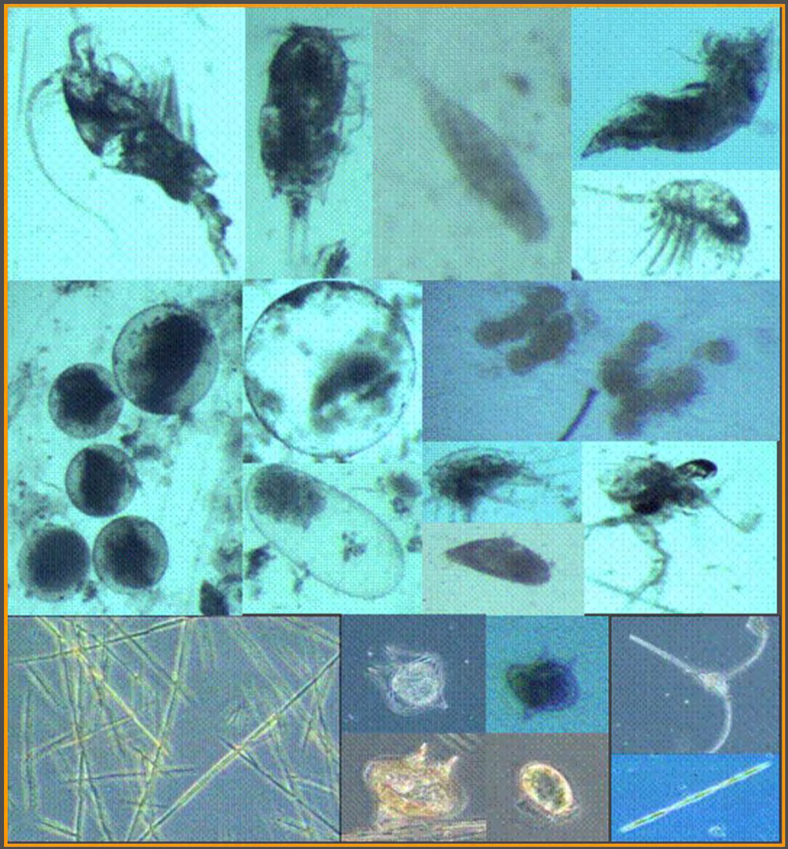
Significantly more gill-rakers and smaller gill-raker gaps in upwelling Atlantic coasts (N Africa & Iberia) than in the Mediterranean Sea.



Andreu 1954, Costalago et al. 2014, J Fish Biol

Diet composition

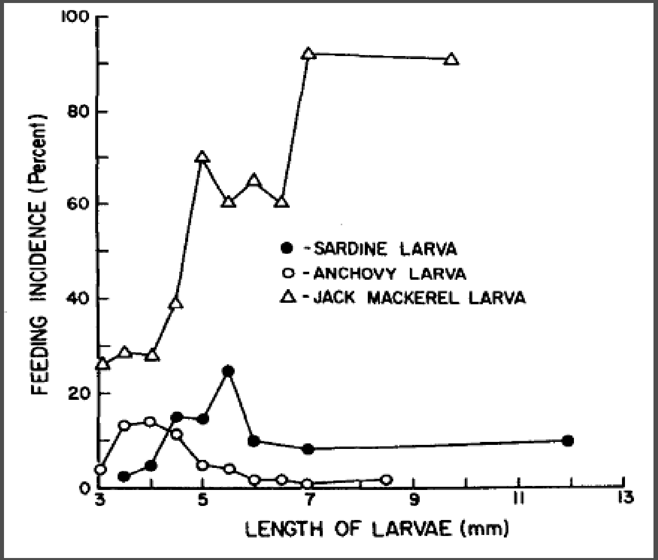
DIET COMPOSITION



Clupeoids are omnivorous planktivores.

Derive the majority of their dietary carbon from zooplankton.

Larvae



As hatching it [clupeoid larvae] is weak, blind, and depends on endowed yolk to survive, Lasker 1985.

Then, first feeding larvae must pass the first hurdle to resist starvation at first-feeding (critical period).

Diet compositon of SPF (straigth gutted species) is difficult to study, due to the high percentage of empty stomachs.

Major effort to date: Arthur et al. 1976: >10.000 *S. sagax* , >2000 *E. mordax* and >500 *T. symmetricus* larval guts analysed.

Feeding incidence <25% in all samples.

Arthur 1976

Engraulis larvae

Stomach content analysis

Laboratory Experimentation

FA and immunochemical analysis

E.mordax: 20-10% feeding incidence

E.encrasicolus:30-20% feeding incidence

E.ringens:
65-80% feeding incidence off Chile (3)

E.japonicus: 10-64% feeding incidence

E.anchoita:<30% feeding incidence

References in Garrido and van der Lingen 2014 and van der Lingen et al. 2009

Sardinops and Sardina larvae

Stomach content analysis

Laboratory Experimentation

FA and immunochemical analysis

S. sagax:
California:20% feeding incidence
70-85% off Chile (3)

S. pilchardus: 30-2% feeding incidence

S. melanostictus: 30-20% feeding incidence

References in Garrido and van der Lingen 2014 and van der Lingen et al. 2009

Engraulis larvae

Stomach content analysis

Laboratory Experimentation

FA and immunochemical analysis

E.mordax:

Eggs, nauplii and copepodite stages of small **copepods**, occasionally pteropods and phytoplankton

Phytoplankton important at first-feeding as well as non-loricate ciliates.Ciliates

E.ringens:

Eggs,nauplii, **copepodites**.

Phytoplankton important at first-feeding as well as ciliates.

E.anchoita:

Eggs, nauplii and copepodite stages of **copepods**, low phytoplankton

E.encrasicolus:

Canary current: **Copepods** & Tintinnids. Inneficiency to capture copepod nauplii at first-feeding.

Benguela: only 3 individuals.

Mediterranean Sea: **Copepods**, tintinnids, bivalve and decapod larvae. First-feeding larvae prefer bivalves over copepod nauplii. Prymnesiophyceae.

Contradictory results of selectivity:calanoids?? Cladocerans??

E.japonicus:

From eggs & nauplii to **copepodite** and adults of *Oithona* and *Paracalanus*. Protists not found with epifluorescence. Contradictory results on selection of *Oithona*. Occasionally phytoplankton.

References in Garrido and van der Lingen 2014 and van der Lingen et al. 2009

Sardinops and Sardina larvae

Stomach content analysis

Laboratory Experimentation

FA and immunochemical analysis

S. sagax:

Benguela: 2 inds (nauplii & harpacticoid **copepod**).

California: Eggs, nauplii, **copepodites** *Oithona, Para/Pseudocalanus*. Occasionally phytoplankton.

Chile: **Copepods** eggs and nauplii at first-feeding.

S. pilchardus:

Canary current: No published study (copepod nauplii, **copepodites**, cladocerans). Ocasionally dinoflagellates.

Mediterranean Sea: Copepods eggs and nauplii, copepodites.

S. melanostictus:

From eggs & nauplii to **copepodite** and adults of *Oithona* and *Paracalanus*. *Oncaea, Microsetella.*

Protists not found with epifluorescence.

References in Garrido and van der Lingen 2014 and van der Lingen et al. 2009

GENERAL CONSIDERATIONS

DIET COMPOSITION

Laboratory experiments are a useful complementary methodology to study larval feeding dynamics, but the natural environment will always be very difficult to reproduce…

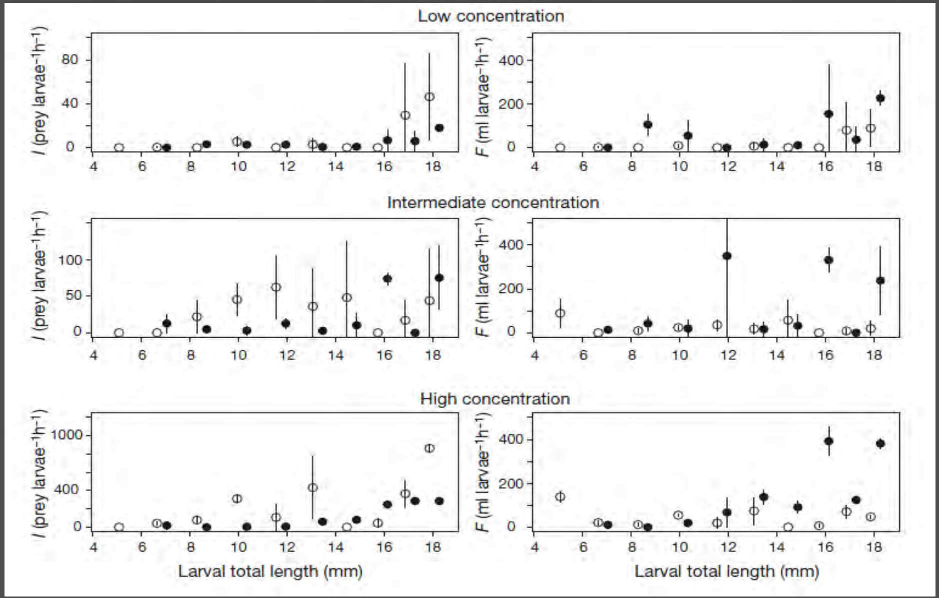
Tank size and color
Illumination
Photoperiod
Larval density
Turbulence
Egg quality
……….

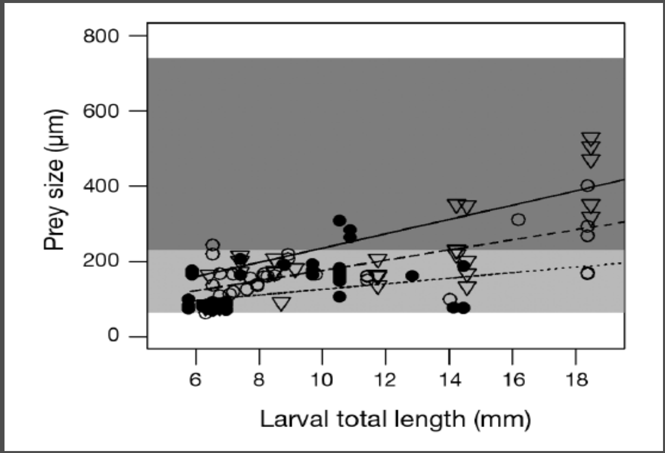
http://projectvital.fc.ul.pt/

GENERAL CONSIDERATIONS

DIET COMPOSITION

Sardina pilchardus larvae





Ingestion rates, digestion rates, feeding behaviour, prey selectivity…..

Caldeira et al. 2014 MEPS, Silva et al. 2014 MEPS

GENERAL CONSIDERATIONS

DIET COMPOSITION

Engraulis juveniles and adults

Stomach content analysis

Laboratory Experimentation

FA , SI and immunochemical analysis

E.mordax:
Mainly zooplankton (**copepods**, followed by **euphausiids**). Also **fish eggs***. Phytoplankton in high numbers but significantly lower biomass.

E.ringens:
Copepods (*Calanus, Centropages, Corycaeus, Oncaea*) but higher proportion of phytoplankton as adults. **Also fish eggs***.

E.anchoita:
Argentinean Coast: **cladocerans, copepods, euphausiids**, **amphipods** and **decapod larvae**. Also , **fish eggs* and larvae**, **appendicularians, salps**

E.encrasicolus:
<u>NE Atlantic & Iberia</u>: **Copepods, fish eggs.** Selection against bivalves, appendicularia, cladocerans.
<u>Benguela</u>: small **copepods,** eggs, nauplii. Ocasionally phytoplankton. Higher efficiency for carbon absorption from zooplankton.
<u>Mediterranean:</u> juv: small **copepods**, **bivalve** and **decapod larvae**. Ad: larger **copepods**, **decapod larvae** and **amphipods**. Selection against siphonophora, appendicularia, doliolids. SI: Cladocerans and Appendicularia

E.japonicus:
Juv: Small **copepods**; Ad: also **euphausiids**, **amphipods**, **fish eggs and larvae**, **bivalve**, **decapod** and **cirriped** larvae, **cladocerans**.

References in Garrido and van der Lingen 2014 and van der Lingen et al. 2009

GENERAL CONSIDERATIONS

DIET COMPOSITION

Sardinops and Sardina larvae

Stomach content analysis

Laboratory Experimentation

FA, SI and immunochemical analysis

S. sagax:

Benguela: Zooplankton (small <1.2 μm ciclopoid and calanoid **copepods**) Phytopl. only ocasionally important. **Fish eggs**.

California: **Euphausiids**, **copepods** and **decapod larvae**. Ad: **Diatoms, dinoflagellates and copepods**.

Humboldt: Calanoid **copepods** and **euphausiids**. Larger prey than in other upwelling areas.

British Columbia: **Euphausiids, copepods** and **diatoms**.

Australia: **Copepods, euphausiids, mysids, ostracods**. Also **fish eggs.**

S. pilchardus:

NE Atlantic: **Copepods, decapods, shiphonophores**, **fish eggs**, **Appendicularians**, **crustacean eggs**.

Canary: **Copepods, decapod larvae**, **fish eggs**, **cirripeds, crustacean eggs** and **phytoplankton** (30/40% resting).

SI: Protein from zooplankton, phytoplankton for reserve materials.

Mediterranean**: Copepods, decapod larvae.**

S. melanostictus:

Kuroshio/Oyashio: **Copepods** (calanoids), **ostracoids, cladocerans, fish eggs** and **phytoplankton**. Also **jellies, appendicularians** and **bivalves**.

SI: *Corycaeus, Microsetella, Paracalanus, cirripeds, cladocerans, stomatopods.*

References in Garrido and van der Lingen 2014 and van der Lingen et al. 2009

GENERAL CONSIDERATIONS

DIET COMPOSITION

Strong spatial and seasonal variability of the diet composition

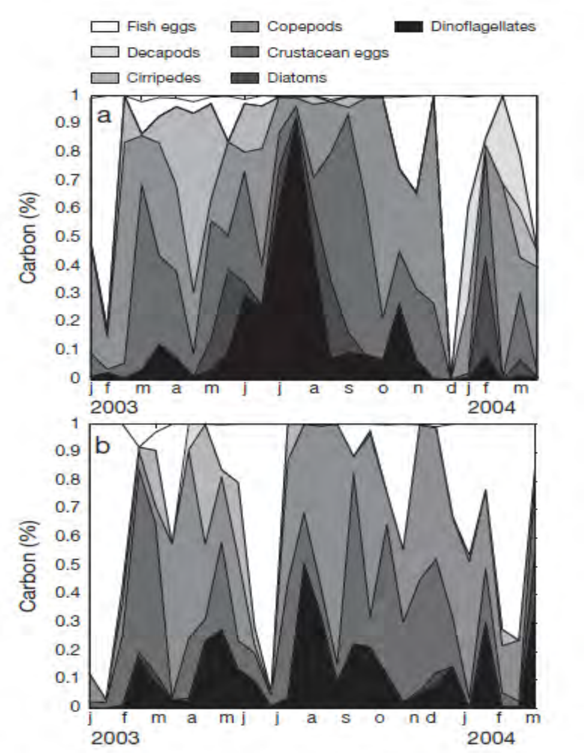


Fig. 3. *Sardina pilchardus*. Cumulative percentage contribution to dietary carbon by prey category in the stomachs of ~18 cm sardines collected every 14 d from (a) Peniche and (b)Portimão

Sardina pilchardus

Garrido et al. MEPS 2008 and *unplubished data*

Feeding behaviour

Small pelagic fish larvae:

Generally selective visual feeders (diurnal).
The ability to resist starvation increases sharply with ontogeny.

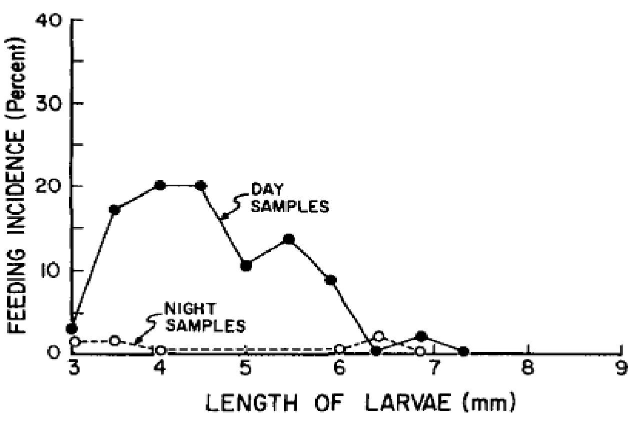
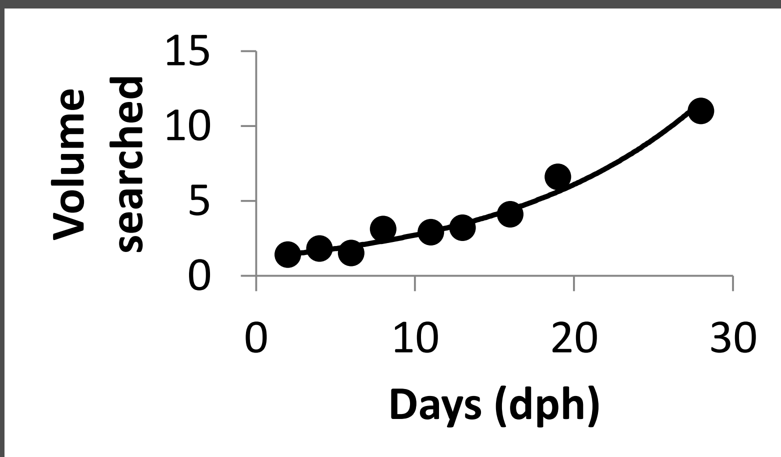


FIGURE 4.–Diurnality of feeding incidence of northern anchovy larvae.

Species	Temp ºC	PNR – from yolk absorption	PNR – from onset of feeding
Clupea harengus	7-8	6	22
Engraulis mordax	16.5	1.5	2.5
Scomber japonicus	19	1.0	1.6
Anchoa mitchilli	24	1.4	1.7

Arthur et al. 1976, Rosenthal & Hempel 1970

The volume of water searched, the number of attacks and successful capture increases with ontogeny.



Clupea harengus

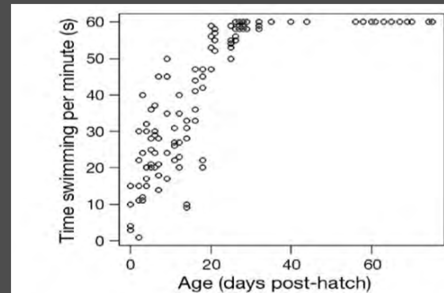


Fig. 2. Time spent swimming by sardine *Sardina pilchardus* larvae during a 60 s period of observation throughout larval ontogeny for larvae reared with high prey concentrations (Diet C)

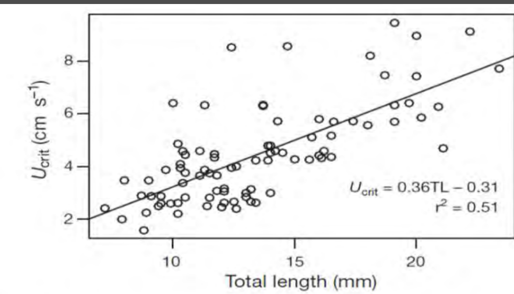
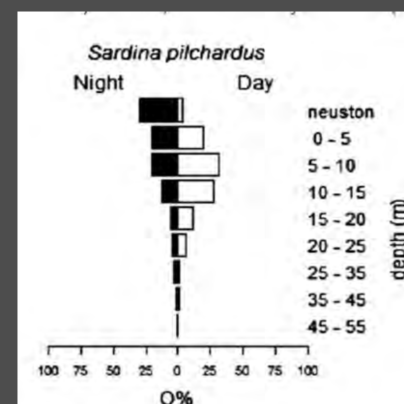


Fig. 4. Critical swimming speed (U_{crit}) of sardine *Sardina pilchardus* larvae throughout ontogeny for larvae from all feeding treatments. Each symbol represents the U_{crit} for an individual larva



Sardina pilchardus

J**uveniles and adults**:

Two feeding modes and switch between the two depending on feeding conditions: generally **filter-feeding** on smaller food particles and **particulate-feeding** (or biting) on larger food particles.

The ability to switch between these feeding modes makes these species highly opportunistic and flexible foragers, which are able to maximize their energy intake through employing the feeding mode most appropriate to a particular food environment.

Filter- and Particulate-feeding

Trophodynamic processes:
Food availability & larval survival

Egg and larval stages are critical for recruitment

Starvation
- Critical period (Hjort 1914)
- Match-mismatch (Cushing 1975)

Predation
- Bigger is better (Miller et al. 1988)
- Stage Duration (Houde 1987)

Physical factors
- Retention, Member/Vagrant Iles & Sinclair (1982)
- Fundamental triad Bakun (1996)

- Year-class strength is determined within the first stages of life and affected by oceanographic conditions.
- Mortality occurring in these early stages is mostly selective.
- Trophodynamically-mediated processes of larval mortality may act mostly through predation.

FOOD AVAILABILITY & LARVAL SURVIVAL

Critical period (at first-feeding) was demonstrated for species for which prey preferences are known. When all the plankton assemblage is used, results do not confirm the theory of the critical period.

Extremely difficult to prove for sardine and anchovy species due to poor data of field studies of feeding dynamics, based on few individuals (high number of **empty stomachs**).

New techniques for capturing larvae are needed: Shorter hauls, light traps??
Different methods to study larval feeding: SIA, FA, experimentation.

Robert et al. ICES J Mar Sci 2014, Beaugrand et al., Nature 2003, Robert et al. ICES J Mar Sci 2009, Irigoien et al. J Plankton Res. 2009, Kunzmann et al. 2014

Trophodynamic processes: Competition and resource partitioning

COMPETITION AND RESOURCE PARTITIONING

Size-based resource partitioning of zooplankton is typically observed between co-occurring anchovies and sardines.

Sardines feed on smaller zooplankton and consume more phytoplankton than do anchovies (lower trophic level).

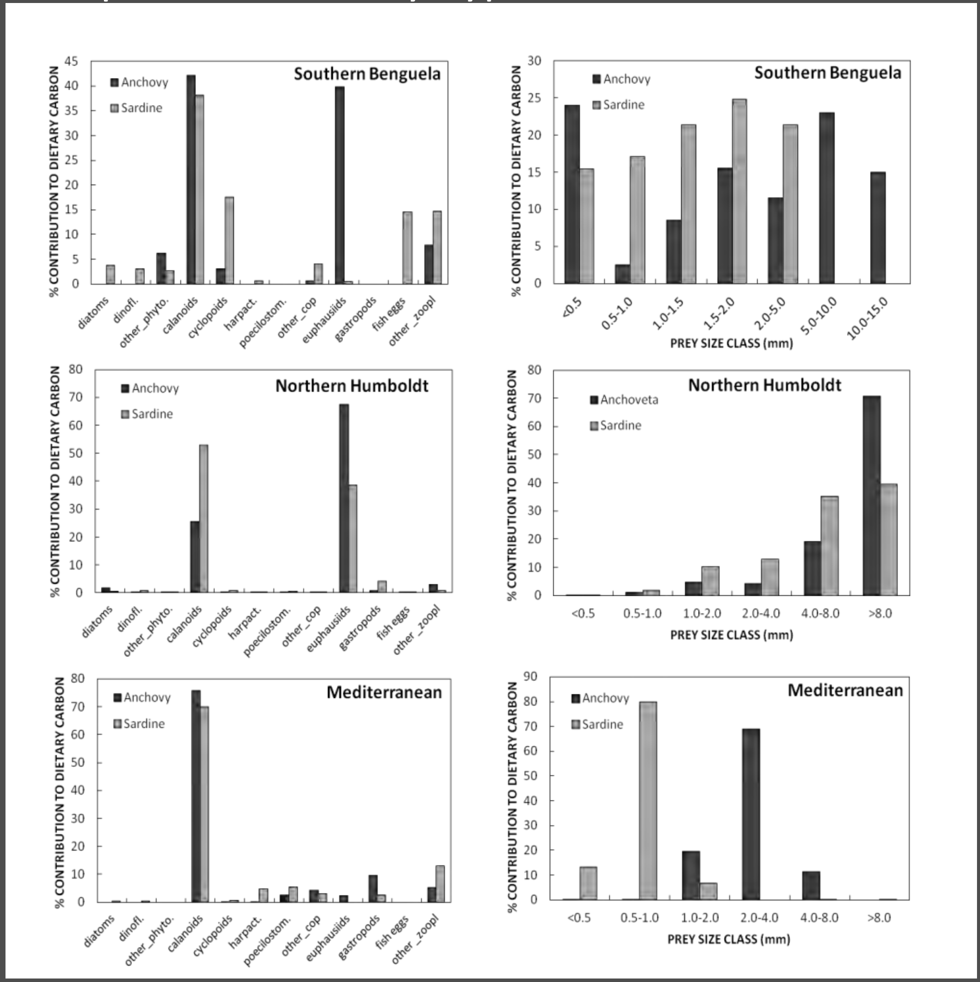
Reasons:

Morphology
Behavior

<u>Trophic dissimilarity hypothesis:</u>

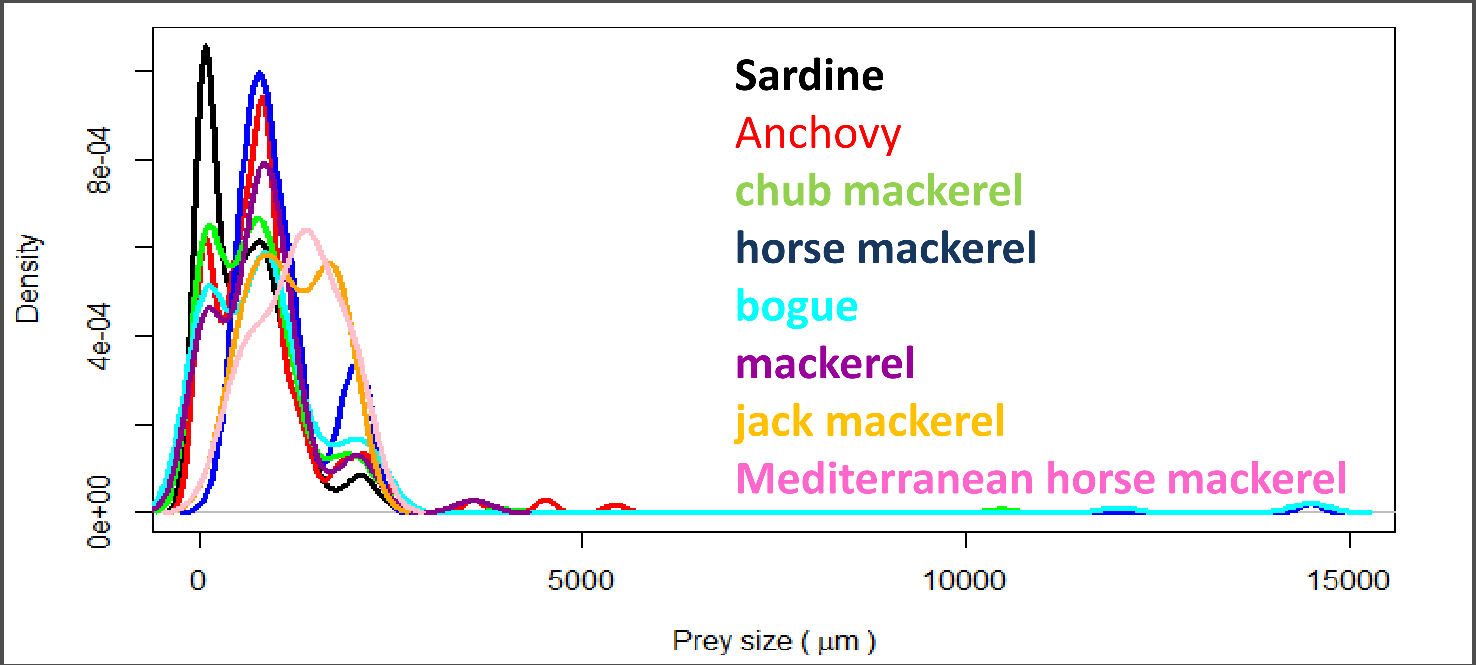
Observed shifts in species dominance may be trophycally-mediated.
Environmentally-mediated changes in the size and/or species composition of the zooplankton community could cause species alternations.

Trophic dissimilarity hypothesis (van der Lingen



COMPETITION AND RESOURCE PARTITIONING

Western Iberia: PREY SIZES



Most important size-class for all SPF: **1000–2000** µm

Mean prey size: Lower for pil than all other

ane: variable from 500 to **> 3000 µm**, depending on the area and maturity stage.

Garrido et al. MEPS 2015

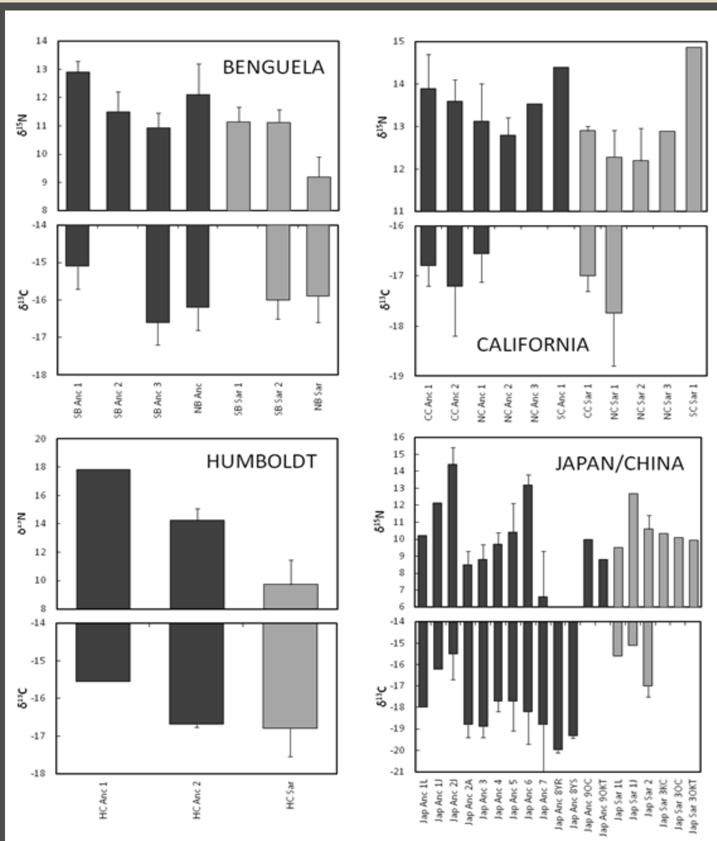
Stable isotopic analysis (SIA)

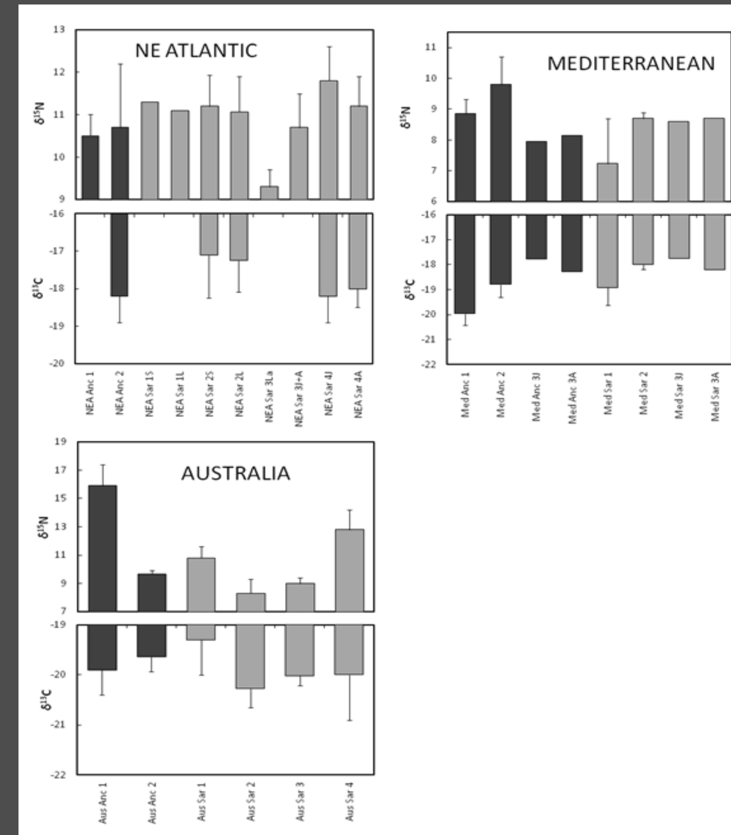
Stable isotopes provide information on the trophic level of species (δ15N;), food-web length, and origin of organic matter (δ13C & δ15N;) ingested by consumers.

Whereas stomach content analyses provide a “snapshot” of a consumer’s diet, SIA provides a broader perspective as isotopes are temporally integrated (40-80 days for fish muscle tissue) and are an expression of assimilated diet.

Post 2002, Fry 2006, Bode et al. 2007, Miller et al. 2010, McCallister et al. 2006

COMPETITION AND RESOURCE PARTITIONING





Dark bars: Anchovy | Light bars: Sardine

Garrido and van der Lingen 2014

Trophodynamic processes: Cannibalism & intraguild predation

CANIBALISM & INTRAGUILD PREDATION

E.mordax:
California: Filters eggs (more frequently), particulate-feeding larvae. **17-32%** egg mortality.

E.ringens:
Cannibalizes more eggs than larvae. **21.9**% egg mortality.

E.anchoita:
Cannibalizes eggs and larvae, mainly adults. Higher during the day and with low mesozooplankton abundance.
27% (northern stock), **1-2%** (Patagonian stock), **8.8%** (Buenos Aires stock).

E.encrasicolus:
NE Atlantic: North and Baltic Seas: fish larvae and (sprat) eggs, higher than herring & sprat; Biscay: **2%** mortality by cannibalism.
Canary: Low number of eggs, adults (not juv).
Mediterranean: Higher feeding intensity during the winter (not spawning) Very low consumption of fish eggs or even non-existing.
Benguela: Higher feeding during the summer. **6%** egg mortality due to cannibalism.

E.japonicus:
Less frequent than for the other spps, although 1 study showed juveniles had 25.8%FO of larvae.

References in Garrido and van der Lingen 2014 and van der Lingen et al. 2009

CANIBALISM & INTRAGUILD PREDATION

Sardinops and Sardina

S. sagax:
Predation of anchovy eggs in all current systems, higher in Benguela (on occasions >50%CC up to 83%CC, estimations of up to **56%** of total **anchovy** mortality) and Australia than California and Humboldt (in anchovy spawning grounds: 62%FO).

S. pilchardus:
NE Atlantic (Biscay): Fish eggs frequent, namely of anchovy.
Canary (NW Iberia): Fish eggs frequently found, particularly cannibalism.**30%(81%)**
Mediterranean Sea: Seldom or absent.

Density-dependent mechanism

Higher when there is lower plankton availability

Eggs > Larvae

S. melanostictus:
Fish eggs seldom found (low FO, low numbers).
Maybe consequence of higher dispersal of eggs and larvae.

References in Garrido and van der Lingen 2014 and van der Lingen et al. 2009

CONCLUSIONS & FUTURE PERSPECTIVES

CONCLUSIONS

LARVAL PHASE

Progressing in the understanding of the feeding ecology of small pelagic fish larvae is important: not really clear most important prey for the majority of fish species. Alternative (or improved) methods to describe diet compositon and prey selectivity in the wild is necessary.

Early larvae of several spps of SPF do not capture copepod nauplii efficiently and must rely on smaller prey (ciliates, naked-phytoplankton cells) that are easily digested. It is essential to properly estimate microzooplankton abundance. Even in non-upwelling areas it can represent 5X more biomass than mesozooplankton (Calbet et al. 2001).

CONCLUSIONS

JUVENILE AND ADULTS

The marked plasticity of the feeding behaviour of SPF requires a high number of fish to be analysed.
While stomach content analysis and prey quantification is very informative, other methods such as SIA are important complementary techniques to describe the trophic position of fish, including to understand large scale variability.

Effect of maternal provisioning on larval survival needs to be clarified.

Thank you!