Trophodynamic Processes and Small Pelagic Fishes

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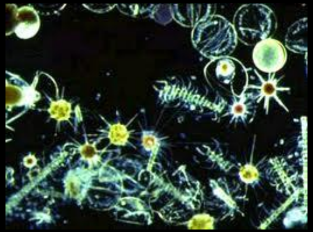

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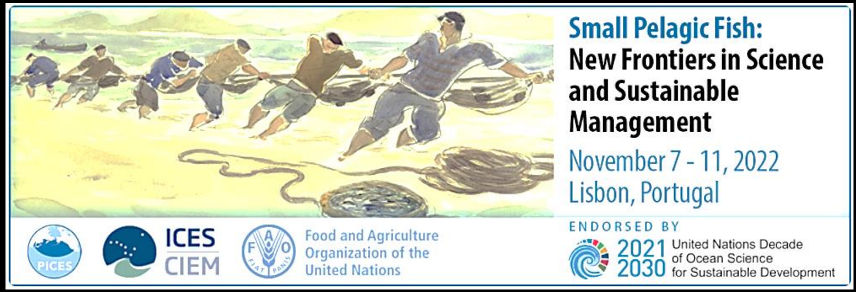


Overview

Describe by way of examples how information on trophodynamic processes involving SPFs has been collected. Comparative approach (SPACC) used

<u>SPFs as predators</u>

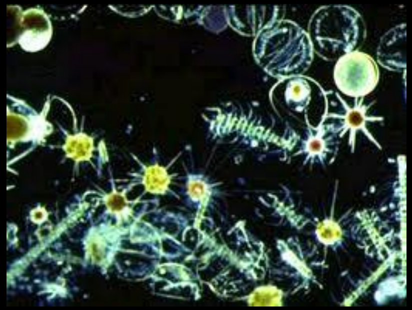
How and what is consumed and assimilated from studies of:

(i) trophic morphology
(ii) diet
(iii) feeding behaviour (and costs)
(iv) biochemical tracers of assimilated diet (stable isotopes)

<u>SPFs as prey</u>

What species forage on SPFs and what consequences do changes in SPF abundance levels have for their predators (models and observations)





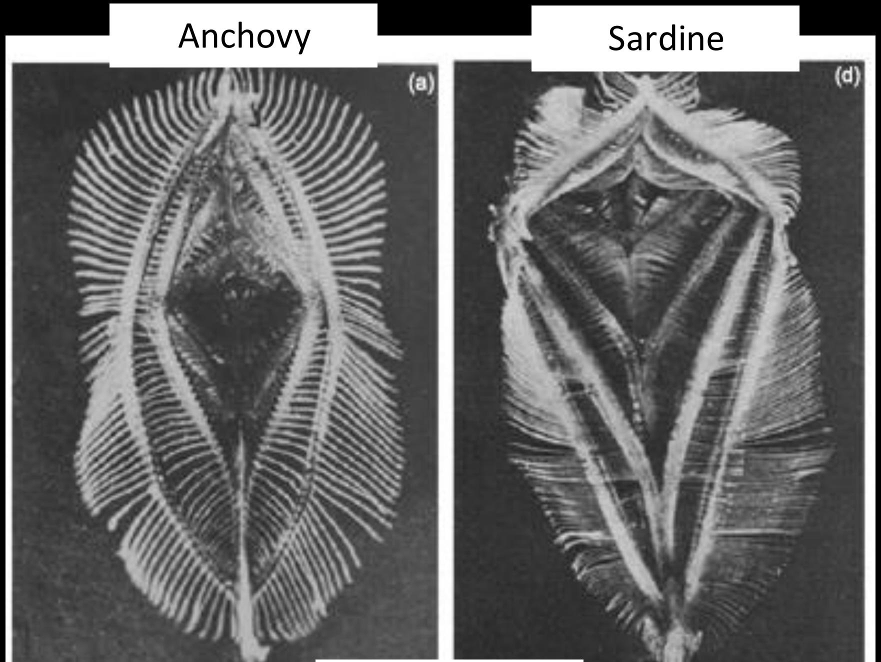


Trophic morphology (i)

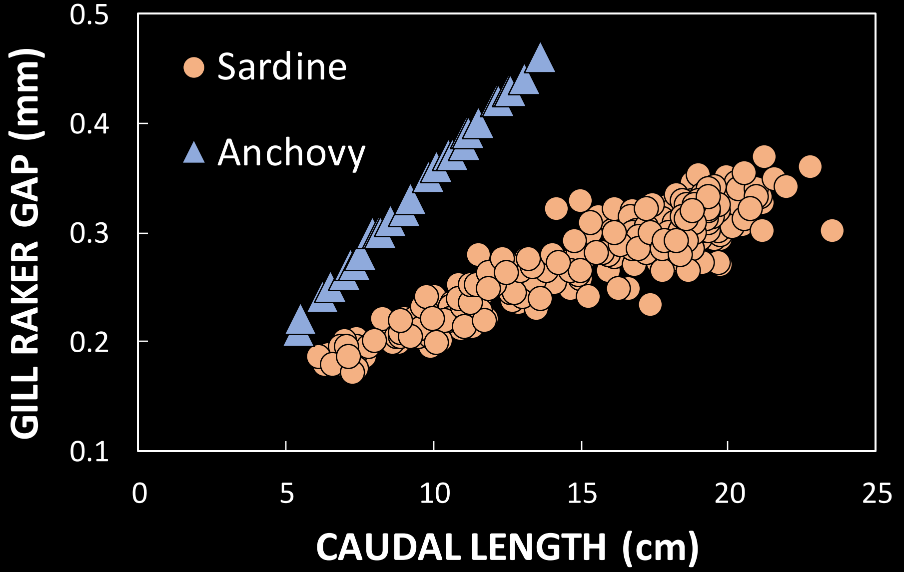
SPFs are planktivorous and use their gill rakers to entrap plankton which are concentrated by the epibranchial organ

SPFs that consume more (or only) phytoplankton have a finer branchial basket (*right*), well-developed epibranchial organs, more pyloric cecae and a longer GIT (*below*) than those that consume more (or only) zooplankton

Species	Diet	Gut : Body length ratio
Cetengraulis mysticetus	Planktonic and benthic diatoms	8.5 : 1
Sardinops sagax	Phytoplankton and zooplankton	1.5 : 1
Engraulis encrasicolus	Phytoplankton and zooplankton	1.1 : 1
Clupea harengus	Zooplankton	0.5 : 1



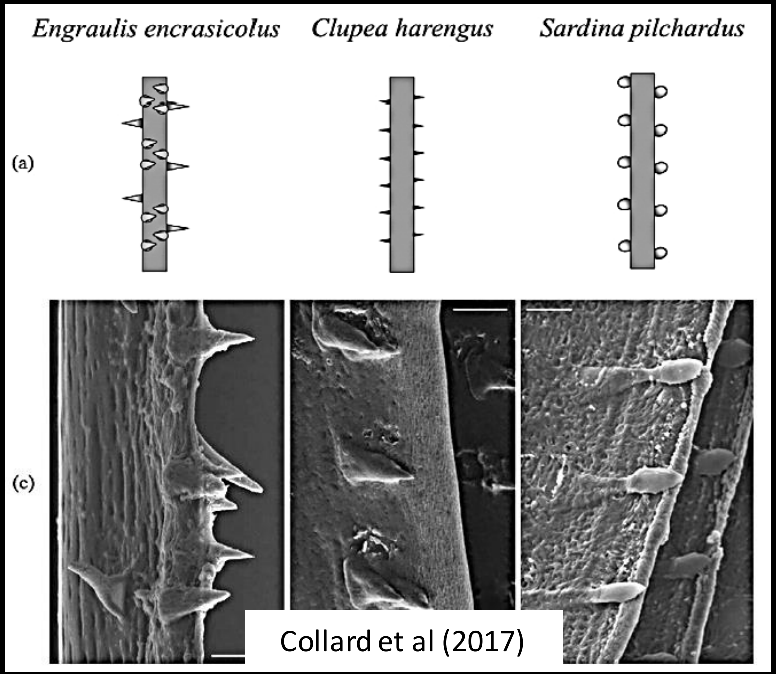
King and MacLeod (1976)

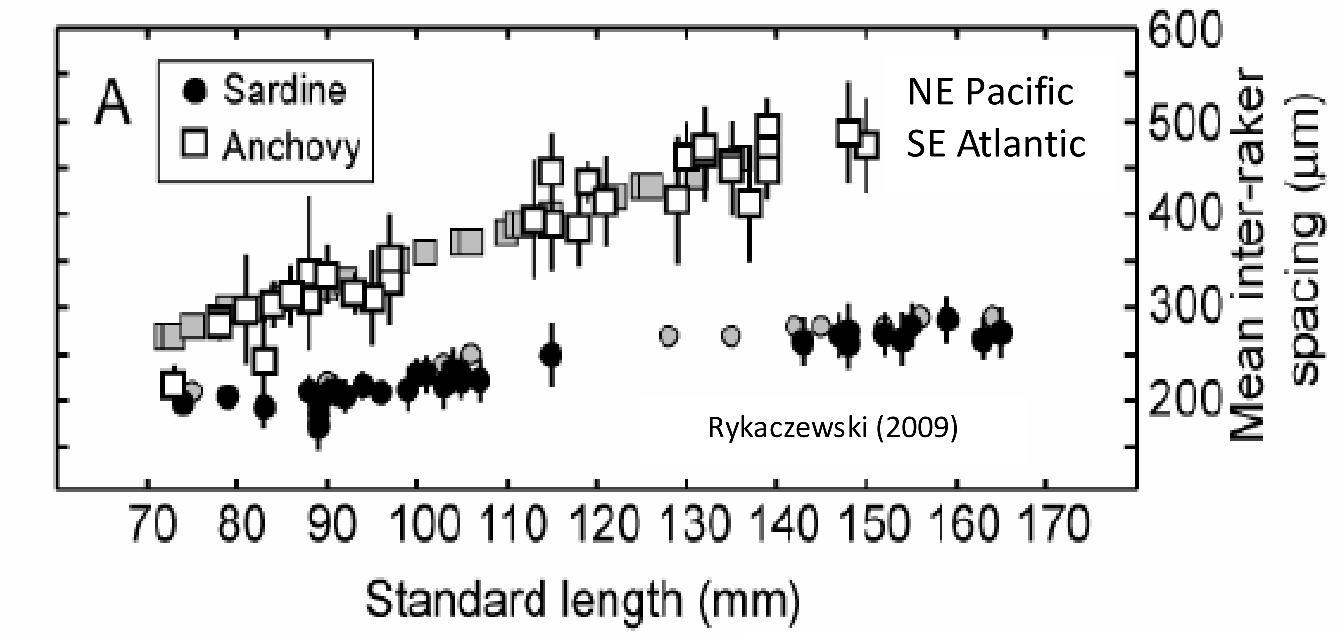


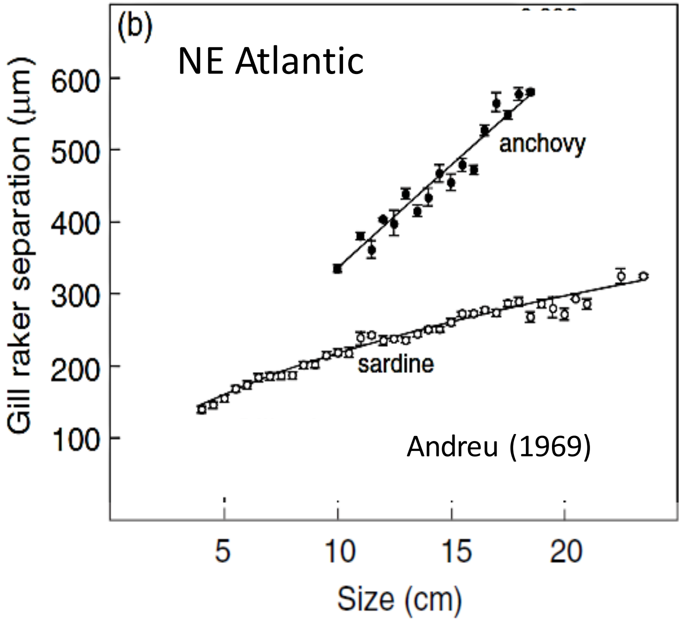
Trophic morphology (ii)

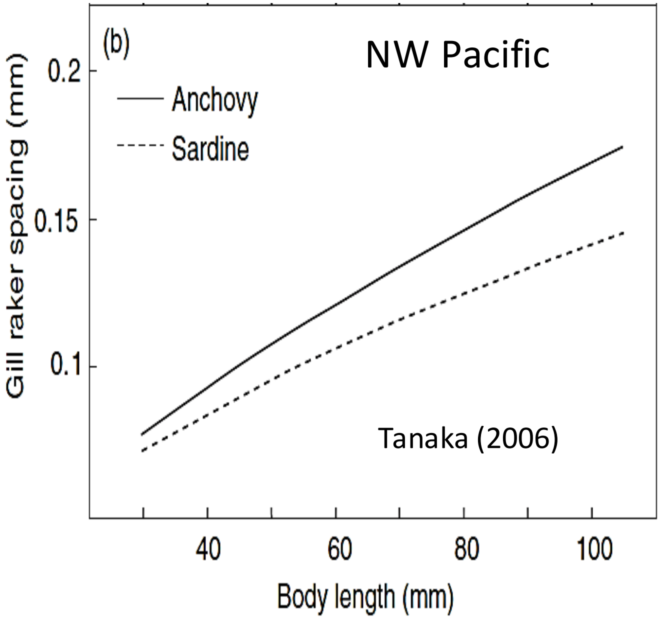
Differences in anchovy (larger) and sardine (smaller) gill raker gap appear consistent across ecosystems: NE Pacific (Calif CS), SE Atlantic (Beng CS) NE Atlantic (Spain) and NW Pacific (Japan)

Also differences in denticle structure









Stomach content analyses (i)

Ingested prey identified, enumerated and measured using a microscope

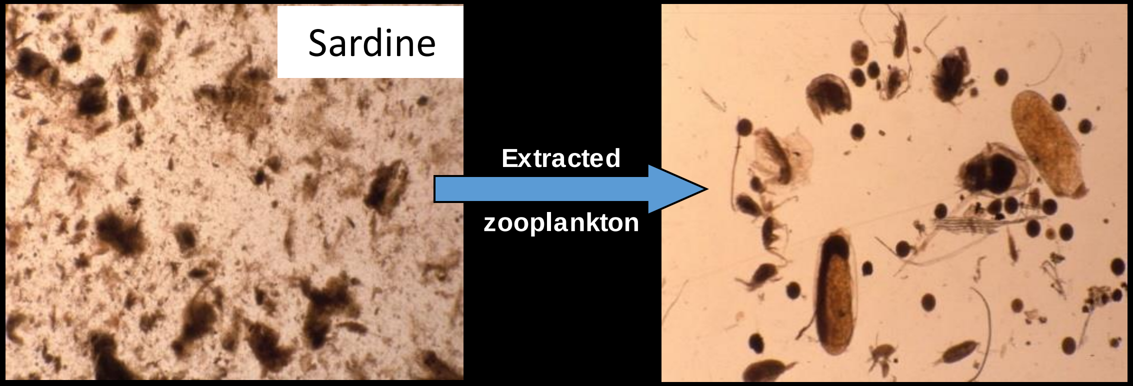
Dietary importance of prey characterized using:

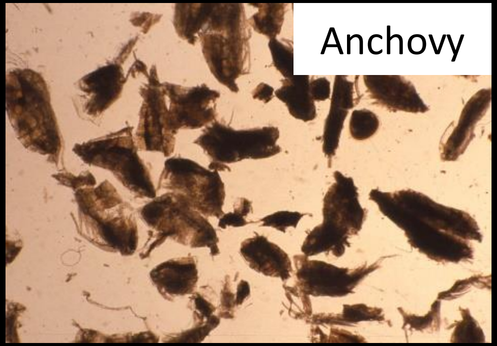
(i) % Frequency of Occurrence (how common in diet)

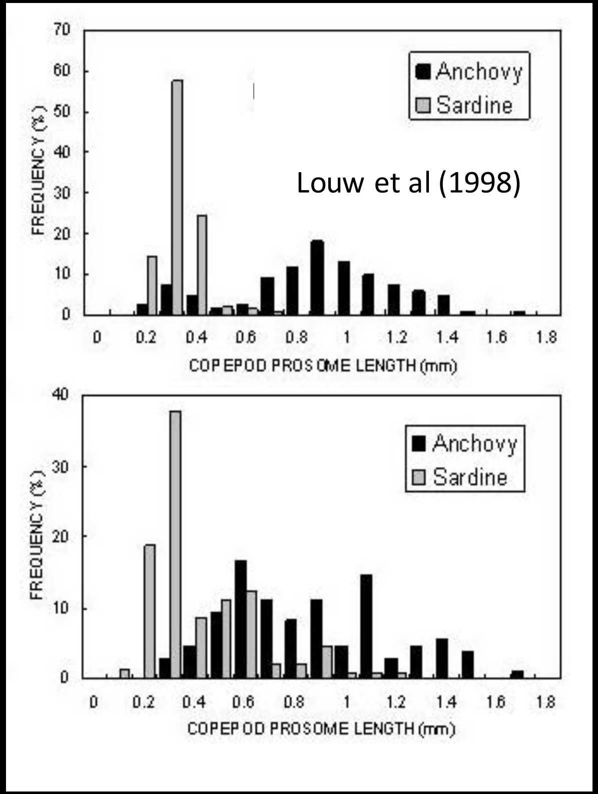
(ii) % Number (how abundant in diet)

(iii) % Mass/Volume/Carbon content - est. from prey type and size (how important in diet)

(iv) % Index of Relative Importance - combines the above three indices







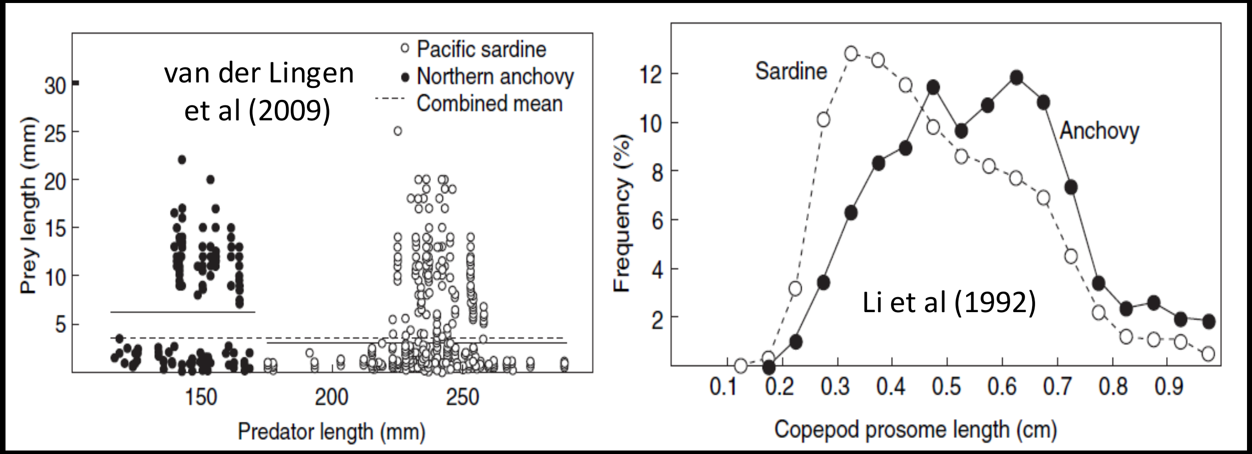
S Benguela sardine consumes phyto- and zooplankton, with smaller zooplankton (calanoid and cyclopoid copepods) major dietary component

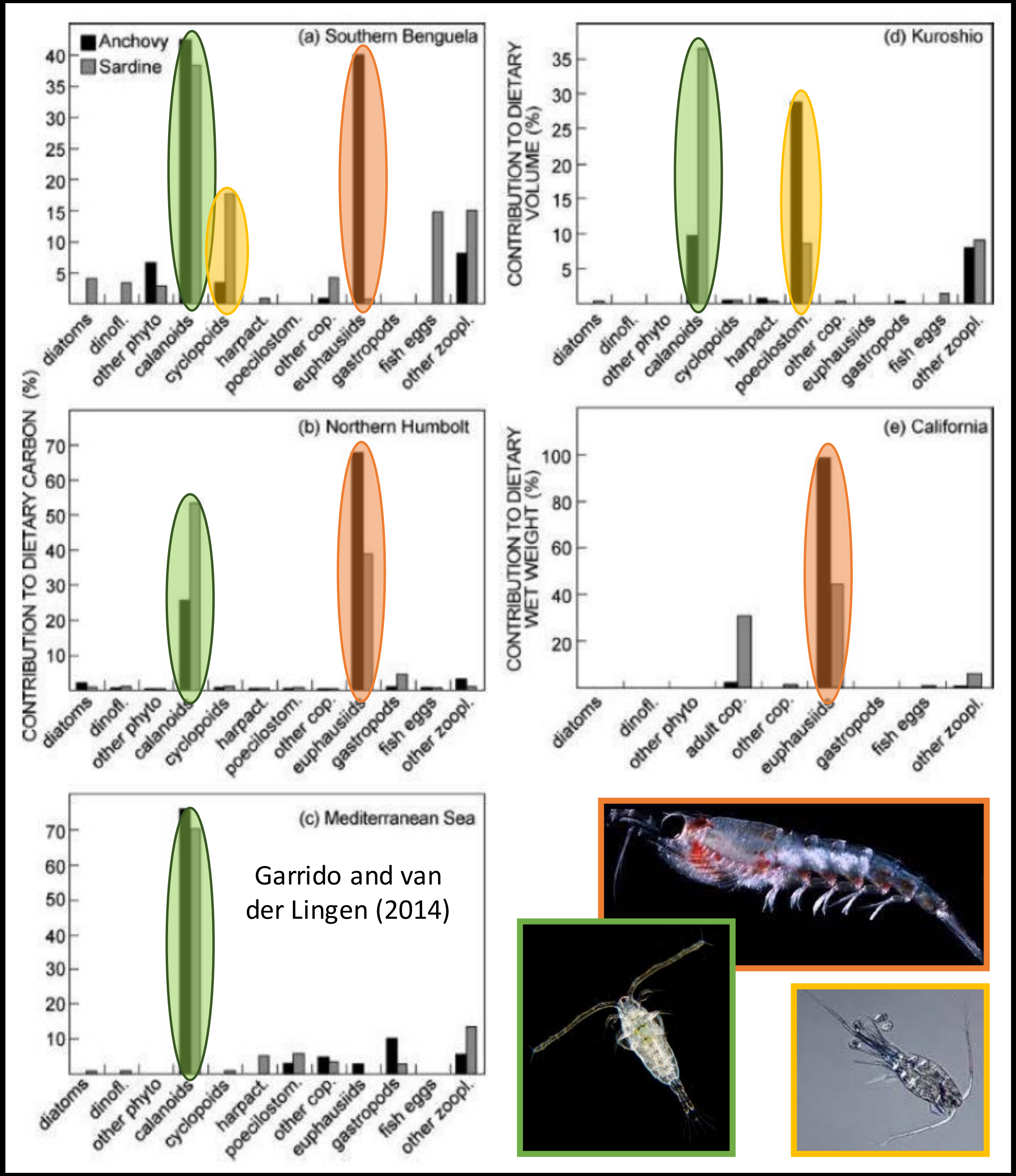
S Benguela anchovy consumes (some) phyto- and zooplankton, with larger zooplankton (calanoid copepods and euphausiids) major dietary component

Stomach content analyses (ii)

Dietary carbon content dominated by zooplankton in co-occurring anchovy and sardine in most systems (*Benguela, California, Humboldt, Kuroshio and Mediterranean; right*) with euphausiids, and calanoid and cyclopoid/poecilostomatoid copepods most important (*right*)

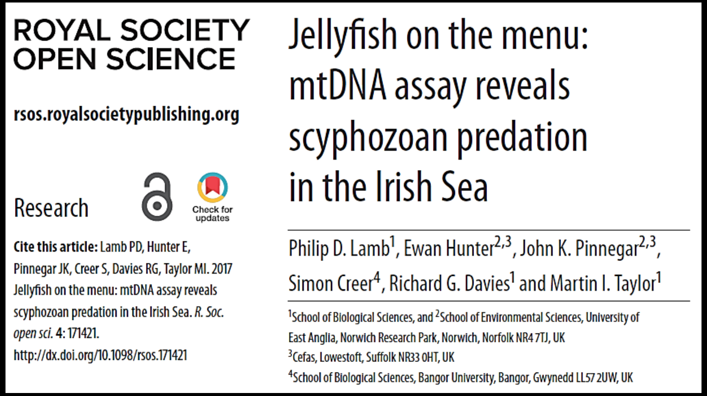
Differences in prey size between anchovy and sardine in many (*Benguela, California, Kuroshio; below*) but not all systems (*e.g. Mediterranean*)





Stomach content analyses (iii)

Molecular gut content assessment of 50 potential jellyfish predators using cnidarian-specific mtDNA primers and sequencing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Cite this article: Lamb PD, Hunter E, Pinnegar JK, Creer S, Davies RG, Taylor MI. 2017 Jellyfish on the menu: mtDNA assay reveals scyphozoan predation in the Irish Sea. *R. Soc. open sci.* 4: 171421. http://dx.doi.org/10.1098/rsos.171421

Jellyfish on the menu: mtDNA assay reveals scyphozoan predation in the Irish Sea

Philip D. Lamb[1], Ewan Hunter[2,3], John K. Pinnegar[2,3], Simon Creer[4], Richard G. Davies[1] and Martin I. Taylor[1]

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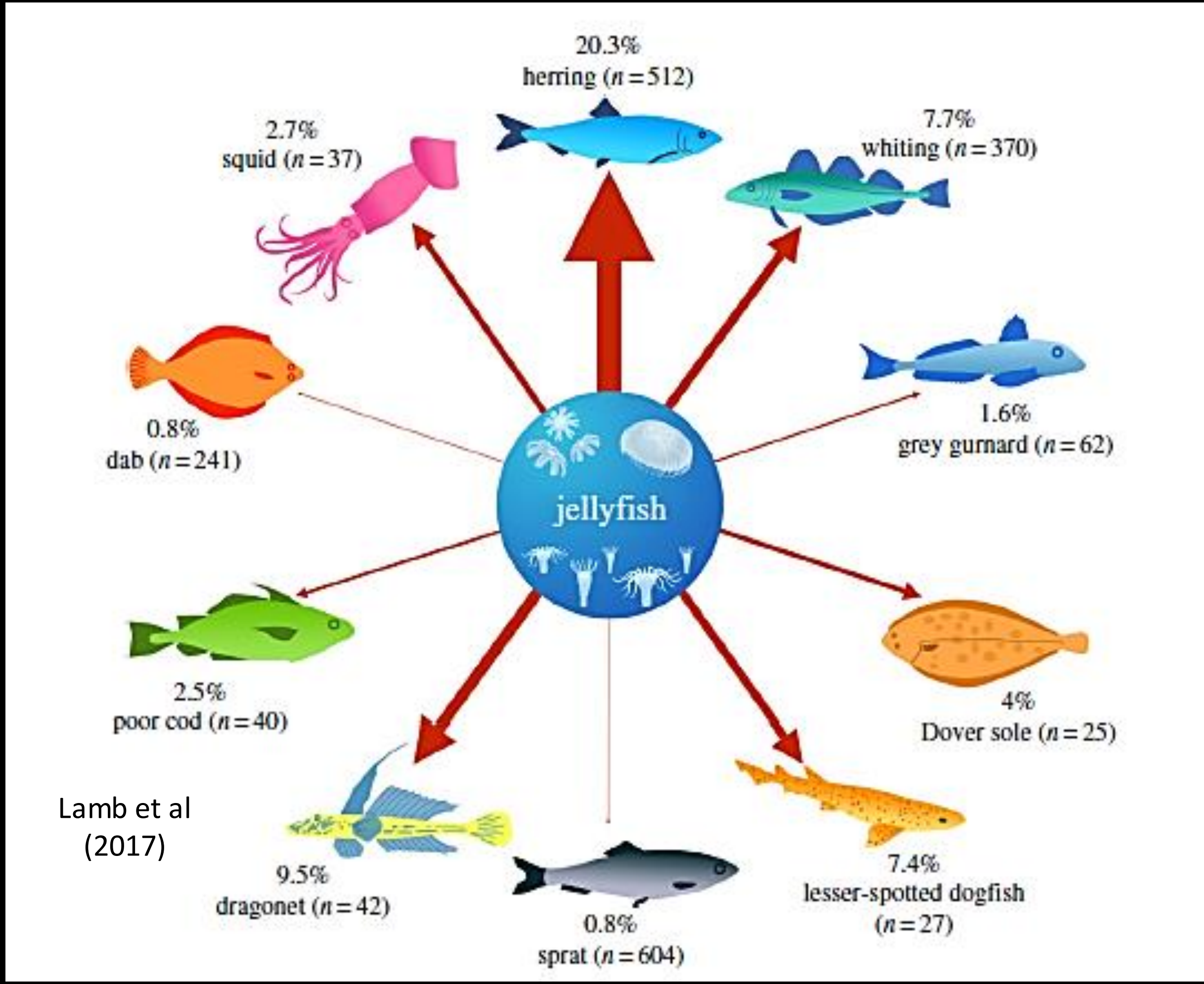


Lamb et al (2017)

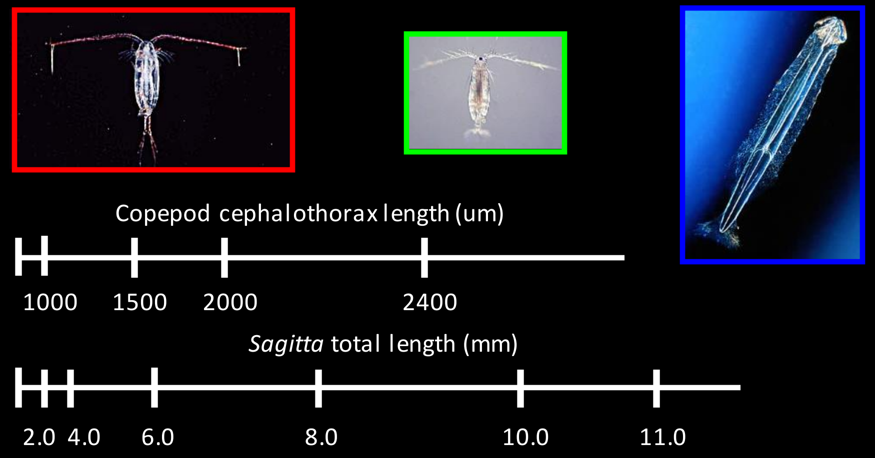
Jellyfish consumed by several predators, with *Aurelia aurita* DNA detected in 20% of herring

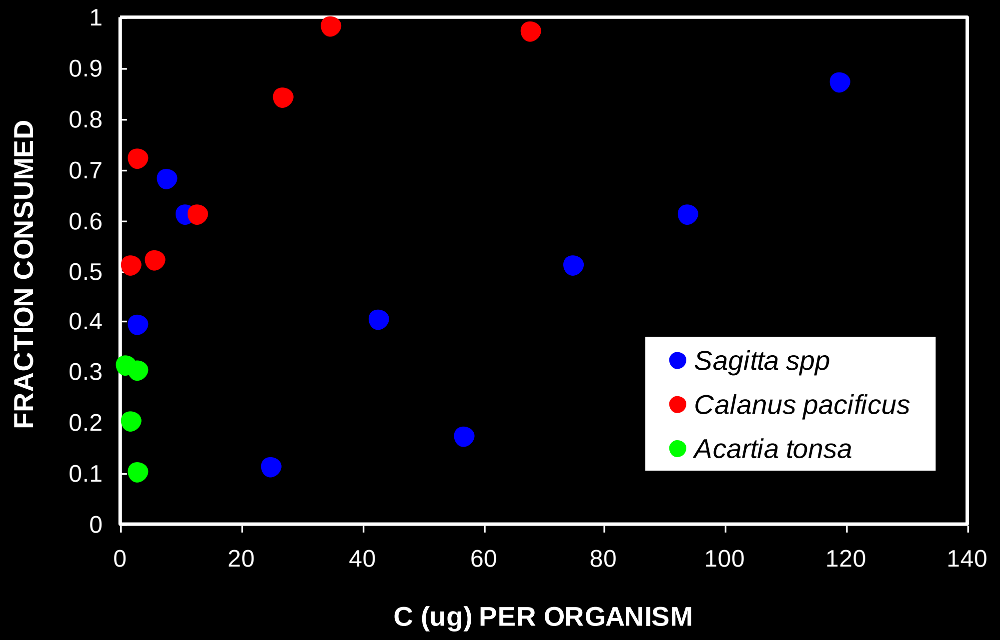
Jellyfish predation may be more common than previously acknowledged; molecular methods particularly advantageous for detection of rapidly-digested prey (*e.g.* gelatinous prey) missed or underestimated by SCA

Feeding behaviour (i)

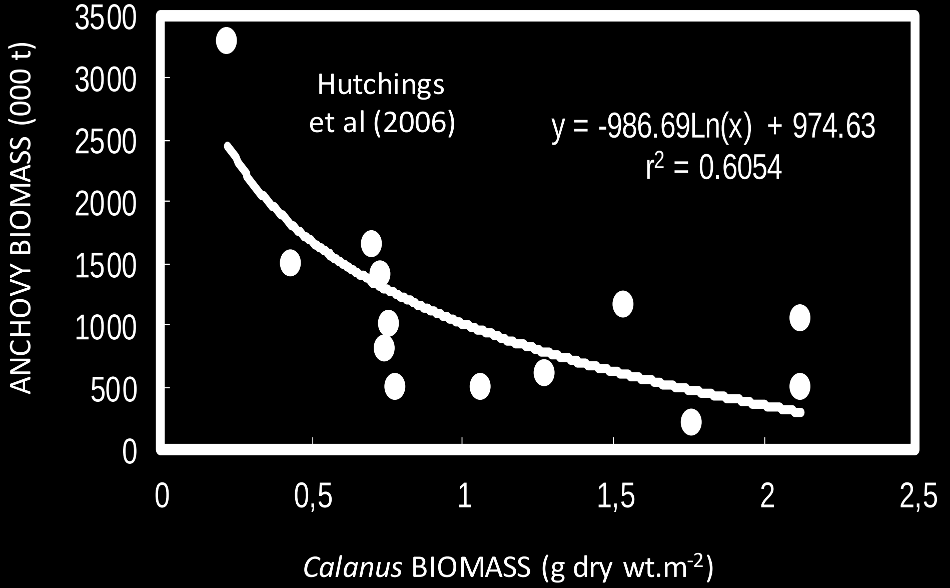
Size-selectivity of Northern anchovy demonstrated by comparing zooplankton samples taken in front of and behind a feeding school; > 90% of largest zooplankton removed (*right*)

Koslow (1981)



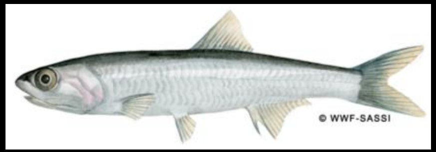


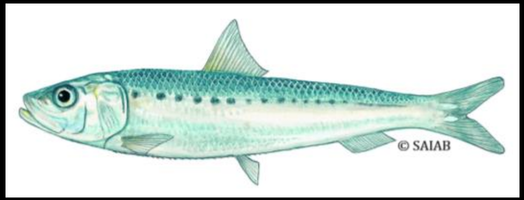
Inverse relationship between European (Cape) anchovy biomass in the S Benguela and large copepod (*Calanus)* abundance from annual surveys (*below*)



SPFs exert top-down control and impact zooplankton size structure and species composition

Feeding behaviour (ii)

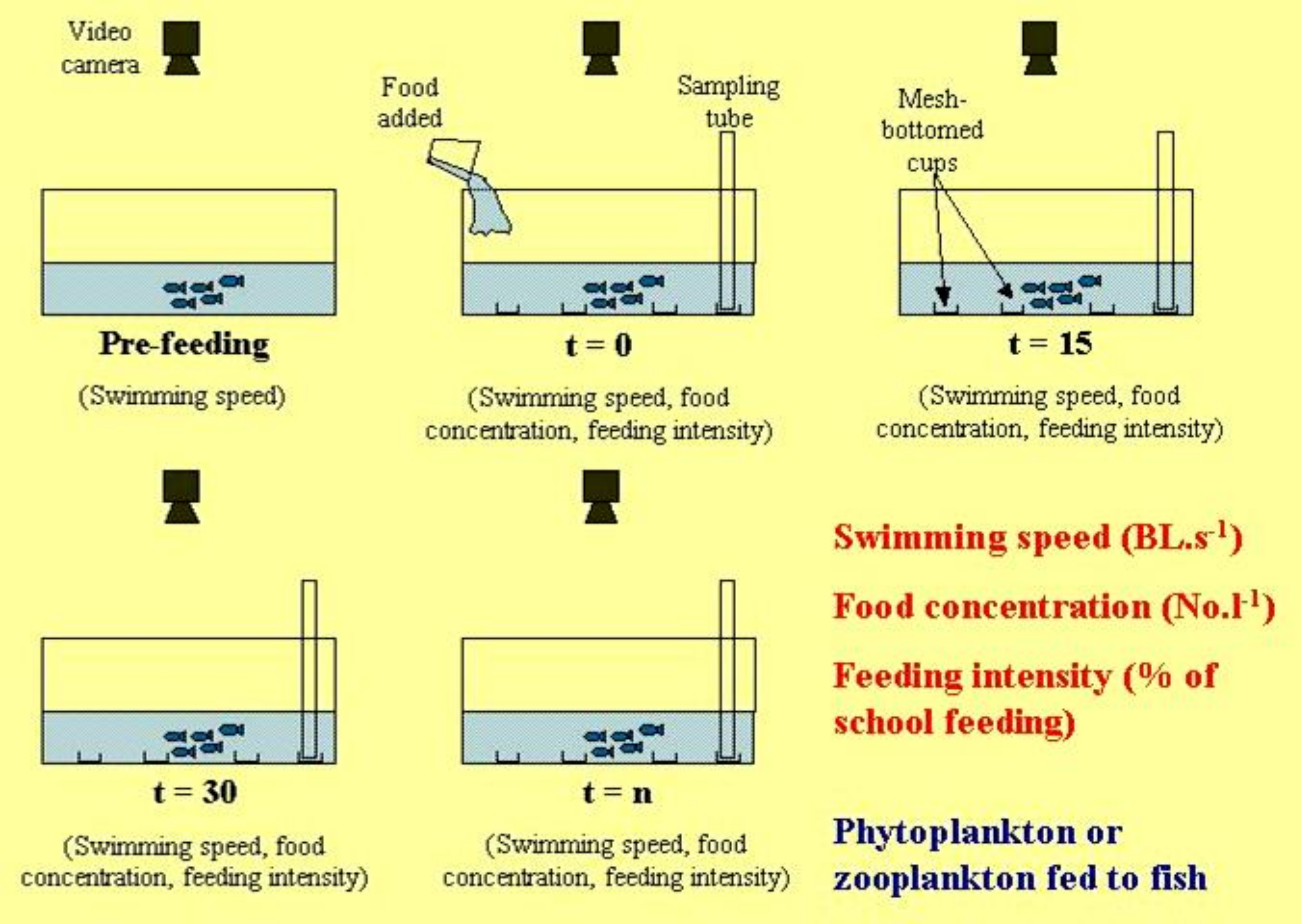




Feeding behaviour (filter- or particulate-feeding), feeding intensity and swimming speed of SPF recorded before, during and after feeding events on different prey types (phytoplankton, small and large zooplankton) added to experimental tanks

Prey concentrations monitored at regular intervals to estimate ingestion (clearance) rates

Respiration rates during different feeding modes also determined

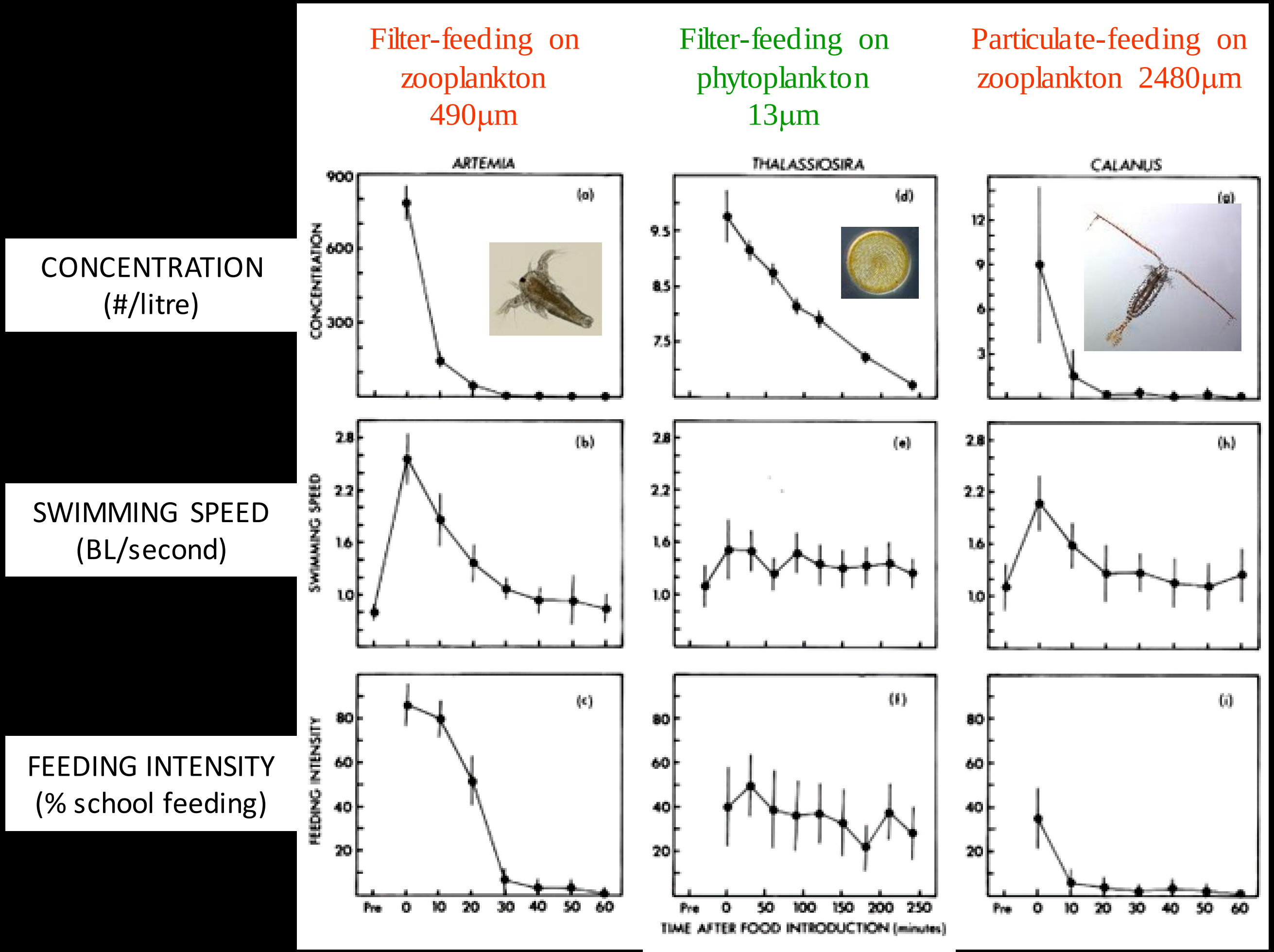


Feeding behaviour (iii)

Choice of feeding behaviour depends on prey size and concentration; SPFs generally F-feed on small (phytop. and small zoop.) and P-feed on large (zoop.) prey

Rapid reduction in zoop. concentrations; swimming speed increases when feeding on zoop. (either mode) but not when F-feeding on phytop.; feeding intensity decreases rapidly as zoop. consumed but remains steady for phytop.

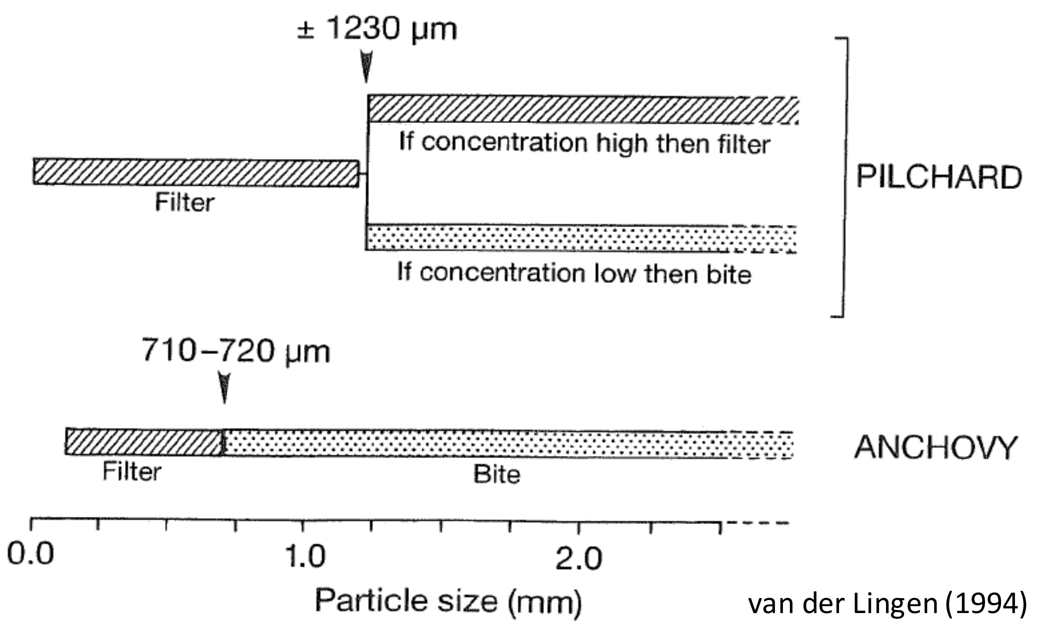
Sardines F-feed more than anchovies do, and both show size-selectivity when P-feeding



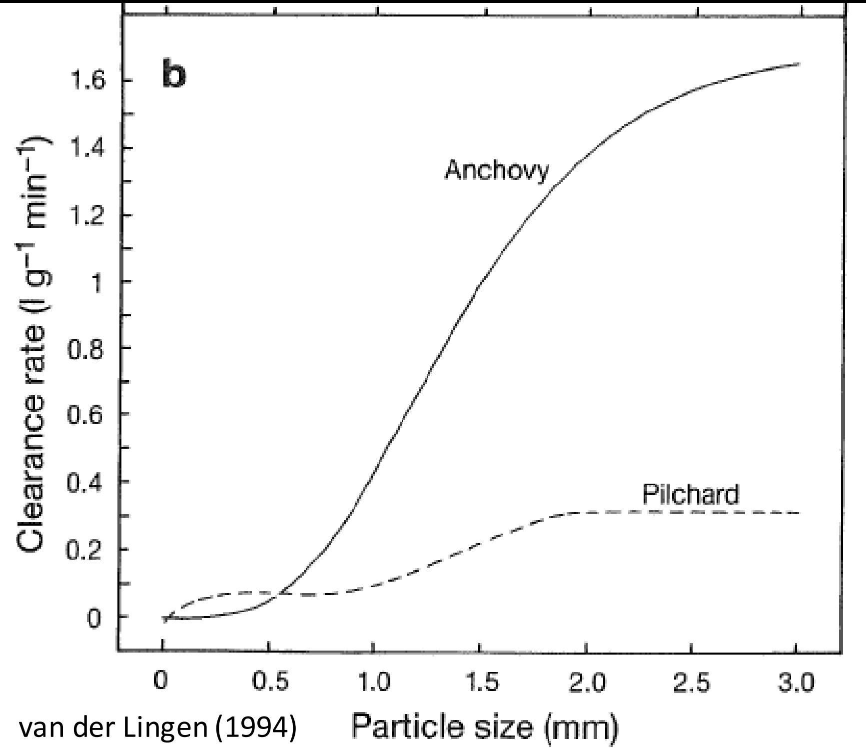
van der Lingen (1994)

Feeding behaviour (iv)

Sardine (= pilchard) filter-feed on particles <1 230µm, and filter-feed on larger prey if present at high concentrations but particulate-feed (on individual prey) if present at low concentrations; anchovy switch from F- to P-feeding at ca. 700 µm (*right*).



van der Lingen (1994)



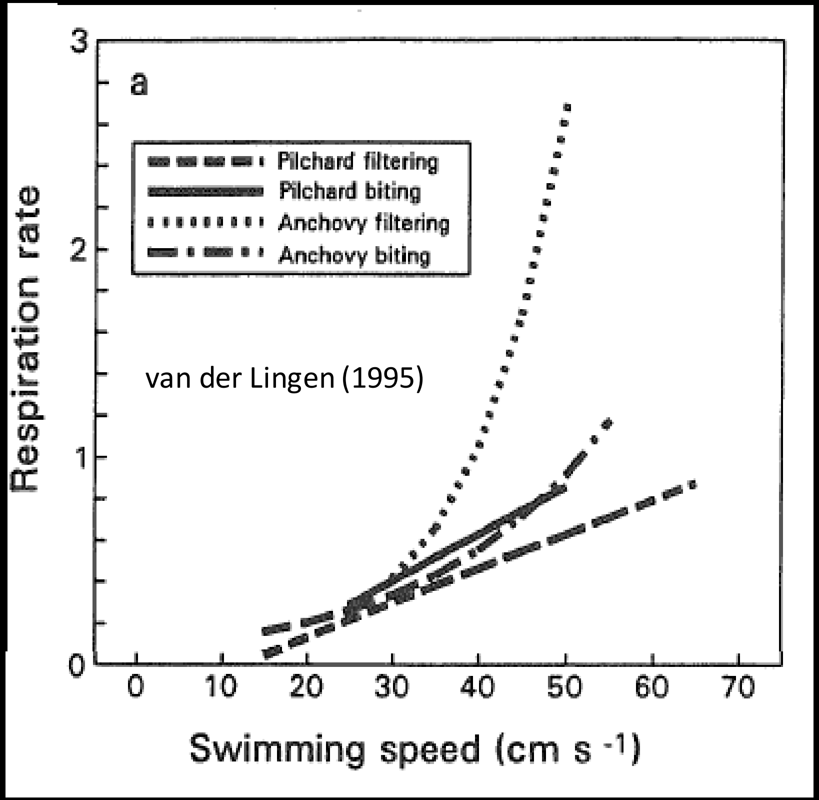
van der Lingen (1994)

Sardine can retain particles down to 20 µm and anchovy down to 200 µm

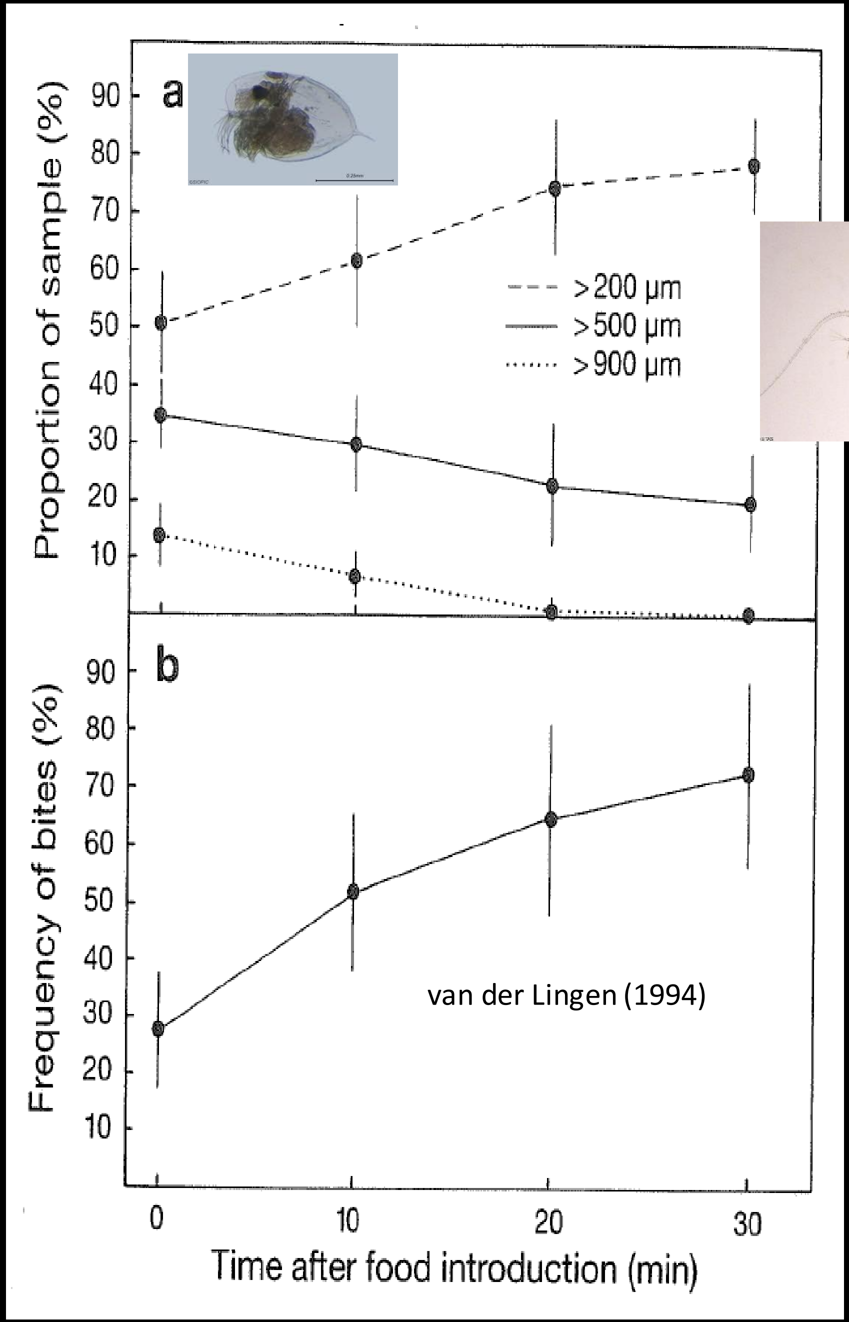
Clearance rate is a function of prey size for both sardine and anchovy, with larger particles removed more rapidly than smaller ones (*left*); on a weight-standardized basis anchovy are more efficient than sardine at removing all prey except those <600 µm.

Feeding behaviour (v)

Sardine display size selectivity when feeding on mixed food assemblages (*right*): prey retained by a 900 µm mesh = adult *Centropages brachiatus* (1500 µm); 500 µm mesh = juvenile *C. brachiatus* (1100µm); 200 µm mesh = *Evadne spinifera* (870 µm)



Filter-feeding energetically cheapest for sardine but energetically most expensive for anchovy (*left*)



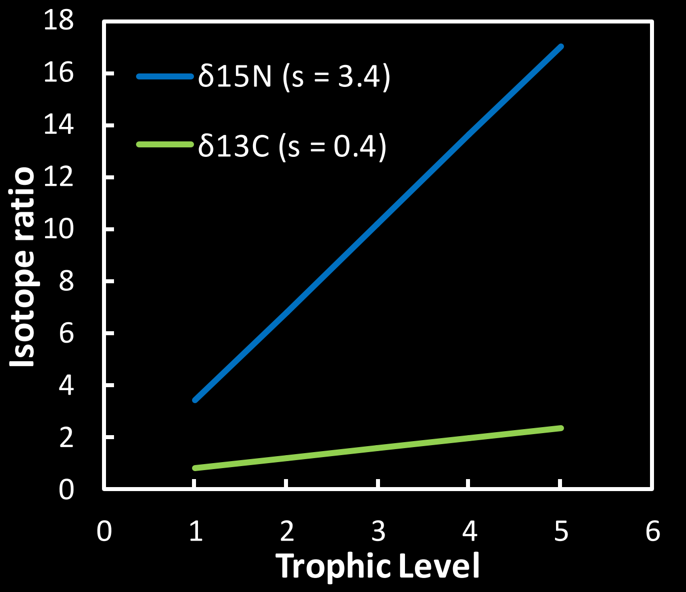
Biochemical tracers [SI] (i)

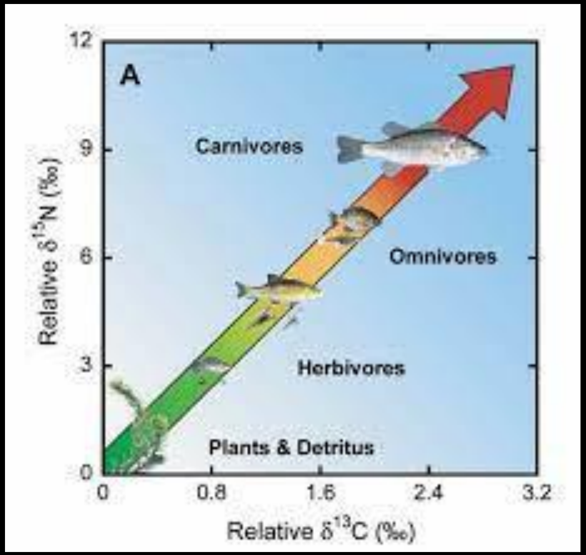
Measurement of the ratios of stable isotopes of nitrogen ($^{15}N/^{14}N$ – denoted as $\delta^{15}N$) and carbon ($^{13}C/^{12}C$ – denoted as $\delta^{13}C$) in organism tissue (typically muscle/fillet in fishes) enables assessment of assimilated diet

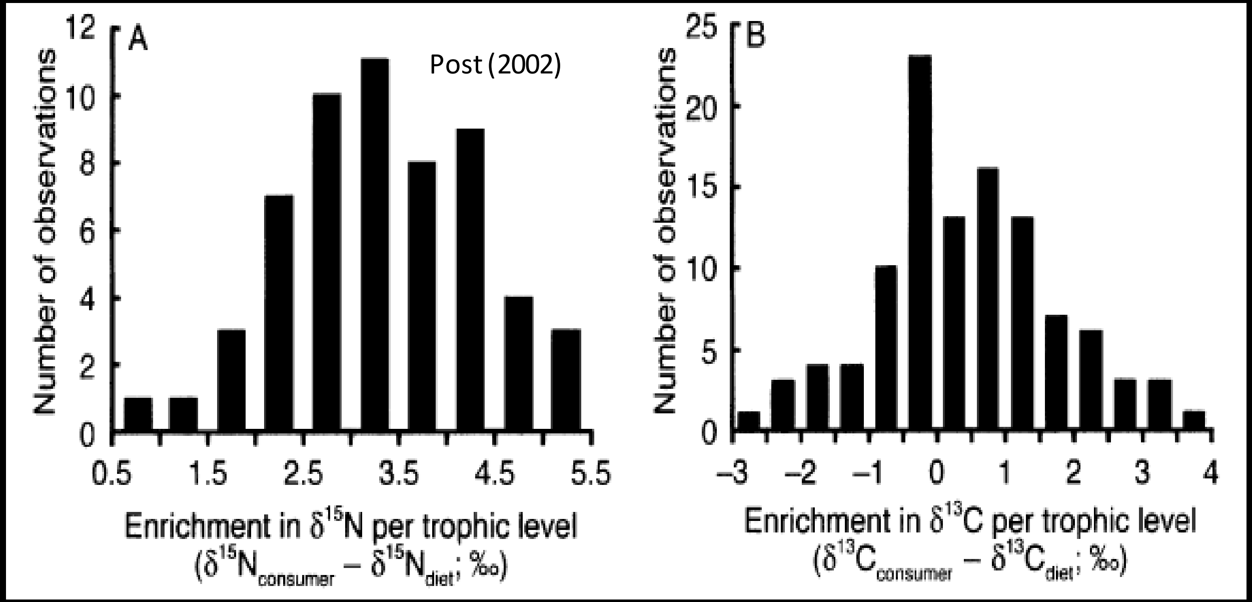
Utility of SIA based on the preferential retention by predators of the heavier isotopes compared to their prey (trophic fractionation) whereby isotope ratios increase with increasing trophic level (*upper*)

$\delta^{15}N$ elucidates relative trophic level (TL) and $\delta^{13}C$ elucidates the source of base production

Mean trophic fractionation values of 3.4‰ per TL for $\delta^{15}N$ and 0.4‰ per TL for $\delta^{13}C$

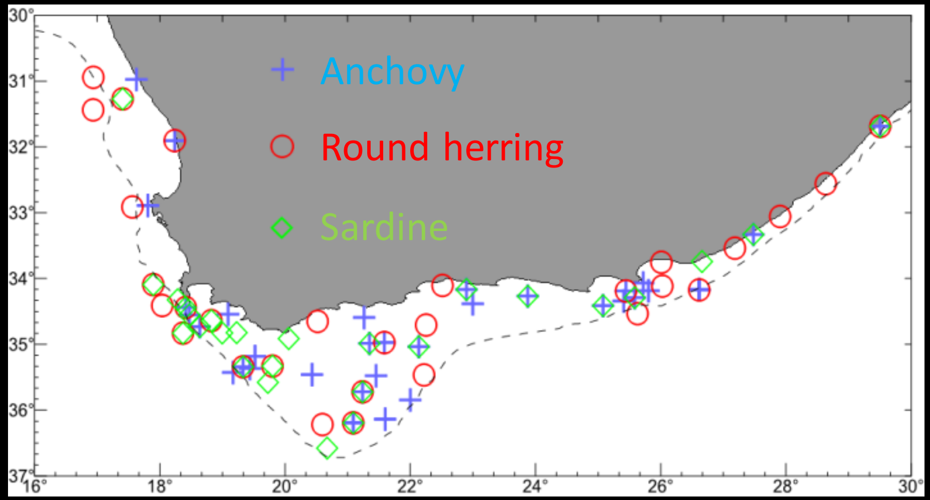




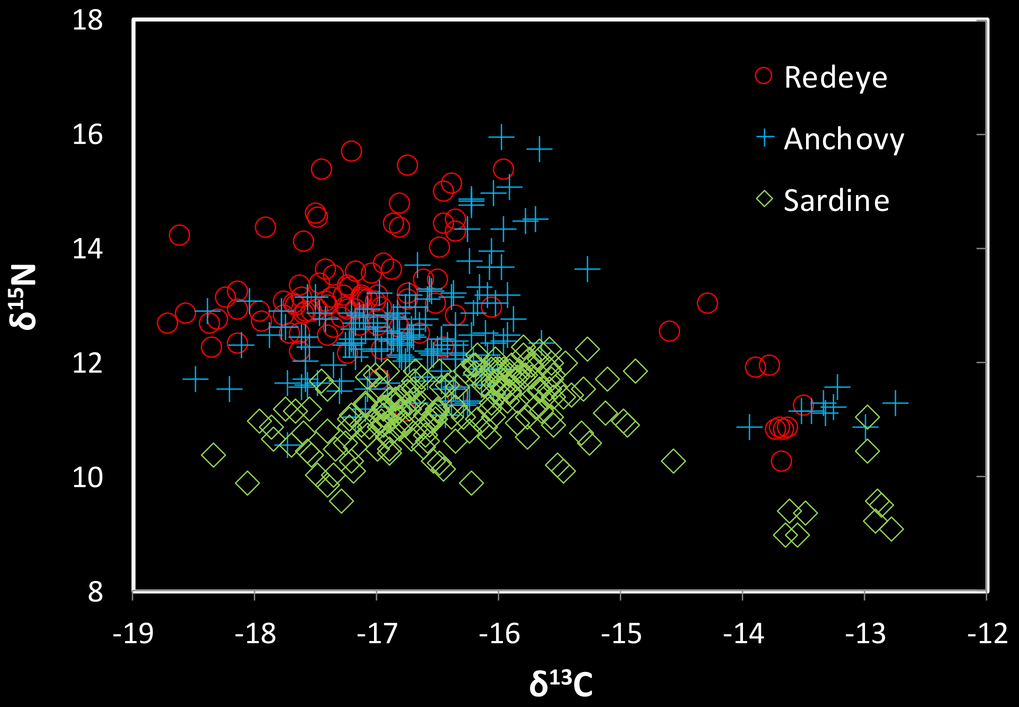


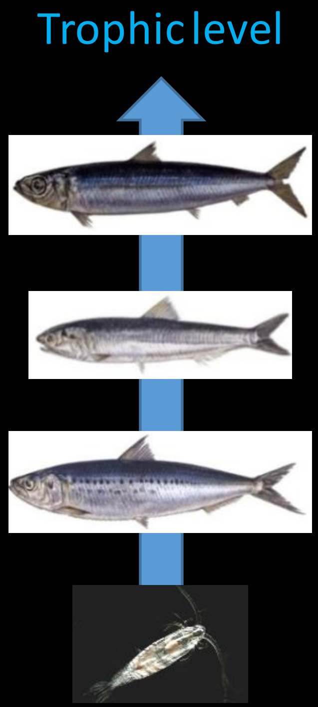
Stable isotope analysis (ii)

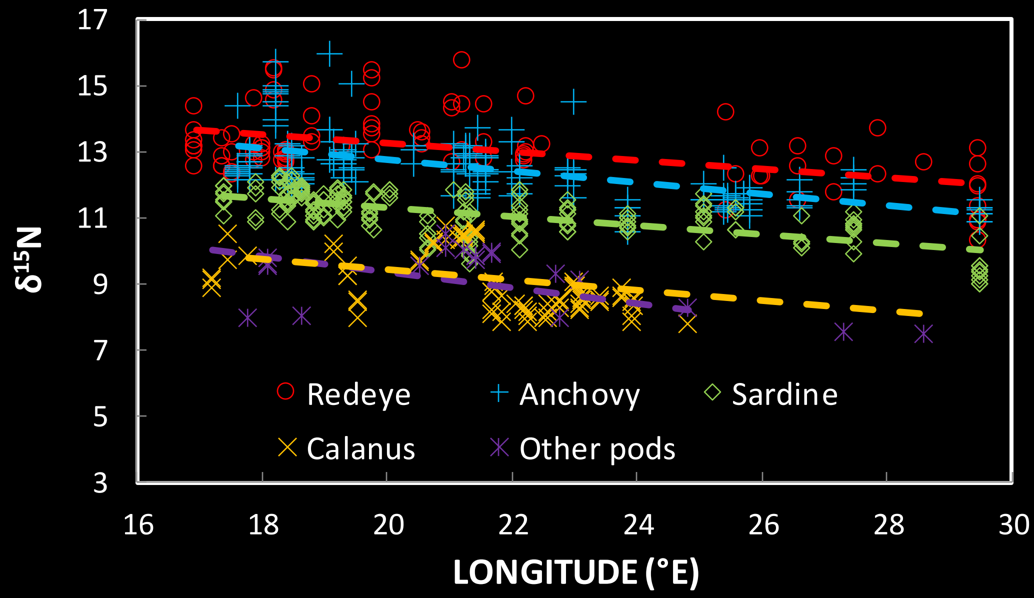
Copepods, anchovy, sardine and redeye round herring collected around the South African coast for determination of $\delta^{13}C$ and $\delta^{15}N$ (*right*)



Interspecific differences in SI signatures (*below*)







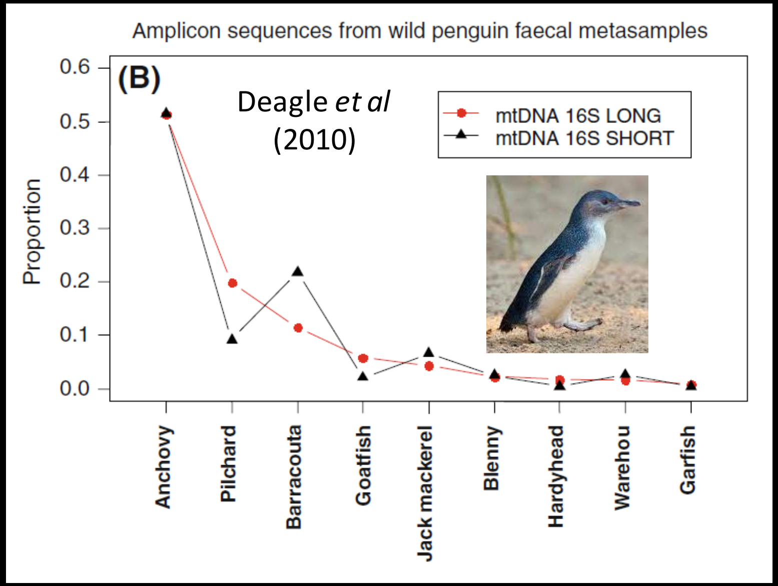
No size effects on ratios of either isotope; significant longitudinal effect on $\delta^{15}N$ for all (*above*)

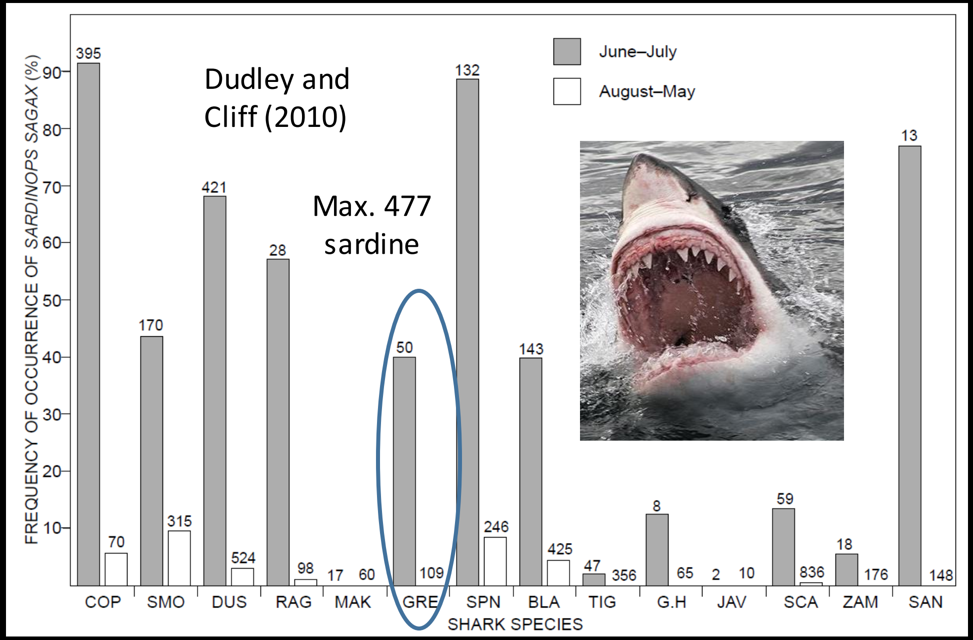
SPFs as prey (i)

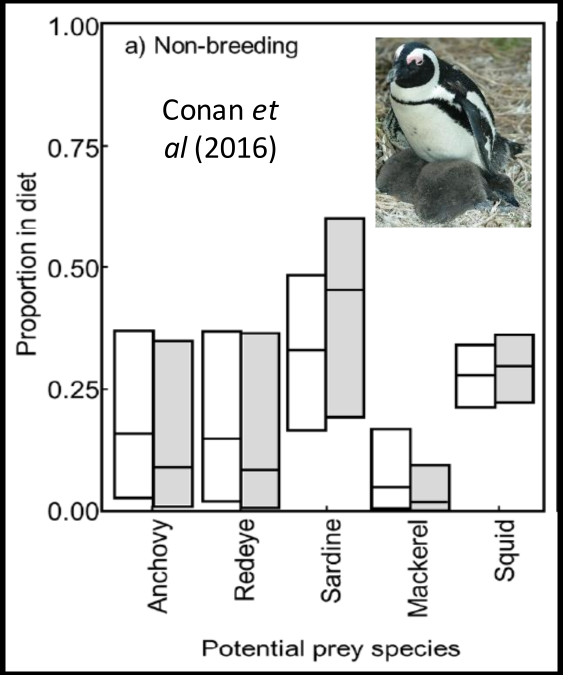


SPFs are the forage of a wide variety of predators including other fishes, marine mammals and seabirds, and many of these predators are highly dependent on SPFs

The occurrence/importance of SPFs in the diets of predators have been examined via stomach content analysis (*shark*), scat analysis (otoliths and DNA *little penguin*), stable isotope mixing models (*African penguin*) and other techniques

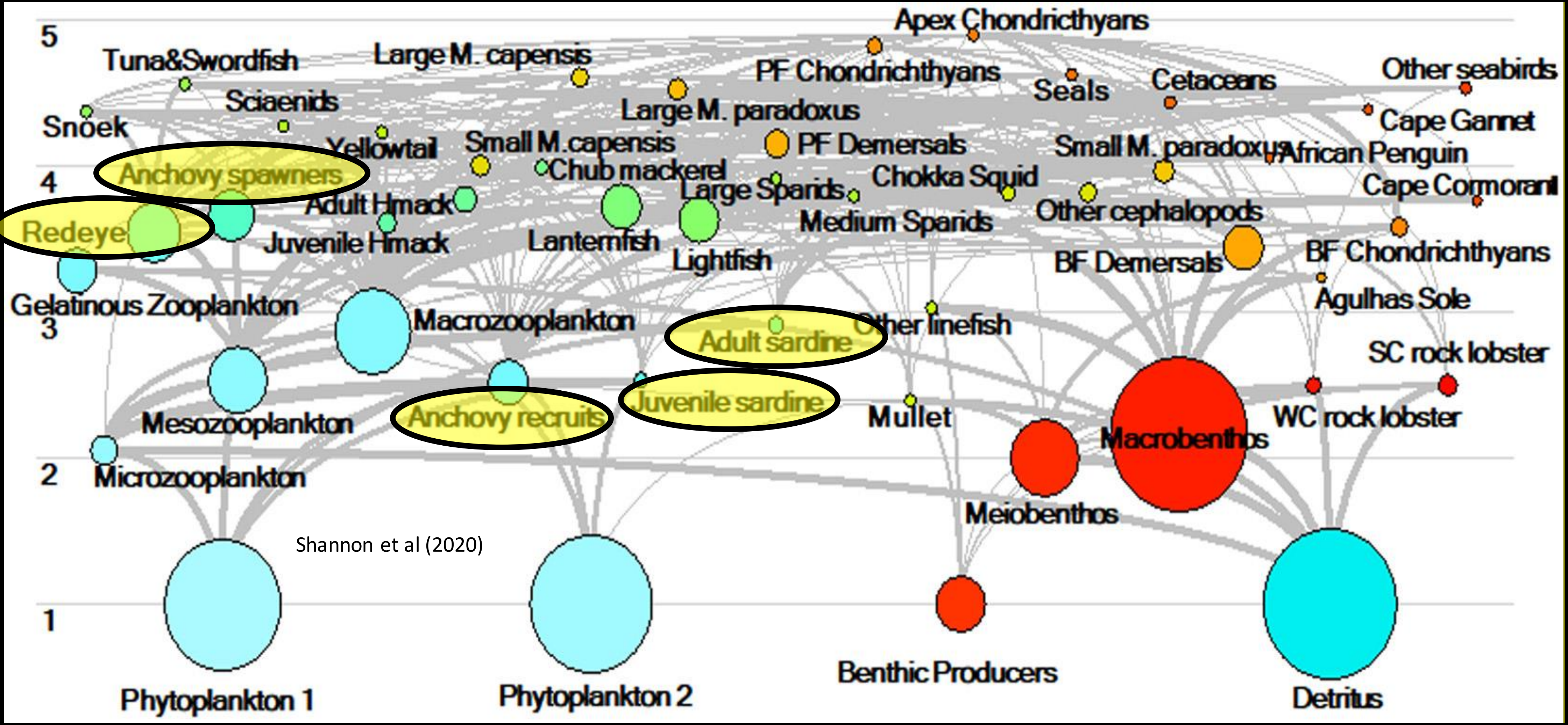






SPFs as prey (ii)

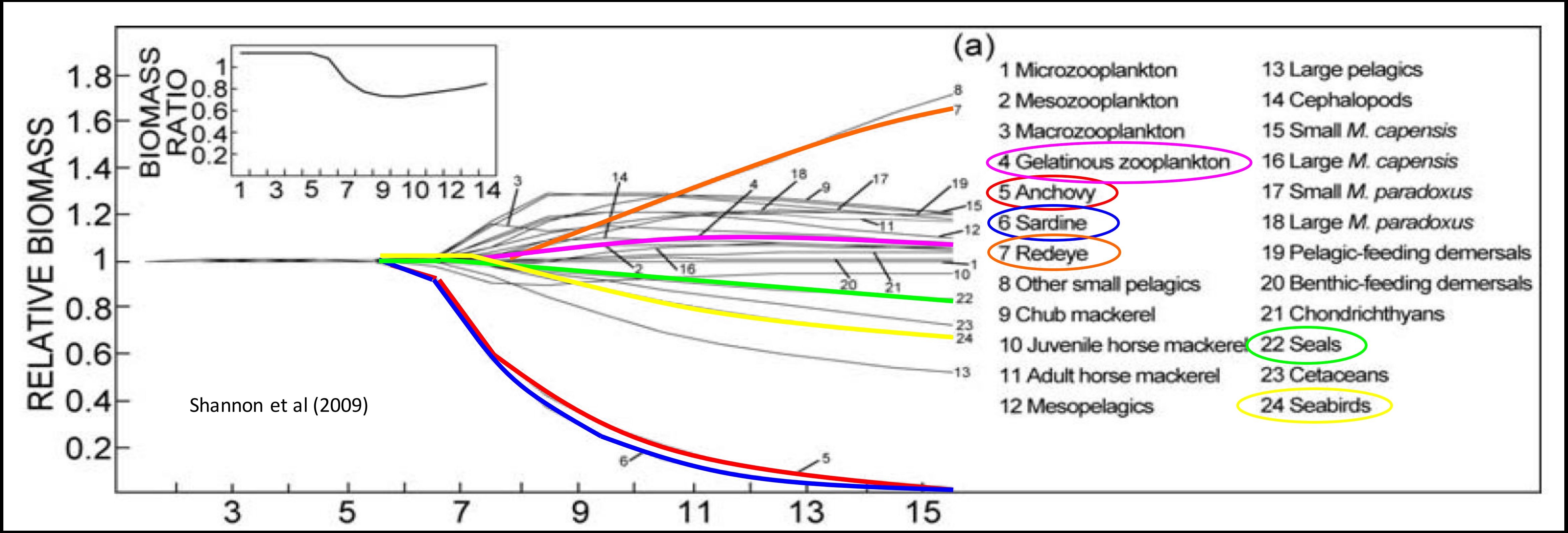
Trophic flows through the S Benguela foodweb (*SPFs identified by yellow elipses*); almost everything (demersal and pelagic fishes, cephalopods, marine mammals and seabirds) eats SPFs!



Shannon et al (2020)

SPFs as prey (iii)

ECOPATH model simulations of the S Benguela run to assess the effect of collapses of anchovy and sardine on the ecosystem. Decrease in predators (particularly avian predators) and the proliferation of other species (*e.g.* competitors) which may not constitute an alternative pathway for the efficient flow of energy to higher trophic levels. Models consistently suggest that gelatinous zooplankton may increase when small pelagic fish stocks decline



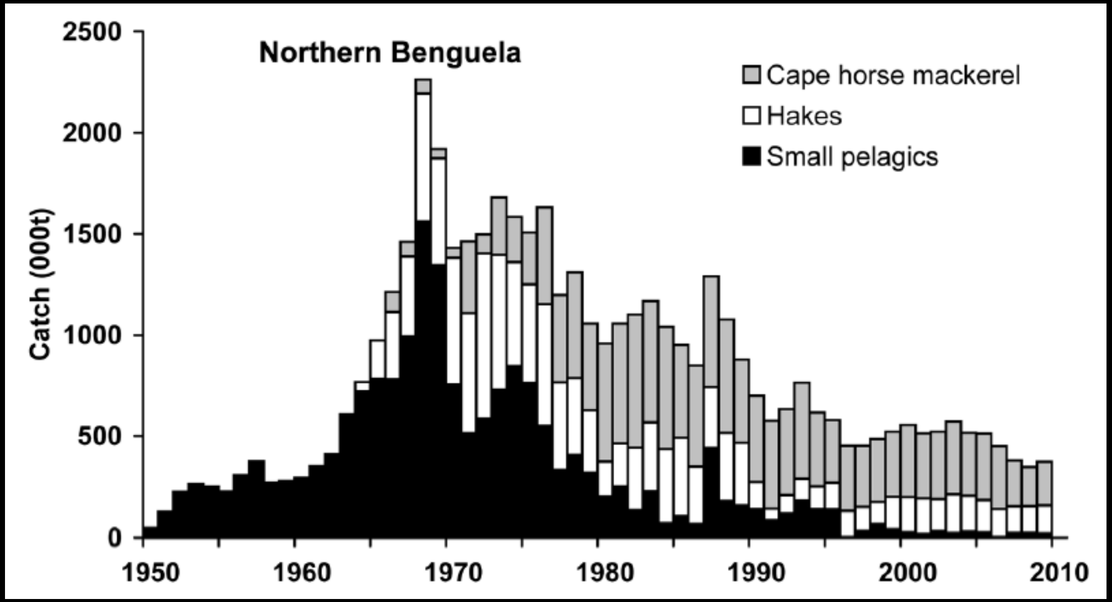
SPFs as prey (iv)

Collapses of SPFs can have serious consequences for their predators

Sardine biomass in the N Benguela was ca. 11 million t (late-1960s) and supported large catches (1.5 million t), but collapsed (*top*) due to overfishing and unfavourable environmental events (warming due to Benguela Niños; low oxygen events)

Some replacement by anchovy following sardine collapse but both species now depleted/absent

Ecosystem shift, with jellyfish and gobies (& horse mackerel) now abundant and increased pelagic-benthic coupling (*bottom*)



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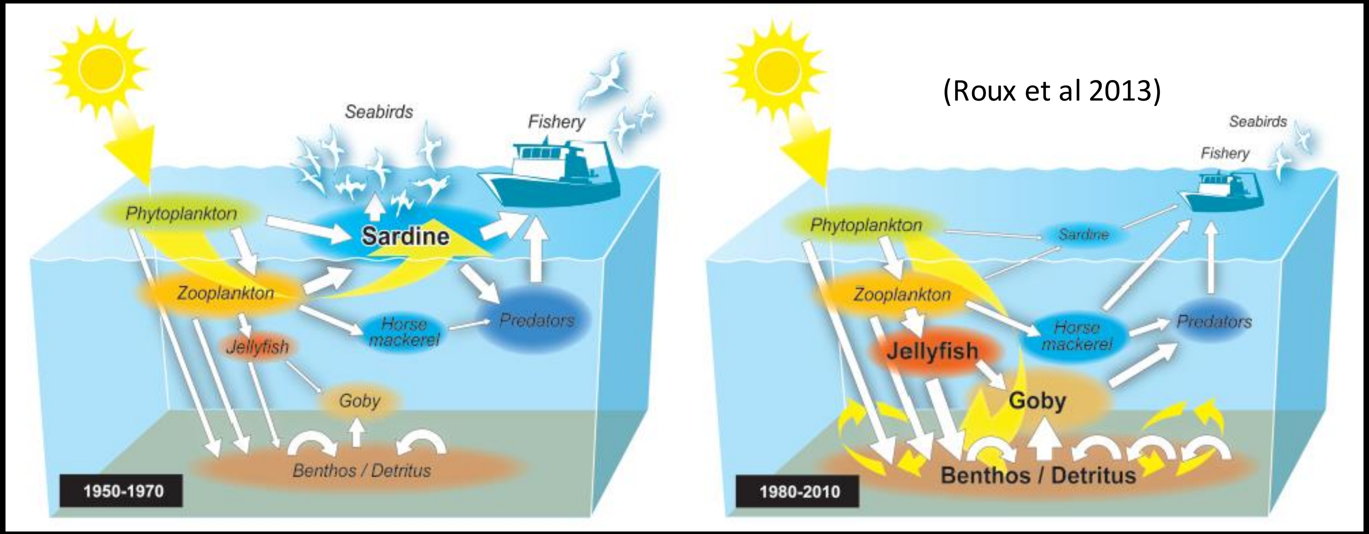
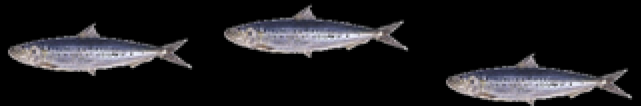


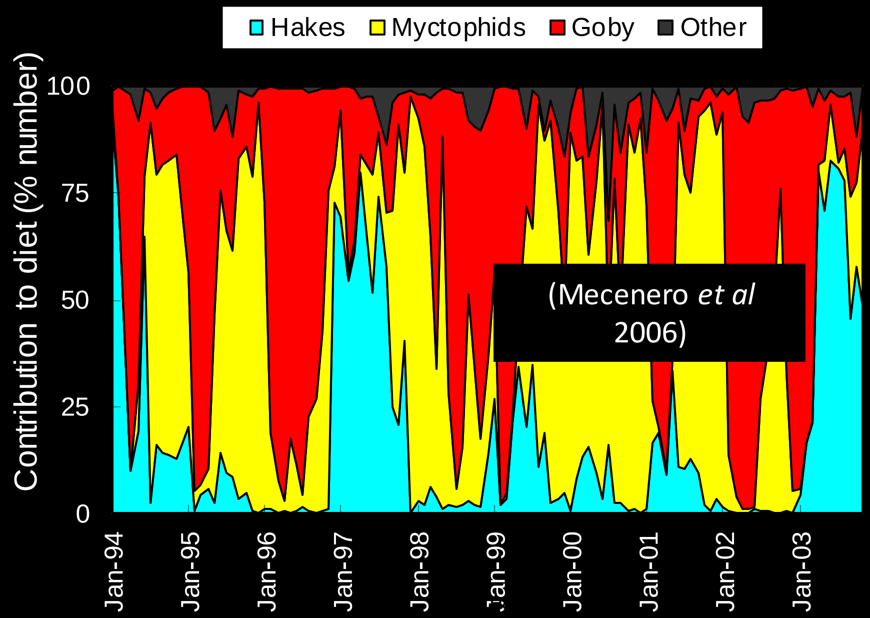
(Roux et al 2013)

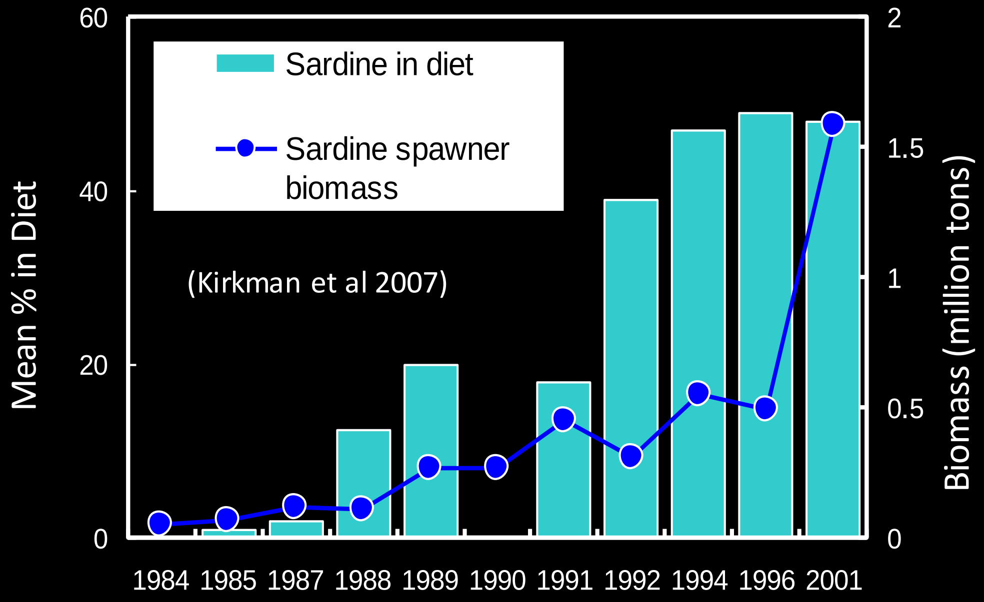
SPFs as prey (v)

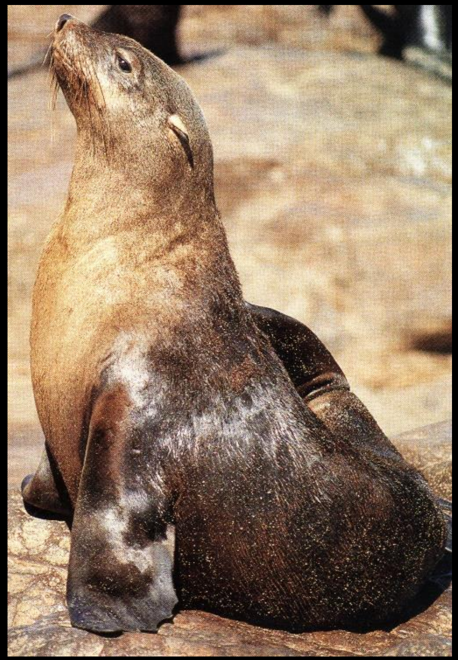


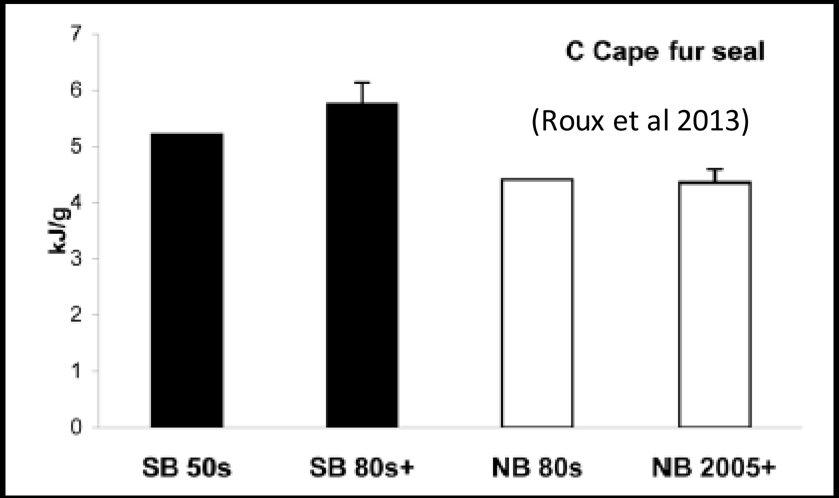
Sardine was a key prey item for many fish, seabird and marine mammal predators in the Benguela and it's occurrence in the diet reflected its abundance (*bottom left*)

Following the collapse in the N Benguela, predators (*seals*) had to switch to alternative prey, esp. pelagic goby (*top right*) resulting in a decreased energy density of their diets (*bottom right*)

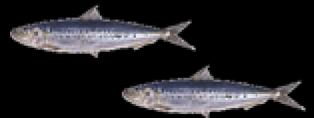




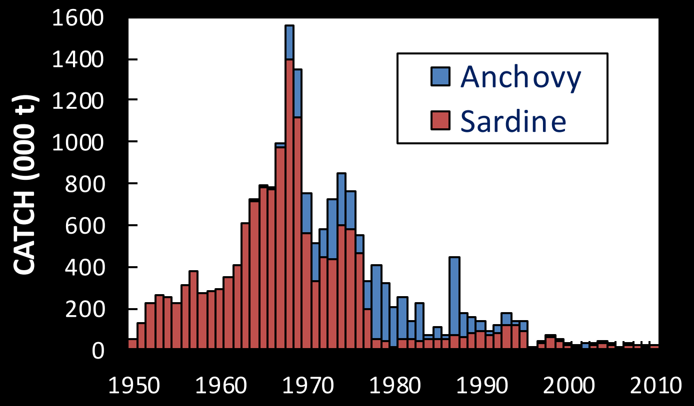


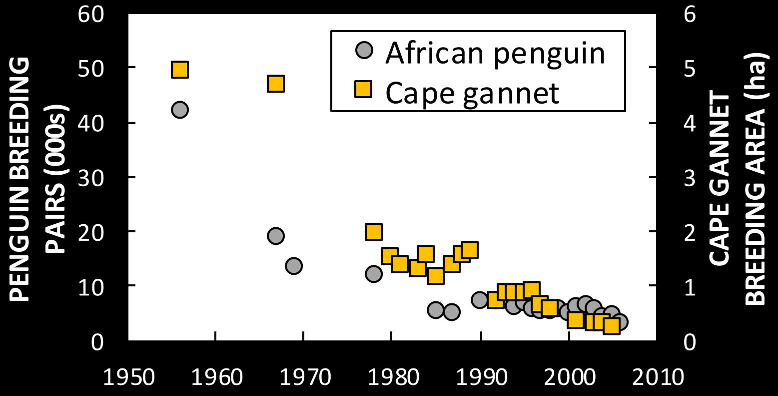


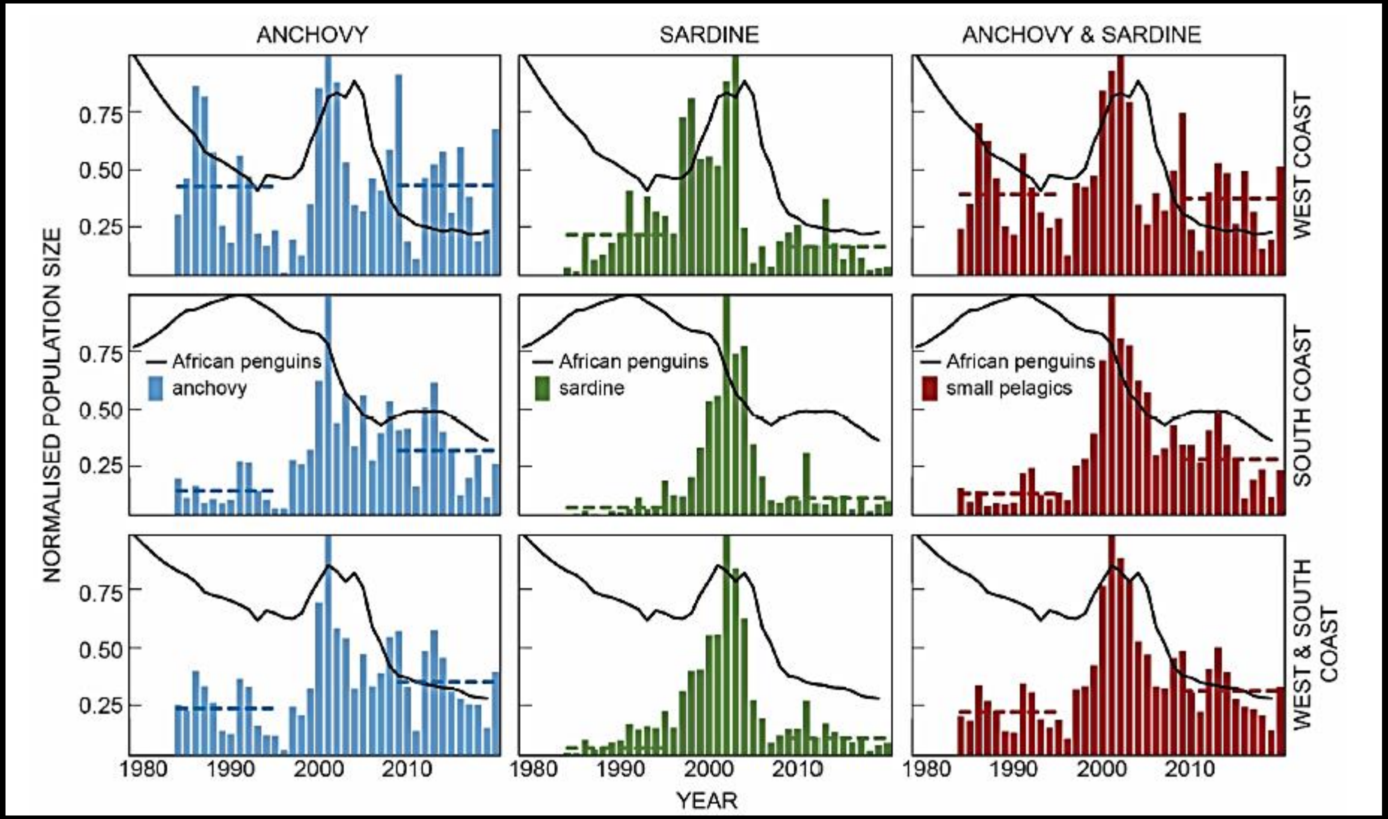
SPFs as prey (vi)



Populations of strongly dependent seabird predators (African penguins, Cape gannets) in the N Benguela that were unable to switch to alternative prey crashed following the removal of SPFs (sardine) from that system (*right*)





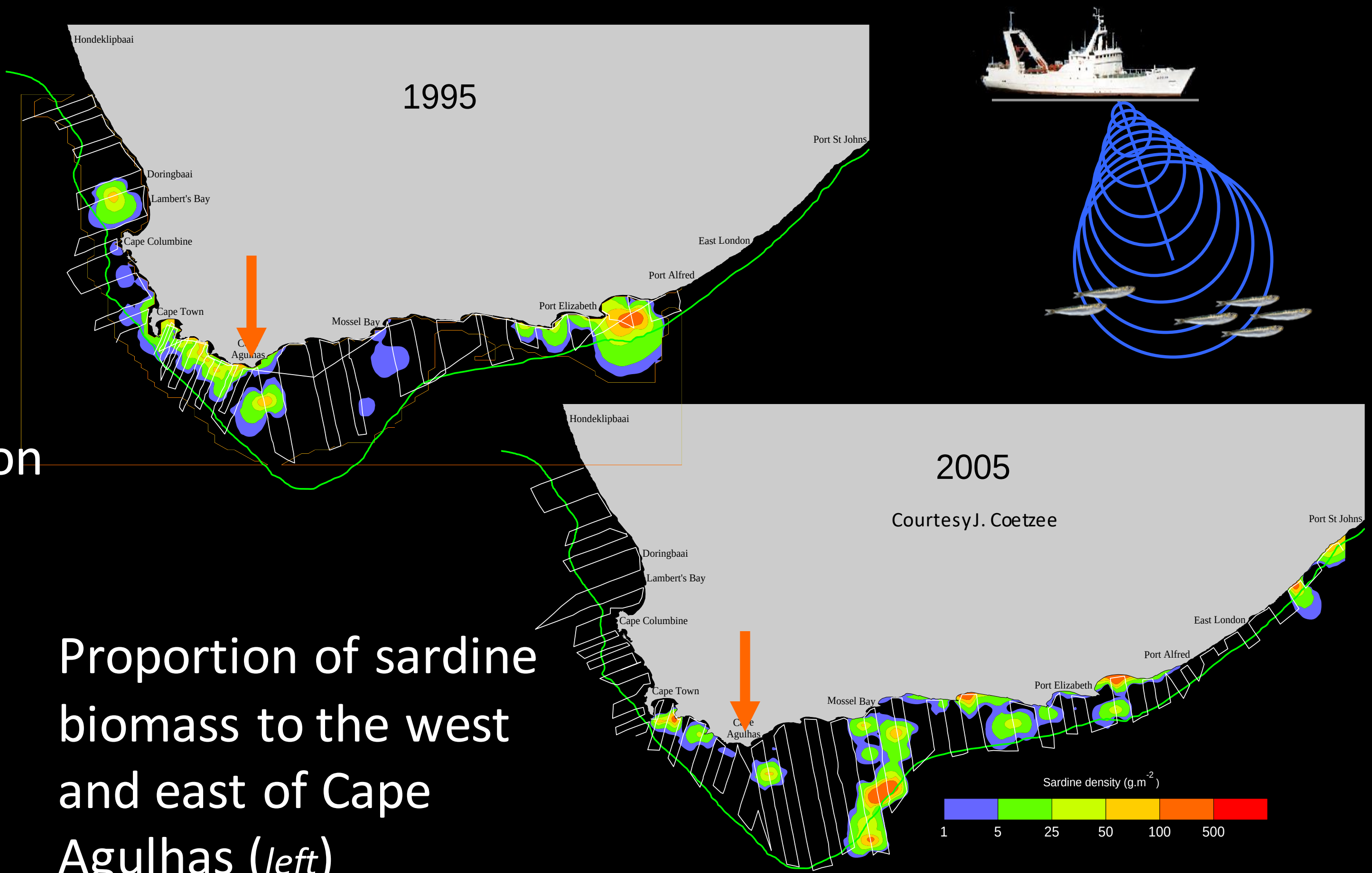


African penguins are also declining in the S Benguela, despite a relatively high biomass of SPFs (*left; normalized population sizes of APs, anchovy and sardine on W, S and W+S coasts*); local food availability or other drivers?

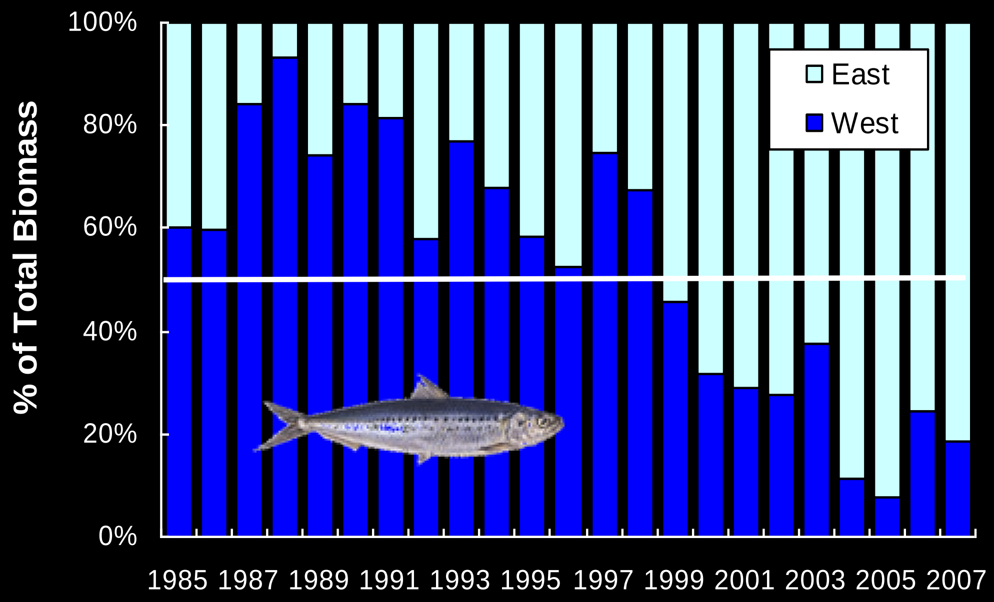
SPFs as prey (vii)

Changed distributions of SPFs can also have serious consequences for their predators

An eastward shift in the relative distribution of sardine in the S Benguela (*acoustic survey maps*)



Proportion of sardine biomass to the west and east of Cape Agulhas (*left*)

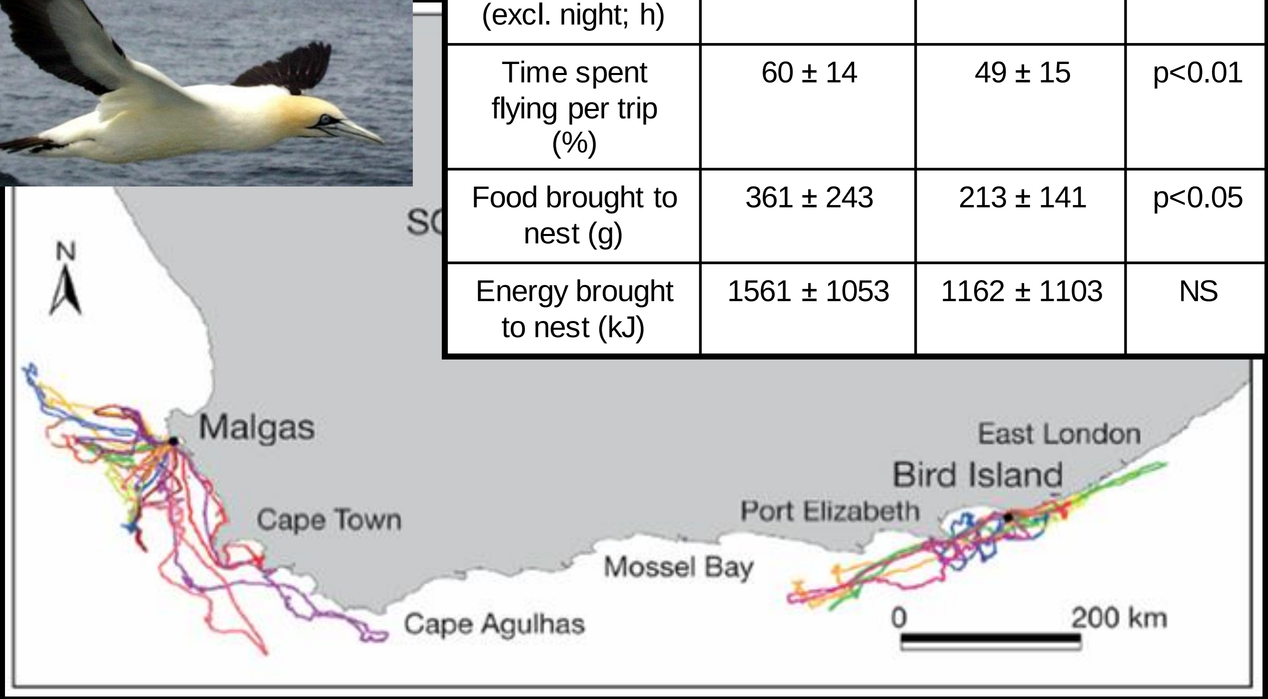


Impacts on a dependent seabird predator, Cape gannet assessed

SPFs as prey (viii)

Foraging behaviour and diet of breeding gannets from west (Malgas) and south (Bird Island) coast colonies examined

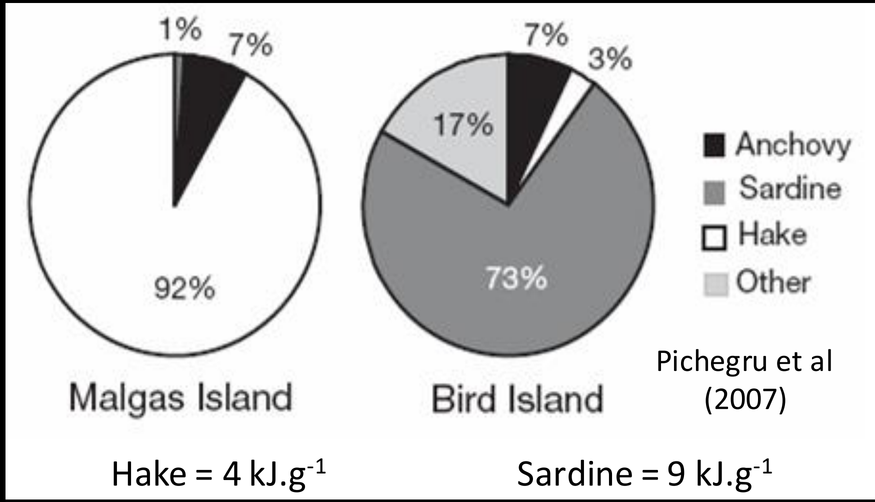
Foraging characteristic	Malgas Island	Bird Island	Sig.
Trip duration (excl. night; h)	17.4 ± 7.2	13.8 ± 17.2	p<0.05
Time spent flying per trip (%)	60 ± 14	49 ± 15	p<0.01
Food brought to nest (g)	361 ± 243	213 ± 141	p<0.05
Energy brought to nest (kJ)	1561 ± 1053	1162 ± 1103	NS



West coast birds worked harder and brought back more food (mainly hake offal from demersal trawlers); south coast birds worked less and brought back less food (mainly sardine)

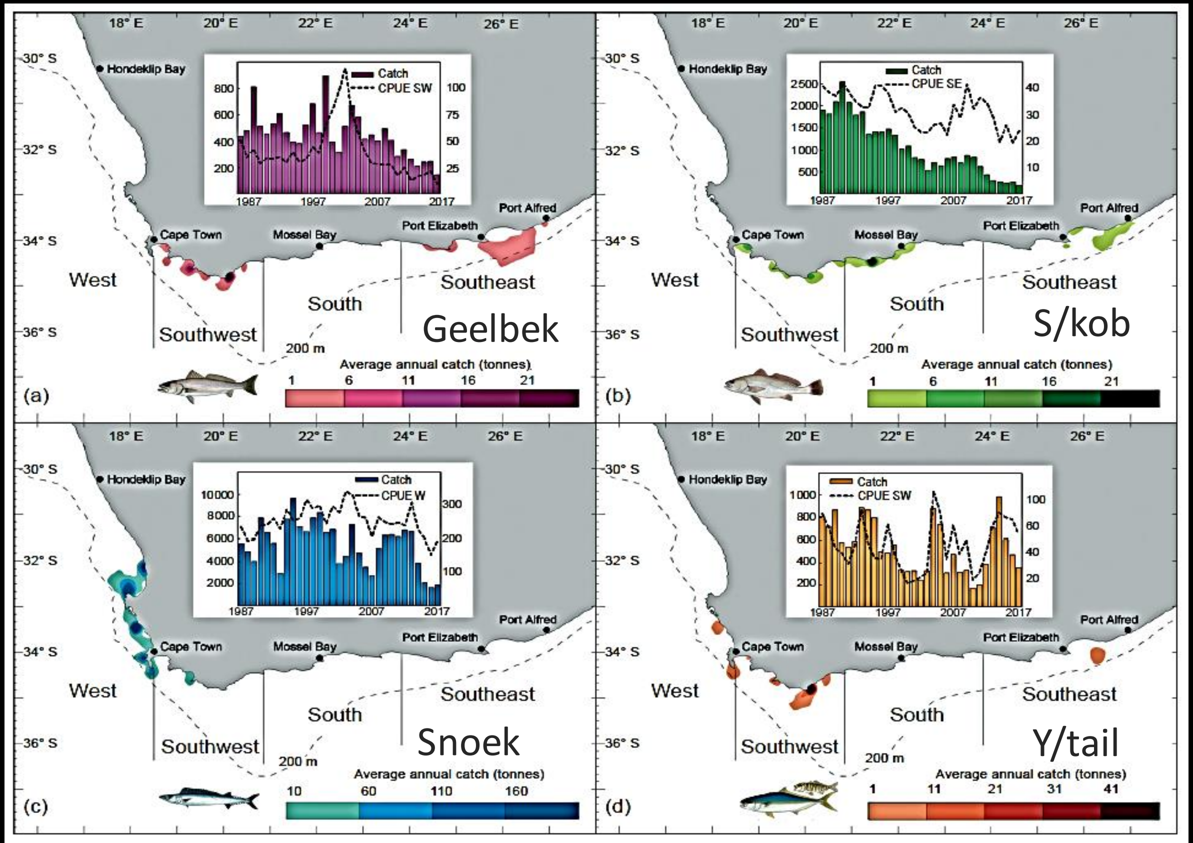
Total energetic content of diets not different but low energy diet does not compensate for increased foraging costs or lack of high value natural prey

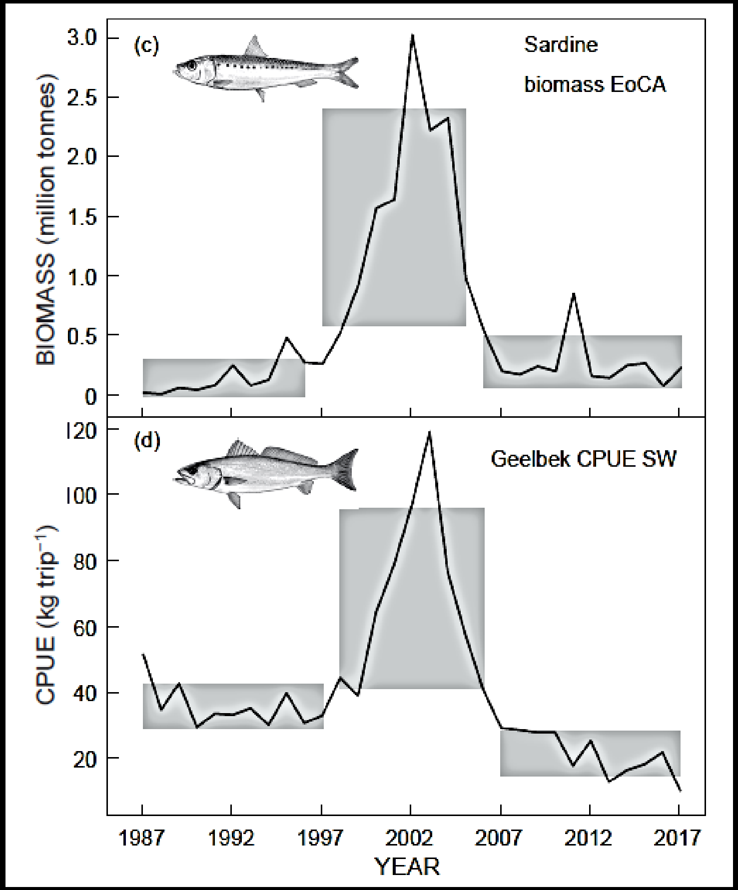
West coast birds showed reduced breeding success and declining numbers; population now Endangered



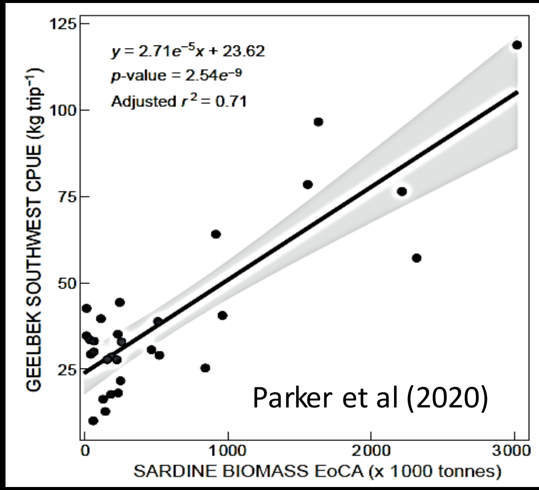
SPFs as prey (ix)

Four commercially-exploited linefish off South Africa feed extensively on SPF: geelbek, silver kob, snoek and yellowtail (*average annual catch distribution, catch and CPUE; right*)





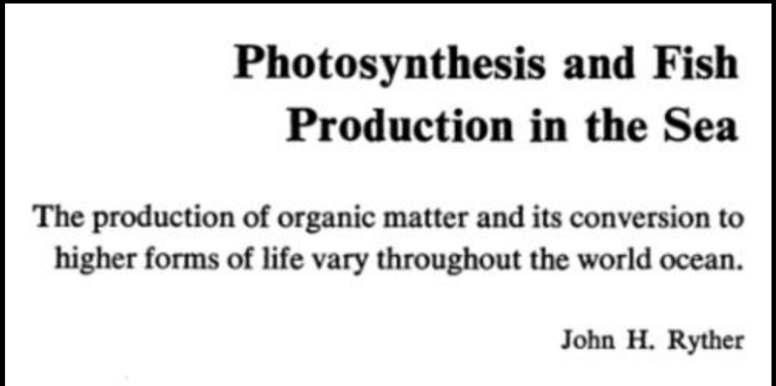
Sequential t-test analysis of regime shifts (STARS) showed close correspondence between geelbek SW CPUE (juveniles) and sardine biomass EoCA (*left*), and SW CPUE in year$_{n+1}$ strongly correlated to sardine biomass EoCA in Year$_n$ (*right*)



Small pelagic fishes and trophodynamic processes (i)

Ryther (1969; *Science*) hypothesized that SPFs attain large abundances because they are primarily phytoplanktivorous and hence benefit from an efficient 2-step food chain

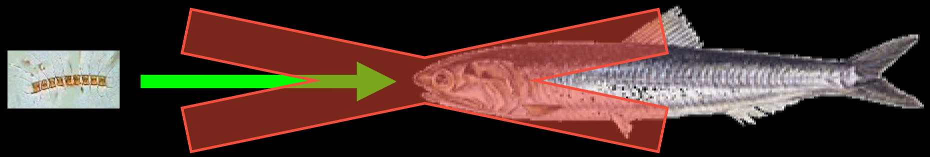
That hypothesis is incorrect; SPFs typically consume both phyto- and zooplankton but most derive the majority of their nutritional input from zooplankton

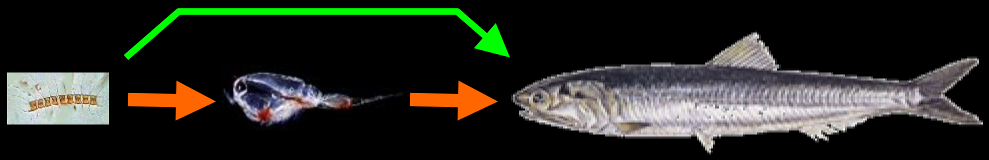


Photosynthesis and Fish Production in the Sea

The production of organic matter and its conversion to higher forms of life vary throughout the world ocean.

John H. Ryther





Small pelagic fishes and trophodynamic processes (ii)

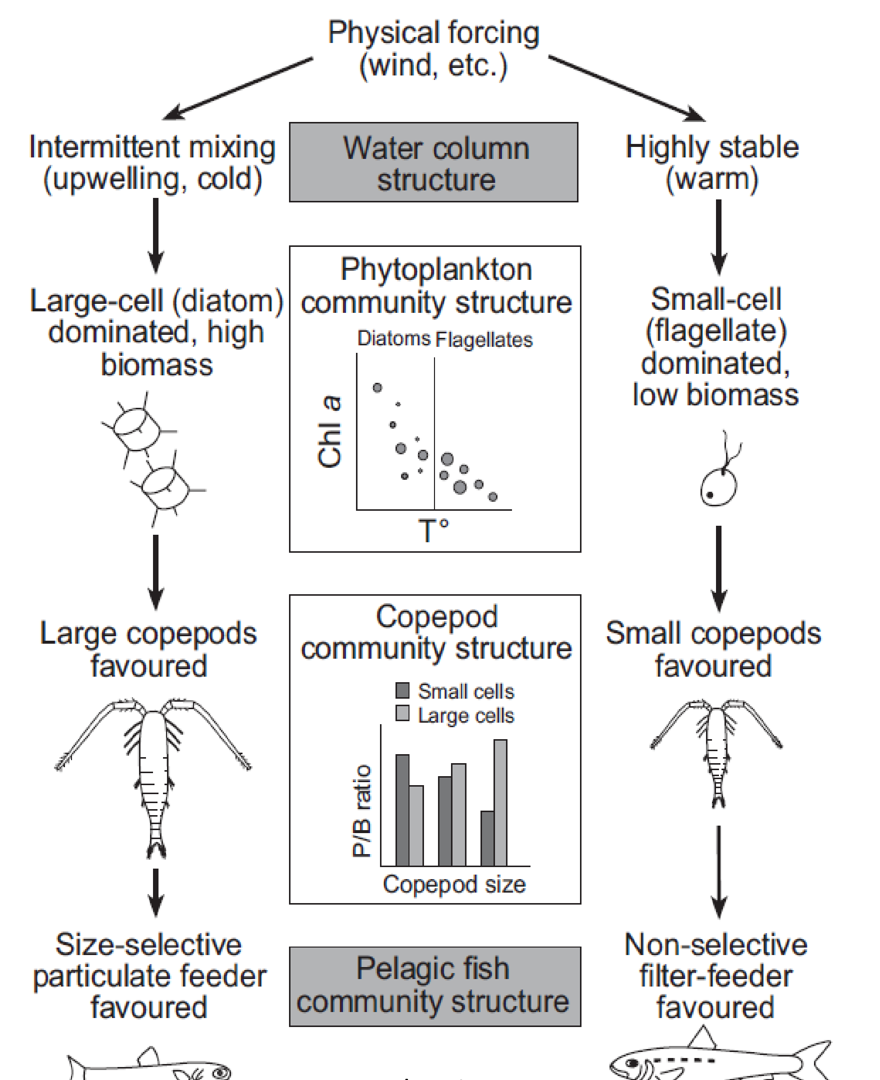
Co-occurring anchovy and sardine species generally utilize different fractions of the zooplankton because of morphological and behavioural differences (especially in EBUS)

Anchovy derive the bulk of their nutrition from larger zooplankton and are positioned at a slightly higher trophic level than sardine (smaller zooplankton, lower trophic level)

“Trophic Dissimilarity Hypothesis” posits that different environmental conditions may favour one species over the other:

Upwelling → large diatoms → larger copepods → anchovy

Stable → small flagellates → smaller copepods → sardine



van der Lingen et al (2006)

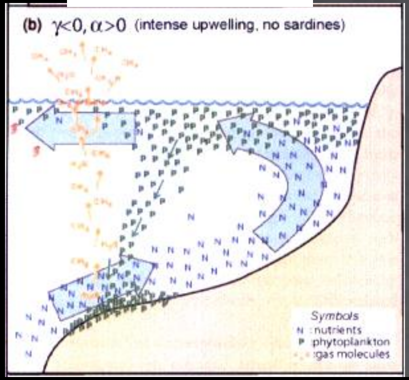
Small pelagic fishes and trophodynamic processes (iii)

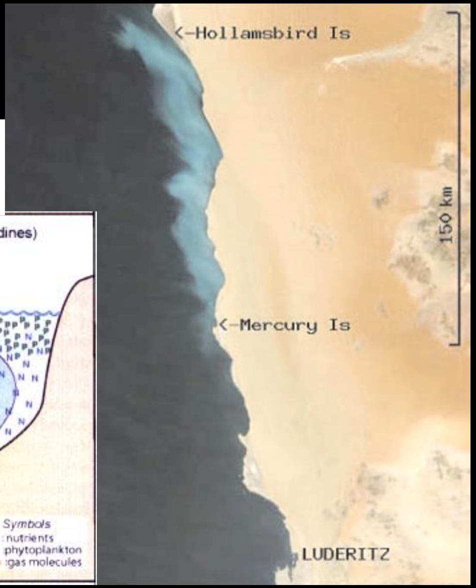
The importance of SPFs as forage for a multitude of predators means they are critical for ecological functioning (and whether the pelagic foodweb is wasp-waist, bone-shaped or beer belly-shaped *sensu* A. Bertrand)

Collapses of SPF populations or changes in their distributions have deleterious impacts on ecosystem functioning and particularly on dependent predators, and these may be irreversible (sulphide eruptions [Bakun and Weeks 2004] and "jellification" [Roux et al 2013] of the N Benguela)

Conservative harvesting levels and the implementation of the Ecosystem Approach to Fisheries Management (EAF) and/or Ecosystem Based Management (EBM) for SPF fisheries are needed

Bakun and Weeks (2004)





JELLYFICATION OF MARINE ECOSYSTEMS AS A LIKELY CONSEQUENCE OF OVERFISHING SMALL PELAGIC FISHES: LESSONS FROM THE BENGUELA

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