

Swimbladders in Mesopelagic Fishes

Bibliography

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NCRL subject guide 2021-06

DOI: [10.25923/a1p9-zh44](https://doi.org/10.25923/a1p9-zh44)

June 2021



U.S. Department of Commerce
National Oceanic and Atmospheric Administration
Office of Oceanic and Atmospheric Research
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Background & Scope

This bibliography is a representative sample of relevant literature on swimbladders in mesopelagic fish and their acoustic properties. References included in this bibliography are mainly from peer-reviewed, academic literature and span the years 1954-2021. The references are listed alphabetically by first author.

Sources Reviewed

The following databases were used to identify sources: Clarivate Analytics' Web of Science: Science Citation Index Expanded and Social Science Index; EconLit; ProQuest's Science and Technology including Aquatic Science Fisheries Abstracts; Elsevier's Science Direct; JSTOR; EBSCO's Academic Search Complete and Environment Complete; NOAA's Institutional Repository; the Biodiversity Heritage Library; BioOne Complete; and Google Scholar.

References

Ali, H. A., Mok, H.-K., & Fine, M. L. (2016). Development and sexual dimorphism of the sonic system in deep sea neobythitine fishes: The upper continental slope. *Deep Sea Research Part I: Oceanographic Research Papers*, 115, 293-308. <https://doi.org/10.1016/j.dsr.2016.07.010>

The anatomy of sound production in continental-slope fishes has been ignored since the work of NB Marshall in the 1960s. Due to food scarcity at great depths, we hypothesize that sonic muscles will be reduced in deep-water neobythitine cusk-eels (family Ophidiidae). Here we describe and quantify dimensions of the swimbladder and sonic muscles of three species from the upper slope. They have four pairs of well-developed sonic muscles (two medial and two lateral) with origins on the skull and insertions on the medial swimbladder (medial pair) or on modified epineural ribs that attach to the lateral swimbladder (lateral pair). Despite minor differences, relatively similar swimbladder dimensions, muscle length and external morphology suggest a conservative body plan. However, there are major differences in sonic muscle mass: medial muscles are heavier in males and made of relatively small fibers (ca 10µm in diameter). Lateral muscles are generally larger in females and consist of larger fibers, as in epaxial trunk muscle. Muscle weight varies between species, and we suggest males produce advertisement calls that vary in amplitude and duration in different species. Due to differences in fiber size, we hypothesize that lateral muscles with larger fibers remain contracted during sound production, and medial muscles with smaller fibers will oscillate to drive swimbladder sound production.

Ariza, A., Landeira, J. M., Escanez, A., Wienerroither, R., de Soto, N. A., Rostad, A., . . . Hernandez-Leon, S. (2016). Vertical distribution, composition and migratory patterns of acoustic scattering layers in the Canary Islands. *Journal of Marine Systems*, 157, 82-91.
<https://doi.org/10.1016/j.jmarsys.2016.01.004>

Diel vertical migration (DVM) facilitates biogeochemical exchanges between shallow waters and the deep ocean. An effective way of monitoring the migrant biota is by acoustic observations although the interpretation of the scattering layers poses challenges. Here we combine results from acoustic observations at 18 and 38 kHz with limited net sampling in order to unveil the origin of acoustic phenomena around the Canary Islands, subtropical northeast Atlantic Ocean. Trawling data revealed a high diversity of fishes, decapods and cephalopods (152 species), although few dominant species likely were responsible for most of the sound scattering in the region. We identified four different acoustic scattering layers in the mesopelagic realm: (1) at 400-500 m depth, a swimbladder resonance phenomenon at 18 kHz produced by gas-bearing migrant fish such as *Vinciguerria* spp. and *Lobianchia dofleini*, (2) at 500-600 m depth, a dense 38 kHz layer resulting primarily from the gas-bearing and non-migrant fish *Cyclothona braueri*, and to a lesser extent, from fluid-like migrant fauna also inhabiting these depths, (3) between 600 and 800 m depth, a weak signal at both 18 and 38 kHz ascribed either to migrant fish or decapods, and (4) below 800 m depth, a weak non-migrant layer at 18 kHz which was not sampled. All the dielly migrating layers reached the epipelagic zone at night, with the shorter-range migrations moving at $4.6 \pm 2.6 \text{ cm s}^{-1}$ and the long-range ones at $115 \pm 3.8 \text{ cm s}^{-1}$. This work reduces uncertainties interpreting standard frequencies in mesopelagic studies, while enhances the potential of acoustics for future research and monitoring of the deep pelagic fauna in the Canary Islands.

Backus, R. H., Craddock, J. E., Haedrich, R. L., Shores, D. L., Teal, J. M., Wing, A. S., . . . Clarke, W. D. (1968). Ceratoscopelus maderensis: Peculiar Sound-Scattering Layer Identified with This Myctophid Fish. *Science*, 160(3831), 991. <https://doi.org/10.1126/science.160.3831.991>

A sound-scattering layer, composed of discrete hyperbolic echosequences and apparently restricted to the Slope Water region of the western North Atlantic, has been identified from the Deep Submergence Research Vehicle Alvin with schools of the meyctophid fish Ceratoscopelus maderensis. By diving into the layer and using Alvin's echo-ranging sonar, we approached and visually identified the sound scatterers. The number of echo sequences observed with the surface echo-sounder ($1/23.76 \times 105$ cubic meters of water) checked roughly with the number of sonar targets observed from the submarine ($1/7.45 \times 105$ cubic meters). The fish schools appeared to be 5 to 10 meters thick, 10 to 100 meters in diameter, and on centers 100 to 200 meters apart. Density within schools was estimated at 10 to 15 fish per cubic meter.

Barange, M. (1990). Vertical migration and habitat partitioning of 6 euphausiid species in the Northern Benguela Upwelling System. *Journal of Plankton Research*, 12(6), 1223-1237.
<https://doi.org/10.1093/plankt/12.6.1223>

The vertical distribution of the adults of six species of euphausiids, *Thysanöessa gregaria*, *Nematoscelis megalops*, *Euphausia americana*, *E.gibboides*, *E.hansenii*, *Stylocheiron longicorne*, as well as the larval stages of *E.hansenii*, were studied during a 48 h cycle at a fixed station in the northern Benguela upwelling system. All the species, except *T.gregaria* and *S.longicorne*, proved to perform diel vertical migration, but both migratory and non-migratory species appeared to be segregated in space during night-time hours, regardless of potential prey (phytoplankton and copepods). It is suggested that water column structure and hydrographic discontinuities caused by a warm, depth-localized intrusion, as well as the reproductive strategies of particular species, are responsible for this pattern. Eggs and larval stages of *E.hansenii* were concentrated near the surface, and the effect of the short-term pulses of the intrusion on their abundance is discussed.

Barange, M., Hampton, I., & Soule, M. (1996). Empirical determination of in situ target strengths of three loosely aggregated pelagic fish species. *ICES Journal of Marine Science*, 53(2), 225-232.
<https://doi.org/10.1006/jmsc.1996.0026>

In situ measurements of target strength (TS) at 38 kHz have been taken from night-time scattering layers of anchovy, pilchard, and Cape horse mackerel in the course of routine surveys. These species have different numerical packing densities, which necessitates treating the TS data differently in each case, as the performance of single-target detectors is strongly dependent on target densities. Evidence for the presence of multiple targets in their TS distributions is presented, and empirical methods of extracting mean target strengths from them described. After careful assessment of the quality of each data point, and the removal of unwanted influences where possible, the data were used to fit TS/length expressions for the three species.

Bardarson, B. (2013). *Modelled target strengths of three lanternfish (family: Myctophidae) in the north east Atlantic based on swimbladder and body morphology*. (MPhil Master of Philosophy), The University of St Andrews, Retrieved from <http://hdl.handle.net/10023/6607>

At mesopelagic depths (200-1000 m), in the oceanic parts of the earth, there are probably the most abundant fish assemblages in the world, often observed on echosounder displays as sound scattering layers extending over vast areas. Lanternfish are believed to be an important part of those layers. In recent years, acoustic backscatter has been used successfully to quantify pelagic fish stocks, where knowledge of individual fish backscatter proportion, the target strength, is essential for reliable estimate. More knowledge on target strength of the lanternfish found in the Northeast Atlantic is needed before they can be properly identified and quantified by acoustics. Air in the swimbladder will cause much stronger backscatter than the fish body. In this study, external morphology and swimbladder morphology of three abundant lanternfish species (*Benthosema glaciale*, *Notoscopelus kroeyerii* and *Myctophum punctatum*) were measured using digital imaging and soft x-ray technology to inform theoretical acoustic target strength (TS) models. The soft x-ray measurements indicated that 71% by number of the adult *B. glaciale* population (sample size (n) = 85) had an air filled swimbladder, while *N. kroeyerii* (n = 127) and *M. punctatum* (n = 99) did not have inflated swimbladders in their adult stage. A distorted wave Born approximation (DWBA) model was used to estimate TS contribution of the fish body while a prolate spheroid resonance scattering model was used for contribution of swimbladder. Further, a comparison was made with exact solution models. At 38 kHz, the commonly used frequency in scientific surveys, *N. kroeyerii* was estimated with the TS length relationship of $22.6 \log(\text{SL}) - 92.8$ while *M. punctatum* had $10.9 \log(\text{SL}) - 81.5$. At same frequency the mean TS of *B. glaciale* was estimated as -64.29 dB with 95% confidence limits of -65.52 and -63.33 dB. Further the TS estimates and scattering properties of all three species were estimated at different frequencies (18, 38, 70, 120 and 200 kHz). These multifrequency TS data will assist with acoustic identification and biomass estimation of lanternfish that, in turn, will enable contribution of much-needed lanternfish data to ecosystem models.

Barr, R. (2001). A design study of an acoustic system suitable for differentiating between orange roughy and other New Zealand deep-water species. *The Journal of the Acoustical Society of America*, 109(1), 164-178. <https://doi.org/10.1121/1.1332381>

Using the simple slab-cylinder acoustic model for fish, developed by Clay and Horne [J. Acoust. Soc. Am. 96, 1661–1668 (1994)], the target strengths of three of New Zealand's deep-water fish species, namely orange roughy, black oreos, and smooth oreos, have been derived. The target strengths derived for the model fish have been found to be in reasonable agreement with currently accepted target strength values. These three model fish were used in a study to test the species discrimination of a chirp sonar system. Chirps of center frequencies 40, 80, and 160 kHz and bandwidth of 10, 20, and 40 kHz have been used to acoustically illuminate the three fish species listed above and the matched, filtered responses to the chirps determined. The effect of the response of transducer or system bandwidth has also been investigated. It has been found that the bandwidth of the chirp is much more important for resolving detail in a fish target than the chirp center frequency. A bandwidth of at least 20 kHz, and preferably 40 kHz, produces matched filtered responses for black and smooth oreos and orange roughy which are quite clearly species specific. Results suggest that with orange roughy it may be possible to size and even sex the targets acoustically.

Barr, R., & Coombs, R. F. (2005). Target phase: An extra dimension for fish and plankton target identification. *The Journal of the Acoustical Society of America*, 118(3), 1358-1371.
<https://doi.org/10.1121/1.1979503>

The acoustic signal backscattered from a fish in water, $\mathcal{L}_{\text{bs}}(f)$, at a frequency, f , differs from the incident signal in both magnitude, $|\mathcal{L}_{\text{bs}}(f)|$, and phase, $\arg[\mathcal{L}_{\text{bs}}(f)]$, and it has been common practice for many years to use the backscatter magnitude from individual fish as an aid to species identification. However, very little use has been made of the phase of the backscattered signal relative to that of the incident acoustic pulse. If the gross phase changes due to propagation through water are compensated for, the residual phase signature is found to contain useful target-specific information. The phase signature can be characterized by estimating the rate at which the echo phase changes, relative to the transmitted pulse, during the echo from a fish. Clear groups are produced when single fish targets from in situ data are plotted in complex target space (target strength versus target rate of change of phase) and this is explored here by computing the acoustic backscatter, in complex target space, from a series of simple large and small model fish targets, both with and without gas-filled swimbladders, using a Monte Carlo technique. It is shown that all the features found in the in situ data can be explained in terms of the size and attitude of the fish. The modeling was carried out at the frequency of 38 kHz, which pertained to the in situ data, and the specific results only apply to this frequency. However, the complex target approach is generally applicable to fish target strength analysis independently of frequency.

Beamish, R. J., Leask, K. D., Ivanov, O. A., Balanov, A. A., Orlov, A. M., & Sinclair, B. (1999). The ecology, distribution, and abundance of midwater fishes of the Subarctic Pacific gyres. *Progress in Oceanography*, 43(2), 399-442. [https://doi.org/10.1016/S0079-6611\(99\)00017-8](https://doi.org/10.1016/S0079-6611(99)00017-8)

We describe the distribution and abundance of the midwater fish community, between 200 m and 500 m, in the North Pacific. The main area of interest was the Subarctic Pacific gyres, but we include species from the Bering Sea and the Sea of Okhotsk. There were 196 species identified in each gyre, 38 of which were common to both gyres. The most abundant species belong to the family Myctophidae and the most ecologically important myctophid probably is *Stenobrachius leucopsarus*. This species could have a biomass of approximately 21 million tonnes (t) in the Subarctic Pacific (including the Bering Sea and Sea of Okhotsk). *S. leucopsarus* is a small (about 8 cm maximum length) fish that lives up to 7 years. It is prey for a variety of other fishes, birds and mammals and may migrate into the mixing layer each evening where it feeds mainly on euphausiids and copepods. The total abundance of midwater fishes appears to be large relative to total catches of other fish in the same areas. The vertical migratory behaviour of some of the residents provides a mechanism to transfer production out of the mixing layer. The movement into the surface layer by some fishes at night indicates that dynamic changes occur in the midwater community between the day and night, and the ecosystem dynamics in the surface layer are different in the day and in the night. This behaviour and the huge biomass relative to commercial species means that the dynamics of fish communities in the Subarctic Pacific are complex and need to be studied over a 24 hour period. The large biomasses may eventually attract commercial interest, thus it is important to establish international, cooperative programs now to learn more about the dynamics of these populations and the relationships with other species.

Becker, K. N., & Warren, J. D. (2015). Material properties of Pacific hake, Humboldt squid, and two species of myctophids in the California Current. *The Journal of the Acoustical Society of America*, 137(5), 2522-2532. <https://doi.org/10.1121/1.4919308>

Material properties of the flesh from three fish species (*Merluccius productus*, *Symbolophorus californiensis*, and *Diaphus theta*), and several body parts of the Humboldt squid (*Dosidicus gigas*) collected from the California Current ecosystem were measured. The density contrast relative to seawater varied within and among taxa for fish flesh (0.9919–1.036), squid soft body parts (mantle, arms, tentacle, braincase, eyes; 1.009–1.057), and squid hard body parts (beak and pen; 1.085–1.459). Effects of animal length and environmental conditions on nekton density contrast were investigated. The sound speed contrast relative to seawater varied within and among taxa for fish flesh (0.986–1.027) and Humboldt squid mantle and braincase (0.937–1.028). Material properties in this study are similar to values from previous studies on species with similar life histories. In general, the sound speed and density of soft body parts of fish and squid were 1%–3% and 1%–6%, respectively, greater than the surrounding seawater. Hard parts of the squid were significantly more dense (6%–46%) than seawater. The material properties reported here can be used to improve target strength estimates from acoustic scattering models, which could increase the accuracy of biomass estimates from acoustic surveys for these nekton.

Belcher, A., Cook, K., Bondyale-Juez, D., Stowasser, G., Fielding, S., Saunders, R. A., . . . Tarling, G. A. (2020). Respiration of mesopelagic fish: a comparison of respiratory electron transport system (ETS) measurements and allometrically calculated rates in the Southern Ocean and Benguela Current. *ICES Journal of Marine Science*, 77(5), 1672–1684. <https://doi.org/10.1093/icesjms/fsaa031>

Mesopelagic fish are an important component of marine ecosystems, and their contribution to marine biogeochemical cycles is becoming increasingly recognized. However, major uncertainties remain in the rates at which they remineralize organic matter. We present respiration rate estimates of mesopelagic fish from two oceanographically contrasting regions: the Scotia Sea and the Benguela Current. Respiration rates were estimated by measuring the enzyme activities of the electron transport system. Regression analysis of respiration with wet mass highlights regional and inter-specific differences. The mean respiration rates of all mesopelagic fish sampled were 593.6 and 354.9 $\mu\text{mol O}_2 \text{ individual}^{-1} \text{ h}^{-1}$ in the Scotia Sea and Benguela Current, respectively. Global allometric models performed poorly in colder regions compared with our observations, underestimating respiratory flux in the Scotia Sea by 67–88%. This may reflect that most data used to fit such models are derived from temperate and subtropical regions. We recommend caution when applying globally derived allometric models to regional data, particularly in cold (<5 degrees C) temperature environments where empirical data are limited. More mesopelagic fish respiration rate measurements are required, particularly in polar regions, to increase the accuracy with which we can assess their importance in marine biogeochemical cycles.

Belcher, A., Saunders, R. A., & Tarling, G. A. (2019). Respiration rates and active carbon flux of mesopelagic fishes (Family Myctophidae) in the Scotia Sea, Southern Ocean. *Marine Ecology Progress Series*, 610, 149–162. <https://doi.org/10.3354/meps12861>

Mesopelagic fish have recently been highlighted as an important, but poorly studied component of marine ecosystems, particularly regarding their role in the marine pelagic food webs and

biogeochemical cycles. Myctophids (Family Myctophidae) are one of the most biomass-dominant groups of mesopelagic fishes, and their large vertical migrations provide means of rapid transfer of carbon to the deep ocean where it can be sequestered for centuries or more. In this study, we develop a simple regression for the respiration rate of myctophid fish using literature-based wet mass and habitat temperature data. We apply this regression to net haul data collected across the Scotia-Weddell sector of the Southern Ocean to estimate respiration rates of the biomass-dominant myctophid species. *Electrona carlsbergi*, *Electrona antarctica*, and *Gymnoscopelus braueri* made a high contribution (up to 85 %) to total myctophid respiration. Despite the lower temperatures of the southern Scotia Sea (-1.46 to 0.95 degrees C), total respiration here was as high (reaching 1.1 mg C m(-2) d(-1)) as in the warmer waters of the mid and northern Scotia Sea. The maximum respiratory carbon flux of the vertically migrating community was 0.05 to 0.28 mg C m(-2) d(-1), equivalent to up to 47 % of the gravitational particulate organic carbon flux in some parts of the Scotia-Weddell region. Our study provides the first baseline estimates of respiration rates and carbon flux of myctophids in the Southern Ocean. However, direct measurements of myctophid respiration, and of mesopelagic fish generally, are needed to constrain these estimates further and incorporate these fluxes into carbon budgets.

Benoit-Bird, K. J., & Au, W. W. L. (2001). Target strength measurements of Hawaiian mesopelagic boundary community animals. *Journal of the Acoustical Society of America*, 110(2), 812-819.
<https://doi.org/10.1121/1.1382620>

A 200-kHz echosounder modified to digitize the envelope of the received echoes directly into a computer was used to measure the ex situ target strength (TS) of live animals from the Hawaiian mesopelagic boundary community as a function of animal size, tilt and roll angle, and biological classification. Dorsal aspect TS (in dB//1 m) at 200 kHz was related to the animal's length: myctophid fish TS = 20 log (standard length in cm) - 58.8, $r^2 = 0.91$, squid TS = 18.8 log (mantle length in cm) -61.7, $r^2 = 0.81$, shrimp TS = 19.4 log (length in cm) - 74.1, $r^2 = 0.83$. Tilting the fish 5 degrees and 10 degrees changed the measured TS by up to 3.0 dB, decreasing TS as the fish was tilted forward and increasing TS as the fish was tilted backwards. In shrimp, forward tilt increased TS while backward tilt decreased TS by up to 3.3 dB. No consistent trend in squid TS change was observed with tilt angle. Roll angles of 5 degrees and 10 degrees increased the TS of all groups by up to 3.0 dB. Myctophid lateral aspect TS was consistently about 6 dB higher than the dorsal TS. Physiological analysis of the fishes' swimbladders revealed that the swimbladder is not the dominant scattering mechanism in the myctophid fishes studied.

Benoit-Bird, K. J., & Warren, J. D. (2015). *Acoustical Scattering, Propagation, and Attenuation Caused by Two Abundant Pacific Schooling Species: Humboldt Squid and Hake*. Retrieved from <https://apps.dtic.mil/sti/citations/AD1013958>

Our long-term goal is to predict the acoustic characteristics expected from aggregations of hake and jumbo squid off the west coast of North America within the frequency range of tactical, low to mid-frequency naval sonars.

Bernal, A., Toresen, R., & Riera, R. (2020). Mesopelagic fish composition and diets of three myctophid species with potential incidence of microplastics, across the southern tropical gyre. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 179.
<https://doi.org/10.1016/j.dsr2.2019.104706>

The species occurrence of mesopelagic fish collected in the scattering layers was studied across the Indian Ocean subtropical gyre during the dry season (2015). Ocean eddies can retain zooplankton and plastic debris, and determine biological composition through advection. The conditions inside the gyre were stabilised by low chlorophyll-a concentrations and a deep nutricline. A diverse assemblage of mesopelagic fish, dominated by myctophids, exhibited diel migrations to the upper water layers for feeding since the early night. Myctophids were concentrated ca. 100 m depth, where the deep chlorophyll maximum was located, and coinciding with the nutricline. Another group of mesopelagic fish remained in deeper waters during the daytime, with a higher occurrence of Stomiiformes (Phoshyctyidae and Sternopychidae) at the 500-600 m Deep Scattering Layer. Moreover, the diets of 220 myctophid specimens belonging to the species Ceratoscopehis warmingii, Diaphus effulgens, and Symbolophorus evermanni, were investigated based on stomach content analysis. Calanoid copepods, mainly Pleuromamma abdominalis, made up 30% of the diet in the three myctophid species, with interspecific differences in the preferred second item: C. warmingii preferred ostracods, D. effulgens, non-calanoid copepods, and S. evermanni, euphausiids. Thus, partial dietary segregation was observed among the three species. We hypothesized that these myctophid diets differed between stations located at the gyre core and its outer edge. Any dietary pattern indicating aggregation of food resources, or an enhancement of the foraging opportunities for myctophids, was discerned as an effect of the gyre advection. However, prey composition diverged between the core and the outer edge stations regardless of the fish species, with a higher dietary representation of P. abdominalis and euphausiids (migratory zooplankton) in the individuals collected in the core-influenced area. A total of six plastic pieces were present in the stomachs of D. effulgens and S. evermanni, in contrast with the high presence of plastic particles found at the surface in most sampling stations (average number of plastic pieces was 41 per hour). The selected myctophid species did not appear to be important transport vectors for micoplastics in comparison with species from other oceans.

Bernardes, I. D., Ona, E., & Gjosaeter, H. (2020). Study of the Arctic mesopelagic layer with vessel and profiling multifrequency acoustics. *Progress in Oceanography*, 182.
<https://doi.org/10.1016/j.pocean.2019.102260>

The range limitation (> 200 m) for high-frequency echosounders does not allow for complete multifrequency studies of the mesopelagic layers from vessel-mounted echosounders. The layers of mesopelagic fish and zooplankton in the Arctic region north of Svalbard (Spitsbergen) were studied using vessel-mounted echosounders and a profiling acoustic probe, using 38; 120; 200 and 333 kHz. Volume density estimates of mesopelagic fish have shown to be marginally higher with the probing system in relation with measured from the vessel-mounted echosounders at 38 kHz. This shows that the swimbladder resonance phenomenon is not occurring in low density layers with limited vertical migration. The use of the profiling probe allowed densities to be calculated with an in situ measured target strength (TS). In depths > 200 m where high-frequency hull-mounted transducers cannot effectively reach, the profiling system measured a mixture of krill and amphipods, down to 600 m. Vertical profiles of measured target categories, from vessel transducers and from the probing system are compared in relation to the biological sampling conducted during the survey. Profiling acoustics are

shown to be a valuable tool to address some limitations in the current surveying methods for studying mesopelagic layers beyond the reach for high-frequency vessel-mounted systems.

Blaxter, J. H. S., & Batty, R. S. (1990). Swimbladder 'behaviour' and target strength. *Rapports et Procès-Verbaux des Réunions Conseil International pour l'Exploration de la Mer*, 189, 233-244. No URL available.

The target strength (TS) of fish is higher when a swimbladder is present. TS depends on the swimbladder volume which increases with fish size and varies with depth. Changes of volume occur during vertical migration; the volume then remains rather stable in physostomes apart from slow losses of gas by diffusion, but physoclists secrete or absorb gas, so tending to restore the original volume. Such adaptation to a depth change is slow compared with the speed of movement of vertical migrants whose TS will change at dusk and dawn.

TS also varies with the orientation of the fish to the echo-sounding beam and may vary with its swimming speed. The highest TS is found with the head tilted down 5-10 degrees. The swimbladder axis is, however, tilted up by the same amount so that it lies normal to the beam. In many species there are day:night differences in activity, swimming speed, tilt angle, density, and vertical stacking, all affecting TS. It is unfortunate that TS depends on a labile organ with a role in buoyancy and posture.

Blaxter, J. H. S., & Hunter, J. R. (1982). The Biology of the Clupeoid Fishes. In *Advances in Marine Biology*. J. H. S. Blaxter, F. S. Russell, & M. Yonge (Eds.), (Vol. 20, pp. 1-223): Academic Press
[https://doi.org/10.1016/S0065-2881\(08\)60140-6](https://doi.org/10.1016/S0065-2881(08)60140-6)

Clupeoid populations have undergone striking increases, followed by precipitous and catastrophic declines, which have caused the collapse of the fishing industry. These fluctuations have been caused by great natural variability in recruitment and by its interaction with fishing policy and economics. A probable combination of overfishing and natural changes also caused declines in other clupeoid stocks during the past few decades. Most clupeoids have a short life span; they recruit at 1-3 years of age and rarely live beyond 5-10 years of age except for some herring stocks, especially the Atlanto-Scandian herring. Early maturation implies that the asymptotic length (L_∞) is reached rapidly and growth is not very significant in older fish. As a result most overfishing of clupeoids is classed as "recruitment" rather than "growth" overfishing. Nevertheless some classic cases exist of particular year-classes dominating a fishery for several years. In such cases, the importance of the year-class lies in its numbers rather than in the weight increase as the fish becomes older. The aim of this chapter is to describe the present status of knowledge on the behavior and physiology of clupeoids with particular reference to their ecology. Some of the advances have been made possible by improvements in the ability to rear larval stages and to catch, transport and keep the older stages in captivity, and by greatly improved techniques such as aerial photography, video systems, sampling gear, and apparatus.

Blaxter, J. H. S., & Tytler, P. (1978). Physiology and Function of the Swimbladder. In *Advances in Comparative Physiology and Biochemistry*. O. Lowenstein (Ed.), (Vol. 7, pp. 311-367): Elsevier
<https://doi.org/10.1016/B978-0-12-011507-5.50010-0>

No abstract available.

Blaxter, J. H. S., Wardle, C. S., & Roberts, B. L. (1971). Aspects of the Circulatory Physiology and Muscle Systems of Deep-Sea Fish. *Journal of the Marine Biological Association of the United Kingdom*, 51(4), 991-1006. <https://doi.org/10.1017/S0025315400018105>

Mesopeiagic fish without swim bladders, found in depths from 100 to 1000 m, have soft bodies with a very high water content (88–95%) low haematocrits (5–9%), small hearts, a low proportion of red muscle, and large lymph ducts. Species possessing swim bladders have a lower water content (70–83%), higher haematocrits (14–35%), larger hearts, more prevalent red muscle and smaller lymph ducts. Some active surface species have still less water (64–74%) and higher haematocrits (48–57%). The soft watery fish appear to use skeletal reduction and high water content as a buoyancy mechanism but there is no evidence, judging from analyses of freezing-point depression of the plasma and muscle fluid, that they maintain an extra low ionic content to assist buoyancy. Although oxygen is probably adequate in the deep water, there may be some constraint on activity because the oxygen-carrying capacity of the blood is low and oxygen may be limited at the tissues. This is partly compensated for by the high proportion of anaerobic white muscle and the large lymph system. These watery fish appear to be best adapted to short bursts of activity. Nevertheless they do make diel vertical migrations which may cause them to reach the limits of their aerobic metabolic systems. The mesopeiagic species with swim bladders are much more similar in their circulatory characteristics to inshore fish. They also make quite substantial vertical migrations with the concomitant problem of adjusting buoyancy by varying the pressure within the swim bladder. Metabolically this is unlikely to be unduly difficult.

Bone, Q. (1973). A Note on the Buoyancy of some Lantern-Fishes (Myctophoidei). *Journal of the Marine Biological Association of the United Kingdom*, 53(3), 619-633.
<https://doi.org/10.1017/S002531540005823>

The buoyancy, lipid levels, and orientation of five species of myctophid from the Biscay area were examined, and it was found that two of the five were probably normally denser than the sea water in which they live. Analysis of the swimbladder gas of *Myctophum punctatum* collected at the surface at night indicated that this species has a less extensive vertical range in this area than elsewhere. A functional classification of myctophids is proposed, based upon density, lipid levels, and the presence or absence of a gas-filled swimbladder.

Boswell, K. M., D'Elia, M., Johnston, M. W., Mohan, J. A., Warren, J. D., Wells, R. J. D., & Sutton, T. T. (2020). Oceanographic Structure and Light Levels Drive Patterns of Sound Scattering Layers in a Low-Latitude Oceanic System. *Frontiers in Marine Science*, 7(51).
<https://doi.org/10.3389/fmars.2020.00051>

Several factors have been reported to structure the spatial and temporal patterns of sound scattering layers, including temperature, oxygen, salinity, light, and physical oceanographic conditions. In this study, we examined the spatiotemporal variability of acoustically detected sound scattering layers in the northern Gulf of Mexico to investigate the drivers of this variability, including mesoscale oceanographic features [e.g., Loop Current-origin water (LCOW), frontal boundaries, and Gulf Common Water]. Results indicate correlations in the vertical position and acoustic backscatter intensity of sound scattering layers with oceanographic conditions and light intensity. LCOW regions displayed consistent decreases, by a factor of two and four, in acoustic backscatter intensity in the upper 200 m relative to frontal boundaries and Gulf Common Water, respectively. Sound scattering layers had greater backscatter

intensity at night in comparison to daytime (25x for frontal boundaries, 17x for LCOW, and 12x for Gulf Common Water). The importance of biotic (primary productivity) and abiotic (sea surface temperature, salinity) factors varied across oceanographic conditions and depth intervals, suggesting that the patterns in distribution and behavior of mesopelagic assemblages in low-latitude, oligotrophic ecosystems can be highly dynamic.

Brooks, A. L. (1977). A study of the swimbladders of selected mesopelagic fish species. In *Oceanic sound scattering prediction*. N. R. Andersen & B. J. Zahuranec (Eds.). New York: Plenum Press.
Retrieved from
<https://search.proquest.com/asfa/docview/15161819/2D70CDB786BF43A4PQ/21?accountid=28258>

The intra- and inter-specific variation in the relationship of fish standard length to swimbladder length, width, and volume was studied in selected mesopelagic fish specimens belonging to 55 species from 9 families. These species are believed to account for most of the volume reverberation occurring throughout a large part of the Sargasso Sea. Regression equations define the relationship of fish length to swimbladder length, width, and volume. For 40 species, bladder volume increases with increasing standard length. Slopes of the regression lines for 14 species are shown to be insignificant from zero. For one species, bladder volume decreases slightly with increasing standard length. Volume of the swimbladder of a given species of given standard length can vary greatly as can the elevations and slopes of the regression lines for different fish species.

Brooks, A. L., & Saenger, R. A. (1991). Vertical Size-Depth Distribution Properties of Midwater Fish off Bermuda, with Comparative Reviews for Other Open Ocean Areas. *Canadian Journal of Fisheries and Aquatic Sciences*, 48(4), 694-721. <https://doi.org/10.1139/f91-086>

The nighttime (N) and daytime (D) size-depth distributions of mesopelagic fish at Ocean Acre, a typical deepwater site in the North Sargasso Sea, are described using archival discrete-depth data from the surface to about 1500-m. The N/D abundance distributions $n(z)$ for a representative group of 18 swimbladdered species indicate that fish are concentrated in the 0-150m euphotic zone at night and in the 400-1000m zone during the day in spring, summer, and winter. Seasonal succession in the average life stage size classes of the bladdered group occurs, but all classes are present year-round due to the variety of specific spawning patterns. The noncoincident N/D depth niches of individual bladdered species apparently are organized to reduce competition. Normalized N/D depth distributions for the bladdered group are similar throughout the year, and appear to be determined, respectively, by the N distribution of zooplankton biomass and the D underwater light field, other hydrographic variables having little direct influence. Also, it seems likely that the form of is relatively insensitive to species composition for such groups. These hypotheses are verified qualitatively by comparing specific and group distribution properties at other ocean sites with those at Ocean Acre.

Butler, J. L. (1970). *Swimbladder morphology and buoyancy of Northeastern Pacific myctophids*. (Master of Science (M.S.)), Oregon State University, Retrieved from <http://hdl.handle.net/1957/28990>

Of the common adult lanternfishes found off Oregon, two species have fat-invested swimbladders (Stenobrachius leucopsarus Eigenmann and Eigenmann 1890 and Stenobrachius nannochir Gilbert

1891), two species have reduced swimbladders (*Lampanyctus ritteri* Gilbert 1915 and *Lampanyctus galis* Gilbert 1891), two species have gas-filled swimbladders ((*Protomyctophum thompsoni* (Chapman 1944)) and (*Protomyctophum crockeri* (Bolin 1939)). Adult *Diaphus theta* Eigenmann and Eigenmann 1891 and adult *Tarletonbeania crenularis* Jordan and Gilbert 1880 however, have either gas-filled or reduced swimbladders. Small individuals of all the above species have gas-filled swimbladders. The primary buoyancy mechanism is lipids for large *S. leucopsarus*, *S. nannochir*, *L. ritteri* and *D. theta*, is reduction of dense material for large *L. regalis*, and is gas for all juveniles and for *P. thompsoni*, *P. crockeri* and some adult *T. crenularis* and *D. theta*.

Butler, J. L., & Pearcy, W. G. (1972). Swimbladder morphology and specific gravit of myctophids off Oregon. *Journal of the Fisheries Research Board of Canada*, 29(8), 1145-&. <https://doi.org/10.1139/f72-170>

Three general types of swimbladders were found in the eight species of myctophids studied: gas-filled, fat-invested, and atrophied or reduced. Small specimens of all species had thin-walled, gas-filled swimbladders. Large specimens of *Stenobrachius leucopsarus* had fat-invested swim-bladders and large *Diaphus theta* had either gas-filled or atrophied swimbladders, as found by other workers. Large *Tarletonbeania crenularis* had either gas-filled or reduced swimbladders, large *Lampanyctus ritteri* and *L. regalis* had reduced swimbladders, and large *Stenobrachius nannochir* had fat-invested swimbladders. *Protomyctophum thompsoni* and *P. crockeri* retained gas-filled swimbladders. High body lipid content was found in *S. leucopsarus*, *S. nannochir*, *L. ritteri* and *D. theta*, and low lipid content was found in the other four species. Myctophids with high lipid content had specific gravities close to that of sea water (1.026–1.030). *Tarletonbeania crenularis* with a reduced swimbladder had a specific gravity of 1.088. *Lampanyctus regalis* had a lower specific gravity (1.040) due to high water content of the tissue. The swimbladder to body volumes in *S. leucopsarus* and *D. theta* were inversely related to body size and lipid content, indicating that lipids assume the primary buoyancy function as the gas-filled swimbladder regresses with age. This change may eliminate the physiological constraints imposed by a gas-filled swimbladder and permit the more extensive diel vertical migrations of adults.

Carter, H. J., & Musick, J. A. (1985). Sexual Dimorphism in the Deep-Sea Fish *Barathrodemus manatinus* (Ophidiidae). *Copeia*, 1985(1), 69-73. <https://doi.org/10.2307/1444791>

Sexual dimorphism in the ophidiid *Barathrodemus manatinus* is found in the elements comprising the sound producing mechanism. Males possess well developed "drumming" muscles associated with the swimbladder, modified anterior vertebrae and a compressed attenuate body. Conversely, females lack these modifications, having relatively deeper, more robust bodies than males.

Castro, M. S., & Bonecker, A. C. T. (2017). Larval fish collected from sound-scattering layers in an offshore tropical area. *Journal of Fish Biology*, 91(6), 1668-1682. <https://doi.org/10.1111/jfb.13487>

The composition of the larval fish assemblage in the sound-scattering layer of the continental shelf waters off the coast of south-eastern Brazil (12 and 22 degrees S), a research project that is part of the Brazilian programme AvaliacAo do Potencial Sustentavel de Recursos Vivos na Zona Economica Exclusiva (REVIZEE), is described. Samples were collected during daylight hours and at dusk at five oceanographic

stations in the winter of 1999 using an Isaacs-Kidd Midwater Trawl (IKMT). The oceanographic stations were chosen based on the detection of plankton layers by acoustic observation. A total of 2192 larval fish were identified, comprising 52 families and 62 species. *Maurolicus stehmanni* (Sternopychidae) was the most abundant species found within the study area, comprising 185% of all identified larvae, followed by *Psilotris celsus* (Gobiidae) at 109%.

Catul, V., Gauns, M., & Karuppasamy, P. K. (2011). A review on mesopelagic fishes belonging to family Myctophidae. *Reviews in Fish Biology and Fisheries*, 21(3), 339-354.
<https://doi.org/10.1007/s11160-010-9176-4>

Myctophids are mesopelagic fishes belonging to family Myctophidae. They are represented by approx. 250 species in 33 genera. Called as “Lanternfishes”, they inhabit all oceans except the Arctic. They are well-known for exhibiting adaptations to oxygen minimum zones (OMZ-in the upper 2,000 m) and also performing diel vertical migration between the meso- and epipelagic regions. True to their name, lanternfishes possess glowing effect due to the presence of the photophores systematically arranged on their body, one of the important characteristic adding to their unique ecological features. Mid-water trawling is a conventional method of catching these fishes which usually accounts for biomass approx. in million tones as seen in Arabian Sea (20–100 million) or Southern ocean (70–200 million). Ecologically, myctophids link primary consumers like copepods, euphausiids and top predators like squids, whales and penguins in a typical food web. Lantern fishes become a major part of deep scattering layers (DSL) during migration along with other fauna such as euphausiids, medusae, fish juveniles, etc. Like any other marine organisms, Myctophids are susceptible to parasites like siphonostomatoid copepods, nematode larvae etc. in natural habitats. They are important contributors of organic carbon in the form of their remnants and fast sinking faeces, which get deposited on ocean beds. Economically, they are a good source of protein, lipids and minerals, which is used as fishmeal for poultry and animal feed and as crop fertilizers. Few species are considered edible, but proper processing difficulties on a higher scale limit myctophids as human food. Myctophids have a life span of approx. 1–5 years and low fecundity rates (100–2,000 eggs per spawn). This trait is a disadvantage, if continuous utilization of their population, for e.g., for fish meal industries etc., occurs without giving them a chance to revive and recover. Hence, research in this area also should be given utmost importance. In this paper, we have tried to compile information and ideas from various sources of myctophid research around the world, particularly from the Indian Ocean, to understand their ecological and economic importance and also to put forth new ideas to bring about conservation and restoration of this vulnerable resource.

Cherel, Y., Fontaine, C., Richard, P., & Labat, J. P. (2010). Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. *Limnology and Oceanography*, 55(1), 324-332.
<https://doi.org/10.4319/lo.2010.55.1.0324>

We report the trophic structure of a myctophid assemblage by measuring the isotopic niches of 14 species living in Kerguelen waters, southern Indian Ocean. Most of the species show distinct isotopic niches that differ by at least one of the two niche axes (delta C-13 habitat and delta N-15 trophic position), indicating trophic partitioning within the assemblage. Strong niche segregation occurs within each of the three most common genera of myctophids (Electrona, Gymnoscopelus, and Protomyctophum), illustrating the different mechanisms (habitat and dietary segregation) that allow coexistence of closely related species. Calculated trophic levels (TLs) of myctophids ranged from 3.3 to 4.2, showing that they are secondary and tertiary consumers in the pelagic ecosystem. The positive

relationship between TL and standard length of fish points out a structuring effect of size, with larger species (*Gymnoscopelus* spp.) occupying a higher trophic position than smaller species (*Krefftichthys anderssoni* and *Protomyctophum* spp.). Myctophids occupy an intermediate trophic position between macrozooplanktonic crustaceans and seabirds and marine mammals within the pelagic ecosystem. However, the TLs of large myctophids overlap those of crustacean-eating seabirds [e. g., *Eudyptes* spp. (crested penguins) and *Pachyptila belcheri*]. The isotopic niche of myctophids indicates that *Aptenodytes patagonicus* (king penguin) adults prey upon *K. anderssoni* when they feed for themselves, thus exemplifying the usefulness of isotopic datasets on potential prey of predators to depict trophic relationships.

Chow, S., Okazaki, M., Watanabe, T., Segawa, K., Yamamoto, T., Kurogi, H., . . . Miyake, Y. (2015). Light-Sensitive Vertical Migration of the Japanese Eel *Anguilla japonica* Revealed by Real-Time Tracking and Its Utilization for Geolocation. *PLoS ONE*, 10(4).
<https://doi.org/10.1371/journal.pone.0121801>

Short-time tracking (one to eight days) of the Japanese eel (*Anguilla japonica*) using ultrasonic transmitter was performed in the tropical-subtropical area adjacent to the spawning area and temperate area off the Japanese Archipelago. Of 16 eels (11 wild and five farmed) used, 10 wild eels displayed clear diel vertical migration (DVM) from the beginning, while the other five farmed eels tracked for 19 to 66 hours did not. During daytime, a significantly positive correlation between migration depth and light intensity recorded on the vessel was observed in the 10 wild eels, indicating that the eels were sensitive to sunlight even at the middle to lower mesopelagic zone (500 to 800 m). During nighttime, the eel migration depth was observed to be associated with the phase, rising and setting of the moon, indicating that the eels were sensitive to moonlight at the upper mesopelagic zone (<300 m). Two of 10 wild eels were in the yellow stage but shared similar DVM with the silver stage eels. Swimbladders of three silver stage eels were punctured before releasing, but very little effect on DVM was observed. The eels very punctually initiated descent upon nautical dawn and ascent upon sunset, enabling us to determine local times for sunrise and sunset, and hence this behavior may be used for geolocating eels. In fact, estimated positions of eels based on the depth trajectory data were comparable or even better than those obtained by light-based archival tag in other fish species.

Christiansen, H., Dettai, A., Heindler, F. M., Collins, M. A., Duhamel, G., Hautecoeur, M., . . . de Putte, A. P. V. (2018). Diversity of Mesopelagic Fishes in the Southern Ocean - A Phylogeographic Perspective Using DNA Barcoding. *Frontiers in Ecology and Evolution*, 6.
<https://doi.org/10.3389/fevo.2018.00120>

Small mesopelagic fish are ubiquitous in the ocean, representing an important trophic link between zooplankton and tertiary consumers such as larger fish, marine mammals and birds. Lanternfishes (Myctophidae) are common worldwide as well as in the Southern Ocean. However, only 17 of the approximately 250 myctophid species occur exclusively in sub-Antarctic or Antarctic waters. It is unclear whether they colonized these latitudes once and diversified from there, or whether multiple colonization events took place in which multiple ancestral phenotypes entered the Southern Ocean at various times. Phylogeographic patterns have been investigated for individual myctophid species, but so far no study has compared species across the Southern Ocean. Here, we present a dataset with previously unpublished cytochrome c oxidase I (COI; n = 299) and rhodopsin (rh1; n = 87) gene sequences from specimens collected at various locations in the Southern Ocean. Our data extend the

DNA barcode library of Antarctic mesopelagic fish substantially. Combined morphological and molecular taxonomy lead to confident species level identification in 271 out of 299 cases, providing a robust reference dataset for specimen identification, independently of incomplete morphological characters. This is highly topical in light of prospective ecological metabarcoding studies. Unambiguous sequences were subsequently combined with publicly available sequences of the global DNA barcode library yielding a dataset of over 1,000 individuals for phylogenetic and phylogeographic inference. Maximum likelihood trees were compared with results of recent studies and with the geographical origin of the samples. As expected for these markers, deep phylogenetic relationships remain partially unclear. However, COI offers unmatched sample and taxon coverage and our results at the subfamily to genus level concur to a large extent with other studies. Southern Ocean myctophids are from at least three distant subfamilies suggesting that colonization has occurred repeatedly. Overall, spatial divergence of myctophids is rare, potentially due to their enormous abundance and the homogenizing force of ocean currents. However, we highlight potential (pseudo-)cryptic or unrecognized species in *Gymnoscopelus bolini*, *Lampanyctus achirus*, and the non-myctophid genus *Bathylagus*.

Clavel-Henry, M., Piroddi, C., Quattrochi, F., Macias, D., & Christensen, V. (2020). Spatial Distribution and Abundance of Mesopelagic Fish Biomass in the Mediterranean Sea. *Frontiers in Marine Science*, 7. <https://doi.org/10.3389/fmars.2020.573986>

Mesopelagic fish, being in the middle of the trophic web, are important key species for the marine environment; yet limited knowledge exists about their biology and abundance. This is particularly true in the Mediterranean Sea where no regional assessment is currently undertaken regarding their biomass and/or distribution. This study evaluates spatial and temporal patterns of mesopelagic fish biomass in the 1994-2011 period. We do that for the whole Mediterranean Sea using two well-established statistical models, the Generalized Additive Model (GAM) and Random Forest (RF). Results indicate that the bathymetry played an important role in the estimation of mesopelagic fish biomass and in its temporal and spatial distribution. The average biomass over the whole time period reached 1.08 and 0.10 t/km², depending on the model considered. The Western Mediterranean and Ionian Seas were the subregions with the highest biomass, while the Adriatic was the area with the lowest. Temporal trends showed different trajectories with steep decrease and a fluctuation, using respectively RF and GAM. This study constitutes the first attempt to estimate the biomass and the spatial temporal patterns of mesopelagic fish using environmental variables as predictors. Given the growing interest in mesopelagic fish, our study sets a baseline to further develop mesopelagic fish biomass assessments in the region. Our results stress the need to improve data collection and quality in the region while identifying appropriate tools to better understand and assess the processes behind mesopelagic fish dynamics in the basin.

Collins, M. A., Stowasser, G., Fielding, S., Shreeve, R., Xavier, J. C., Venables, H. J., . . . Van de Putte, A. (2012). Latitudinal and bathymetric patterns in the distribution and abundance of mesopelagic fish in the Scotia Sea. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 59, 189-198. <https://doi.org/10.1016/j.dsr2.2011.07.003>

Mesopelagic fish are a key component of the pelagic ecosystem throughout the world's oceans. Opening and closing nets were used to investigate patterns in the distribution and abundance of mesopelagic fish from the surface to 1000 m on a series of transects across the Scotia Sea from the ice-edge to the Antarctic Polar Front. A total of 141 non-target net hauls were undertaken during three cruises (Nov

2006, Jan 2008 and Mar 2009), with 7852 teleost fish captured, representing 43 species in 17 families. A further 1517 fish were caught in targeted net hauls. The dominant families were the Myctophidae (6961 specimens: 21 species) and Bathylagidae (1467 specimens: 4 species). Few fish were caught in the upper 400 m during daylight, which was attributed to a combination of net avoidance and diurnal vertical migration. Species composition was linked to depth and location and was closely associated with oceanographic features. Diversity was lowest in cold water at the most southerly stations, which were dominated by *Electrona antarctica*, *Gymnoscopelus braueri* and *Bathylagus antarcticus*. Further north, diversity increased with the addition of species such as *Krefftichthys anderssoni*, *Protomyctophum bolini* and *Electrona carlsbergi*. The depth integrated biomass of myctophids was similar across the latitudinal transect and produced an estimate of 4.5 million tonnes in the Scotia Sea. Bathylagids were patchily distributed, but were abundant in the lower mesopelagic zone (> 400 m) and are potentially significant zooplankton consumers. Given the biomass of the myctophids and bathylagids coupled with the vertical migrations of many species, these fish are likely to play a significant role in carbon export from the surface waters to the deep ocean.

Collins, M. A., Xavier, J. C., Johnston, N. M., North, A. W., Enderlein, P., Tarling, G. A., . . . Cunningham, N. J. (2008). Patterns in the distribution of myctophid fish in the northern Scotia Sea ecosystem. *Polar Biology*, 31(7), 837-851. <https://doi.org/10.1007/s00300-008-0423-2>

The mesopelagic fish community of the northern Scotia Sea was investigated during the austral autumn using multi-frequency acoustics, opening and closing nets and pelagic trawls fished from the surface to 1,000 m. The Family Myctophidae (15 species in 5 genera) dominated the ichthyofauna, with larval notothenids caught over the South Georgia shelf and bathylagids and stomiids abundant in deeper hauls. The biomass of myctophids was estimated to be 2.93 g wet weight 1,000 m(-3), with *Electrona carlsbergi*, *E. antarctica*, *Protomyctophum bolini*, *P. choriodon*, *Gymnoscopelus braueri*, *G. fraseri*, *G. nicholsi* and *Krefftichthys anderssoni*, being the most abundant species. Analysis of community structure indicated a high level of depth stratification within the myctophids, with evidence of diurnal vertical migration in some, but not all, species. Length-frequencies of *G. braueri*, *G. nicholsi*, *E. antarctica* and *K. anderssoni* were multimodal, suggesting that all life stages may be present in the northern Scotia Sea. In contrast, *P. choriodon*, *P. bolini*, *G. fraseri* and *E. carlsbergi* had unimodal distributions despite having multi-year lifecycles, indicating that they probably migrate into the region from warmer areas to the north.

Coombs, R. F., & Barr, R. (2004). Acoustic remote sensing of swimbladder orientation and species mix in the oreo population on the Chatham Rise. *The Journal of the Acoustical Society of America*, 115(4), 1516-1524. <https://doi.org/10.1121/1.1649998>

A method for combining in situ measurements and theoretical swimbladder-derived estimates of target strength of the deep-water fish, black and smooth oreos, is described. The technique uses Monte Carlo simulation and yields fish length–target strength relationships suitable for use in estimating biomass from echo integration acoustic surveys. The relationships are derived from estimates of the mean and standard deviation of the tilt angle distributions of the wild fish generated by the method. The relationships may also be used to estimate proportions of the two oreo species in the wild. The mean tilt angle of black oreos in the wild was about 10° with a standard deviation of 8°. For smooth oreos it was close to zero with a standard deviation of about 4°. The target strength relationships derived for biomass estimation purposes were $TSB = -78.05 + 25.3 \log_{10}(L) + 1.62 \sin(0.0815L + 0.238)$ and

$TSS = -82.16 + 24.6 \log_{10}(L) + 1.03 \sin(0.1165L - 1.765)$, where L is the fish length and TSB and TSS are the target strengths of black and smooth oreos respectively.

D'Aoust, B. (1970). *Physiological Constraints on Vertical Migration by Mesopelagic Fishes*. Paper presented at the International Symposium on Biological Sound Scattering in the Ocean, Warrenton, VA. Retrieved from <https://babel.hathitrust.org/cgi/pt?id=mdp.39015001558512&view=1up&seq=102>

The major factor limiting the extent and rate of upward excursion by mesopelagic fishes is the rate at which gas can be removed from the swimbladder. Downward migration carries only the burden of additional physical work of gas secretion and overcoming decreased buoyancy, whereas (depending on the size of the swimbladder) too rapid ascent involves the risk of embolism. Using simple decompression models of bubble resolution and considering present knowledge of swimbladder physiology, maximum possible rates of ascent are calculated for hypothetical fishes of different sizes over a range of initial:final pressure ratios. Exceptions to the predicted limits are noted and discussed and the ecological advantage of a swimbladder to such species is considered.

D'Elia, M., Warren, J. D., Rodriguez-Pinto, I., Sutton, T. T., Cook, A., & Boswell, K. M. (2016). Diel variation in the vertical distribution of deep-water scattering layers in the Gulf of Mexico. *Deep-Sea Research Part I-Oceanographic Research Papers*, 115, 91-102. <https://doi.org/10.1016/j.dsr.2016.05.014>

Sound scattering layers (SSLs) are important components of oceanic ecosystems with ubiquitous distribution throughout the world's oceans. This vertical movement is an important mechanism for exchanging organic matter from the surface to the deep ocean, as many of the organisms comprising SSLs serve as prey resources for linking the lower trophic levels to larger predators. Variations in abundance and taxonomic composition of mesopelagic organisms were quantified using repeated discrete net sampling and acoustics over a 30-h survey, performed during 26-27 June 2011 at single site (27 degrees 28'51 " N and 88 degrees 27'54 " W) in the northern Gulf of Mexico. We acoustically classified the mesopelagic SSL into four broad taxonomic categories, crustacean and small non-swimbladdered fish (CSNSBF), large non-swimbladdered fish (LNSBF), swimbladdered fish (SBF) and unclassified and we quantified the abundance of mesopelagic organisms over three discrete depth intervals; epipelagic (0-200 m); upper mesopelagic (200-600 m) and lower mesopelagic (600-1000 m). Irrespective of the acoustic categories at dusk part of the acoustic energy redistributed from the mesopelagic into the upper epipelagic (shallower than 100 m) remaining however below the thermocline depth. At night higher variability in species composition was observed between 100 and 200 m suggested that a redistribution of organisms may also occur within the upper portion of the water column. Along the upper mesopelagic backscatter spectra from CSNSBF migrated between 400 and 460 m while spectra from the other categories moved to shallower depths (300 and 350 m), resulting in habitat separation from CSNSBF. Relatively small vertical changes in both acoustic backscatter and center of mass metrics of the deep mesopelagic were observed for CNSBF and LNSBF suggesting that these animals may be tightly connected to deeper (below 1000 m) mesopelagic habitats, and do not routinely migrate into the epipelagic.

Davison, P. C., Koslow, J. A., & Kloser, R. J. (2015). Acoustic biomass estimation of mesopelagic fish: backscattering from individuals, populations, and communities. *ICES Journal of Marine Science*, 72(5), 1413-1424. <https://doi.org/10.1093/icesjms/fsv023>

Acoustic survey methods are useful to estimate the distribution, abundance, and biomass of mesopelagic fish, a key component of open ocean ecosystems. However, mesopelagic fish pose several challenges for acoustic biomass estimation based on their small size, wide depth range, mixed aggregations, and length-dependent acoustic reflectance, which differentiate them from the larger epipelagic and neritic fish for which these methods were developed. Foremost, there is a strong effect of depth on swimbladder resonance, so acoustic surveys of mesopelagic fish must incorporate depth-stratification. Additionally, the 1-3 cm juveniles of many species are not only more abundant, but can also be stronger acoustic backscatterers than the larger adults that comprise most of the biomass. The dominant species in terms of biomass may thus be weak acoustic backscatters. Failure to properly incorporate depth, the full size distribution, and certain less-abundant species into mesopelagic acoustic analyses could lead to errors in estimated biomass of up to three orders of magnitude. Thus, thorough validation, or "ground-truthing", of the species composition, depth structure, population size distribution, capture efficiency of the sampling device, and acoustic properties of the fish present is critical for credible acoustic estimates of mesopelagic fish biomass. This is not insurmountable, but requires more ancillary data than is usually collected.

Deng, X. (2009). *Comparative studies on the structure of the ears of deep-sea fishes*. University of Maryland, College Park, MD. Retrieved from <http://hdl.handle.net/1903/9491>

Many deep-sea fishes have sensory adaptations for living at great depths with very limited light. While such adaptations are best known in the visual system, it is likely that there are also adaptations in the auditory system that enable deep-sea fishes to use the "auditory scene." However, there are few data on the inner ear of deep-sea fishes. The purpose of this study was to add to those data. Since deep-sea fishes are rarely taken alive, this study was done through comparative anatomical investigations. Three families were chosen from two major deep-sea fish fauna: benthopelagic and mesopelagic. In *Antimora rostrata* (family Moridae, deep-sea cods), the inner ear structure and its coupling to the swim bladder were analyzed and compared with similar systems found in shallow-water fishes. Part of the membrane labyrinth is thick and rigid. The elaborate structure of the saccular epithelium and the close contact between the ear and swim bladder suggests enhanced hearing sensitivity. In the family Melamphaidae (bigscales and ridgeheads), five species from three genera show broad interspecific variation in the saccular otolith shapes, including having a long otolithic "stalk" in two genera. The presence of this "stalk" corresponds with a gradual change in the saccular maculae. A special type of ciliary bundle on the saccule may have enhanced sensitivity to bundle displacements. Ears were compared between six species of Macrouridae (grenadiers and rattails) that live at different depths. The saccule/lagena size ratio seems to increase with depth, especially between a mesopelagic and a benthopelagic species in the genus *Nezumia*, in which the benthopelagic species has an enlarged saccule associated with sound production. These findings support the hypothesis that some deep-sea fishes have evolved specializations for inner ear function. While it is not possible to test hearing in deep-sea fishes, the various adaptations found suggest that at least some such species have evolved specialized structures to enable them to use sound in the deep-sea. Some features in the ears of deep-sea fishes that have never been seen in the ears of other vertebrates, which further reveals the structural diversity of fish inner ears in general.

Deng, X., Wagner, H.-J., & Popper, A. N. (2011). The inner ear and its coupling to the swim bladder in the deep-sea fish *Antimora rostrata* (Teleostei: Moridae). *Deep Sea Research Part I: Oceanographic Research Papers*, 58(1), 27-37. <https://doi.org/10.1016/j.dsr.2010.11.001>

The inner ear structure of *Antimora rostrata* and its coupling to the swim bladder were analyzed and compared with the inner ears of several shallow-water species that also have similar coupling. The inner ear of *Antimora* has a long saccular otolith and sensory epithelium as compared to many other fishes. Some parts of the membranous labyrinth are thick and rigid, while other parts are thinner but attached tightly to the bony capsule. The partially rigid membranous labyrinth, along with its intimate connection to the swim bladder, may help the inner ear follow the sound oscillations from the swim bladder with better precision than would occur in a less rigid inner ear. In addition, the saccular sensory epithelium has an elaborate structure and an anterior enlargement that may be correlated with increased hearing sensitivity. Some of the features in the inner ear of *Antimora* may reflect the functional specialization of deep-water living and support the hypothesis that there is enhanced inner ear sensitivity in some deep-sea fishes.

Denton, E. J., & Marshall, N. B. (1958). The buoyancy of bathypelagic fishes without a gas-filled swimbladder. *Journal of the Marine Biological Association of the United Kingdom*, 37(3), 753-767. <https://doi.org/10.1017/S0025315400005750>

The upper reaches of the deep ocean contain many bathypelagic fishes with a capacious, gas-filled swimbladder. But living within and below this region are also numerous species in which this hydrostatic organ is absent or markedly regressed (Marshall, in preparation). In the neritic province nearly all the fishes that swim freely at the various water levels (and can stay poised at a particular level without undue effort) have a well-developed swimbladder, the capacity of which is about equal to 5 % of the body volume (Jones & Marshall, 1953). Having this amount of gas, these fishes are able to keep their weight in water close to the vanishing point. If such a fish were deprived of its swimbladder, it could keep at a constant level only by exerting a down-ward force equivalent to 5 % of its weight in air. The swimbladder thus saves the fish the energy needed for such effort, which is quite appreciable.

DeWitt, F. A. (1972). Bathymetric Distributions of Two Common Deep-Sea Fishes, *Cyclothona acclinidens* and *C. signata*, off Southern California. *Copeia*, 1972(1), 88-96. <https://doi.org/10.2307/1442785>

The deep-sea fishes *Cyclothona acclinidens* and *C. signata* were sampled by trawl from the bathypelagic and mesopelagic zones, respectively, off Santa Barbara, California. Few adults of *C. acclinidens* were captured near shore in the relatively shallow Santa Barbara Basin. Morphologically, these two bristlemouths differ in accordance with their respective adaptations to deep and shallow habitats. Adults of *C. acclinidens* resemble typical bathypelagic fishes in that they have black skin, a non-pneumatic swimbladder invested with fat, a feeding mechanism adapted to capture a relatively wide variety of prey, and large gills for increased oxygen uptake in an oxygen-minimum layer. Individuals of *C. signata* have a pneumatic swimbladder and a feeding mechanism adapted to select relatively small prey from dense concentrations of zooplankton. Unlike many mesopelagic fishes, however, *C. signata* is not countershaded or strongly counterlighted, but is disruptively colored and probably camouflaged even in well-lighted waters near the surface. The mesopelagic young of *C. acclinidens* resemble *C. signata* in coloration. Bathymetric distributions of catch per unit effort varied little for either species between day and night. Likewise, there was no significant difference in the patchiness of their distributions between

day and night. Therefore, they probably do not regularly ascend toward the surface at night, as do many mesopelagic fishes. *C. signata* captures were distributed bimodally, with abundance maxima at the shallow and deep extremes of the mesopelagic zone. Therefore, individuals of *C. signata* may indeed commute between the cool and dark deep waters and the food-rich surface waters, but at irregular intervals.

Diachok, O. (2001). Interpretation of the spectra of energy scattered by dispersed anchovies. *The Journal of the Acoustical Society of America*, 110(6), 2917-2923. <https://doi.org/10.1121/1.1413996>

The spectra of backscattered energy by dispersed anchovies, which were reported by Holliday (1972), reveal several peaks at frequencies that correspond to theoretically calculated resonance frequencies of year classes of anchovies. Theoretical calculations are based on concurrent measurements of distributions of swim bladder dimensions and a modified form of Minnaert's (1933) equation.

Differences between calculated and measured values of the mean lengths of the second-, third-, and fourth-year classes are within experimental uncertainties ($\pm 8\%$). The calculated mean lengths of juvenile anchovies are in good agreement with historical measurements of the bounds on this parameter (Butler, 1989). Matching of theoretical calculations and measurements of backscattered energy level versus frequency yields estimates of the total Q of the spectral line, QT , and the relative number density per year class. The resultant estimate of QT of adult anchovies is approximately 4.4. This value of QT is consistent with laboratory measurements of the Q of individual anchovies, Q_0 (~ 7 at 15 m) and measurements of length distributions of year classes and depth distributions. Resultant estimates of relative number densities of year classes were consistent with historical measurements of the relative number densities of year classes of anchovies in the Southern California Bight.

Do, M. A., & Surti, A. M. (1990). Estimation of dorsal aspect target strength of deep-water fish using a simple model of swimbladder backscattering. *The Journal of the Acoustical Society of America*, 87(4), 1588-1596. <https://doi.org/10.1121/1.399406>

A practical model for estimating target strength of gas-filled swimbladdered fish is described using the scattering function of a finite cylinder. Two equivalent cylinders are derived from measurements of swimbladder length, surface area, and volume. The scattering functions of both equivalent cylinders were tested using data available for gadoids, then applied in the estimation of target strength of deep-water hoki (*Macruronus novaezealandie*). Molds of 23 hoki swimbladders were constructed for measurements of their internal dimensions. Estimates of target strength using the scattering function of the equivalent surface area cylinder agree closely with estimates by other methods for gadoids. Estimates using the scattering function of the equivalent volume cylinder are lower, but approach the former estimates when the swimbladders are fully inflated. The advantage of using the latter method is the simplicity in measuring the swimbladder volume. The dorsal aspect target strength of hoki were estimated at four frequencies, 38, 49, 70, and 120 kHz for several distribution functions of fish tilt angle.

Dornan, T. (2019). *Southern Ocean mesopelagic fish: Scales, drivers and the effects of environmental variability*. (Doctor of Philosophy), University of Bristol, Bristol, UK. Retrieved from https://research-information.bris.ac.uk/ws/portalfiles/portal/225124456/PhD_TDornan_RedactedFINAL.pdf

In the Southern Ocean, the mesopelagic zone 200 – 1000 m below sea level holds vast resources of fish, yet they remain one of the least investigated components of the Antarctic ecosystem. Sampling challenges have led to considerable uncertainty regarding mesopelagic fish biomass, limiting our ability to monitor populations or quantify their contribution to ecosystem function. Active acoustic methods, where pulses of sound are transmitted into the water column and the “backscattered” signal from organisms are detected by a transducer, enable us to sample the water column at greater spatial and temporal scales than conventional net sampling. However, to reliably interpret acoustic data we require information on the species present and their acoustic properties, which has been lacking for the Southern Ocean region. In this thesis I document the use of X-ray computed tomography scans to clarify swimbladder morphology of members of the mesopelagic fish community. I report a switch from fish possessing gas-filled swimbladders that contribute strongly to backscatter at low latitudes, to fish lacking gas-filled swimbladders at high latitudes. This contributes to the ubiquitous southward decline in acoustic backscatter that contrasts with latitudinal biomass patterns recorded from net samples. Patterns in acoustic data indicate that diel vertical migration of fish may be suppressed at high latitudes, which has implications for biogeochemical cycling. Acoustic backscatter was strongly related to sea surface temperature, daylight hours and sea ice extent. These relationships, coupled with taxon-specific calculations of acoustic Target Strength, yielded Southern Ocean mesopelagic fish biomass estimates considerably greater than previous net-based estimates. Overall, these findings indicate that knowledge of the acoustic properties of mesopelagic species, alongside core information on their relative abundance in the environment, can enable active acoustic data to become a powerful tool for researching, monitoring and managing the Southern Ocean ecosystem.

Duhamel, G., Chazeau, C., & Sinegre, R. (2017). The benthic and pelagic phases of *Muraenolepis marmorata* (Muraenolepididae) off the Kerguelen Plateau (Indian sector of the Southern Ocean). *Cybium*, 41(4), 303-316. <https://doi.org/10.26028/10.26028/cybium/2017-414-001>

Muraenolepis marmorata life cycle is poorly investigated. This benthic species occurs mainly on the shelf slope and deep-sea as juvenile and adult stages but its early life is strictly pelagic off the Kerguelen Plateau. The upper layers (0-500 m) of the pelagic waters off the shelf are used by fingerlings both day and night during summertime. Dense aggregations (swarms) are sometimes observed by echo sounder (gas swim bladder detection) then have been confirmed by midwater trawl sampling. Fingerlings reach the size of about 55 mm before disappearing (ontogenetic migration to the bottom) from the pelagic catches in autumn. *M. marmorata* and the myctophid *Krefftichthys anderssoni* are the only species to be present during the day in the upper layers of the water column off the Kerguelen Plateau. *M. marmorata* becomes a prey for top predators such as king penguins (*Aptenodytes patagonicus*) in their known depth diving range of their foraging area. Strong interannual variations in density of fingerlings are noted. The biomass of *M. marmorata*, evaluated in the bathymetric range 100-1000 m, was about 300 tonnes, which places the species at the 17th rank of the 19 demersal species occurring on the shelf and slope of the Kerguelen Islands.

Duhamel, G., Koubbi, P., & Ravier, C. (2000). Day and night mesopelagic fish assemblages off the Kerguelen Islands (Southern Ocean). *Polar Biology*, 23(2), 106-112.
<https://doi.org/10.1007/s003000050015>

Mesopelagic fish assemblages were investigated in the Polar Frontal Zone off the Kerguelen Islands during summer 1995, in parallel with a king penguin tracking study. During the day, the upper offshore water layers (0-200 m) have low potential prey diversity and abundance with only three fish species: a lanternfish, Krefftichthys anderssoni, a member of the Muraenolepididae, Muraenolepis marmoratus, and the early stages of the nototheniid, Lepidonotothen squamifrons. The mesopelagic fish community, including the typical myctophids, first appears in the deeper layer (300 m). At night, the surface layer (50 m) is invaded by the mesopelagic Myctophidae Electrona antarctica, Gymnoscopelus braueri, G. piabilis, G. fraseri, G. nicholsi, Protomyctophum bolini and P. tenisoni. Deeper (> 100 m), a diene of species assemblages from the coast to offshore is observed.

Escobar-Flores, P. C., Ladroit, Y., & O'Driscoll, R. L. (2019). Acoustic Assessment of the Micronekton Community on the Chatham Rise, New Zealand, Using a Semi-Automated Approach. *Frontiers in Marine Science*, 6(507). <https://doi.org/10.3389/fmars.2019.00507>

Micronekton are a key component of the pelagic food web of the Chatham Rise east of New Zealand. The Chatham Rise is an important fishing area for hoki (Macruronus novaezelandiae), New Zealand's largest finfish fishery, and a predator on mesopelagic fish. Four fisheries oceanographic voyages provided multi-frequency acoustic data (18, 38, 70, 120, and 200 kHz) and midwater trawls, which were used to define a classification tree to separate micronektonic organisms. We carried out validation and sensitivity analyses that showed that we were able to classify pearlside (*Maurolicus australis*) and euphausiids. Other mesopelagic targets (mainly myctophids) were classified together based on their acoustic frequency response. Using scripting in the open-source software ESP3, we applied our classification tree to an independent time series of acoustic data from trawl surveys on the Chatham Rise between 2009 and 2018, that was not used for model development or validation. Our methodology allowed us to study temporal and spatial patterns of *M. australis*, euphausiids, and total backscatter in the water column. Total backscatter associated with micronekton has varied over the last 10 years, with no clear trend. The abundance of euphausiids showed a significant decreasing trend over the last 10 years. Abundance of *M. australis* also decreased since 2012, though this was not significant. This work contributes to on-going efforts to monitor and detect changes in the pelagic ecosystems.

Escobar-Flores, P. C., O'Driscoll, R. L., & Montgomery, J. C. (2018). Predicting distribution and relative abundance of mid-trophic level organisms using oceanographic parameters and acoustic backscatter. *Marine Ecology Progress Series*, 592, 37-56. <https://doi.org/10.3354/meps12519>

Data on the distribution and abundance of mid-trophic level organisms (MTLOs) in the pelagic open-ocean ecosystem are normally sparse or absent. Consequently, ecosystem models are limited in their ability to support decision-making for issues ranging from fisheries management to ecosystem resilience to climate change. We used acoustic data collected at 38 kHz frequency across the Southern Ocean (SO) between 2008 and 2014 to develop explanatory and predictive models for acoustic backscatter, a proxy for MTLO abundance in the epi- and mesopelagic zones. Boosted regression trees and generalised additive mixed models were used to develop simple predictive models for backscatter in the epi- and mesopelagic zones, using sea surface temperature, time of day (day/night) and depth. The resulting

models predicted backscatter reasonably well in the Pacific sector of the SO, and in an independent dataset in the Indian sector of the SO. Our predictive models may provide a tool for inferring abundance and distribution of MTLOs in other parts of the SO.

Escobar-Flores, P. C., O'Driscoll, R. L., Montgomery, J. C., Ladroit, Y., & Jendersie, S. (2020). Estimates of density of mesopelagic fish in the Southern Ocean derived from bulk acoustic data collected by ships of opportunity. *Polar Biology*, 43(1), 43-61. <https://doi.org/10.1007/s00300-019-02611-3>

The demand for information on mid-trophic level (MTL) organisms in open-ocean marine ecosystems has led to initiatives to collect acoustic data opportunistically in different regions around the world. Although, bulk acoustic data can provide information on the distribution patterns and dynamics of MTL organisms, it is necessary to convert acoustic-derived indices into biologically relevant quantities for parameterising and validating ecosystem and trophic models. A 7-year time series of acoustic data collected by ships of opportunity (SOOP) in the New Zealand sector of the Southern Ocean, information on species' distribution derived from trawl samples collected in research voyages, and target strength (TS) estimates obtained using a resonance-scattering model and literature TS-length relationships, were used to obtain the first estimates of density of mesopelagic fish in this region. Estimates of mesopelagic fish density decreased from north to south reflecting changes in species composition and scattering properties across three latitudinal regions (Northern, Central and Southern). Density estimates ranged from 16.4-40.1 in the north to 4.4-13.4 g m⁻² in the south. Catches revealed that the Northern region was dominated by Lampanyctodes hectoris and Protomyctophum sp. (Myctophidae) and Maurolicus australis (Sternopychidae); the Central and Southern regions were dominated by the myctophids Electrona antarctica and Protomyctophum sp. and the Antarctic krill, Euphausia superba. Information on species composition was the main source of uncertainty in the density estimates, highlighting the need for more biological sampling. This study demonstrates that it is possible to integrate acoustic data collected opportunistically with auxiliary information from research voyages and literature to provide estimates of mesopelagic fish biomass in remote areas.

Flynn, A. J., & Williams, A. (2012). Lanternfish (Pisces: Myctophidae) biomass distribution and oceanographic-topographic associations at Macquarie Island, Southern Ocean. *Marine and Freshwater Research*, 63(3), 251-263. <https://doi.org/10.1071/mf11163>

Lanternfishes, which are important prey for demersal and diving predators at Macquarie Island in the Southern Ocean, have spatial patterns of distribution over the Macquarie Ridge that suggest biomass is enhanced where the Subantarctic Front (SAF) interacts with a break in the topography of the Ridge (the 'Ridge Gap'). The summertime lanternfish assemblage, documented here for the first time, comprised 23 taxa, dominated by Krefftichthys anderssoni and Gymnoscopelus braueri. Mean lanternfish biomass was highest (3.13 g 1000 m⁻³) in the Ridge Gap habitat. Lowest mean biomass (0.71 g 1000 m⁻³) was recorded up-current of the SAF over the Abyssal Plain and intermediate biomass (1.26 g 1000 m⁻³) was recorded over the Macquarie Ridge. At Ridge Gap, a high abundance of K. anderssoni was recorded in the shallowest stratum (0-250 m) during the day. We hypothesised that the oceanographic-topographic interaction between the SAF and Ridge Gap creates eddy systems and productivity fronts that passively entrain and/or actively attract lanternfishes to the Ridge Gap area. This oceanographic-topographic interaction depends on the spatial stability of the SAF in relation to the Macquarie Ridge and Ridge Gap and is vulnerable to climate-mediated change that may have flow-on effects to predators with commercial and conservation significance.

Foote, K. G. (1980). Importance of the swimbladder in acoustic scattering by fish - a comparison of gadoid and mackerel target strengths. *Journal of the Acoustical Society of America*, 67(6), 2084-2089. <https://doi.org/10.1121/1.384452>

Previous determinations of the swimbladder contribution to the fish backscattering cross section have been hindered by ignorance of the acoustic boundary conditions at the swimbladder wall. The present study circumvents this problem by direct comparison of target strengths of three gadoid species and mackerel- anatomically comparable fusiform fish which respectively possess and lack a swimbladder. The relative swimbladder contribution to both maximum and averaged dorsal aspect backscattering cross sections is shown to be approximately 90% to 95%, which is higher than most other estimates. The new results were established for fish of 29- to 42-cm length and acoustic frequencies of 38 and 120 kHz.

Foote, K. G. (2001). Acoustic Scattering by Marine Organisms. In *Encyclopedia of Ocean Sciences*. J. H. Steele (Ed.), (pp. 44-53). Oxford: Academic Press <https://doi.org/10.1006/rwos.2001.0311>

No abstract available.

Freer, J. J., Tarling, G. A., Collins, M. A., Partridge, J. C., & Genner, M. J. (2019). Predicting future distributions of lanternfish, a significant ecological resource within the Southern Ocean. *Diversity and Distributions*, 25(8), 1259-1272. <https://doi.org/10.1111/ddi.12934>

Aim: Lanternfish (Myctophidae) are one of the most abundant and ecologically important families of pelagic teleosts, yet how these species will respond to climate change is unclear, especially within polar regions. The aim of this study was to predict the impact of climate change on the distribution of Southern Ocean lanternfish and to relate these predicted responses to species traits. **Location:** Circumpolar, 35-75 degrees S. **Methods:** We used MaxEnt ecological niche models to estimate the present and predict the future distributions of 10 biomass-dominant lanternfish species throughout the region. Future conditions were simulated using eight climate models, in both stabilizing (RCP 4.5) and rising (RCP 8.5) emission scenarios, for the time periods 2006-2055 and 2050-2099. Species responses were then related to their realized thermal niche (i.e., thermal tolerance range), latitudinal preference and body size. **Results:** Despite large variation between climate model simulations, all but one species are consistently predicted to undergo a poleward distribution shift. Species show contrasting projections relating to a gain or loss of suitable habitat which was best explained by their thermal niche. Overall, high-latitude Antarctic species were found to have narrower thermal niches and a higher likelihood of losing habitat than sub-Antarctic species. **Main conclusions:** The direction of a species response was dependent on the interplay between physiology (realized thermal niche) and biogeography (latitudinal preference). Antarctic species with restricted thermal niches and limited available habitat in which to disperse will be the most vulnerable group of Southern Ocean lanternfish in the face of climate change. Predicted range shifts may alter the size structure of the myctophid community as smaller, sub-Antarctic species reach further south. This could have implications for trophic interactions and thus the wider Southern Ocean ecosystem.

Frouzova, J., Kubecka, J., & Mrkvicka, T. (2011). Differences in acoustic target strength pattern between fish with one- and two-chambered swimbladder during rotation in the horizontal plane. *Fisheries Research*, 109(1), 114-118. <https://doi.org/10.1016/j.fishres.2011.01.026>

Pattern of target strength (TS) during 360 degrees rotation in the horizontal plane was studied for six common European fish species: brown trout (*Salmo trutta*), perch (*Perca fluviatilis*) bream (*Abramis brama*), roach (*Rutilus rutilus*), carp (*Cyprinus carpio*), and bleak (*Alburnus alburnus*). Trout and perch have one-chambered swimbladders, and the other species have two-chambered swimbladders. In general, the lowest TS was recorded when the head or tail faced the sonar beam and the highest values when the side was perpendicular to the sonar beam. The TS distribution differed between fish with one- and two-chambered swimbladders. For two-chambered fish, the TS transition between minima and maxima was linear, and the median of the TS value was similar to the mean. For one-chambered fish, TS distribution was skewed and the median TS was considerably smaller than the mean. The relationship between TS and fish aspect relative to the sonar beam, can be described by a linear model for fish with two-chambered swimbladders and by a quadratic model for fish with one-chambered swimbladders. This study provides new general equations for modeling the dependence of TS on any body aspect in the horizontal plane as well as equations for common European fish species.

Fujino, T., Sadayasu, K., Abe, K., Kidokoro, H., Tian, Y., Yasuma, H., & Miyashita, K. (2009). Swimbladder Morphology and Target Strength of a Mesopelagic Fish, *Maurolicus japonicus*. *The Journal of the Marine Acoustics Society of Japan*, 36(4), 241-249. <https://doi.org/10.3135/jmasj.36.241>

The relationship of target strength (TS), tilt angle and the effect of swimbladder resonance were examined using a theoretical scattering model for *Maurolicus japonicus* (30.4-46.8 mm standard length (SL)) at 38 kHz and 120 kHz, based on swimbladder measurements. The effect of tilt angle on TS was seen at 120 kHz, but was minimal at 38 kHz. The effect of resonance on TS was clear at 38 kHz, but was minimal at 120 kHz. This was due to the small size (average 11 % of SL) and oval shape with a relatively high aspect ratio (average 0.48) of the swimbladder. Considering the effect of resonance, the TS-SL relationships at 38 kHz were estimated: $TS = 10.0 \log_{10}SL - 61.3$ at 200 m depth. Considering the effect of tilt angle, the average TS (TSavg) -SL relationship at 120 kHz was estimated: $TSavg = 16.5 \log_{10}SL - 75.1$.

Gallet, A., Koubbi, P., Leger, N., Scheifler, M., Ruiz-Rodriguez, M., Suzuki, M. T., . . . Duperron, S. (2019). Low-diversity bacterial microbiota in Southern Ocean representatives of lanternfish genera *Electrona*, *Protomyctophum* and *Gymnoscopelus* (family Myctophidae). *PLoS ONE*, 14(12). <https://doi.org/10.1371/journal.pone.0226159>

Myctophids are among the most abundant mesopelagic teleost fishes worldwide. They are dominant in the Southern Ocean, an extreme environment where they are important both as consumers of zooplankton as well as food items for larger predators. Various studies have investigated myctophids diet, but no data is yet available regarding their associated microbiota, despite that the significance of bacterial communities to fish health and adaptation is increasingly acknowledged. In order to document microbiota in key fish groups from the Southern Ocean, the bacterial communities associated with the gut, fin, gills and light organs of members of six species within the three myctophid genera *Electrona*, *Protomyctophum* and *Gymnoscopelus* were characterized using a 16S rRNA-based metabarcoding approach. Gut communities display limited diversity of mostly fish-specific lineages likely involved in

food processing. Fin and skin communities display diversity levels and compositions resembling more those found in surrounding seawater. Community compositions are similar between genera *Electrona* and *Protomyctophum*, that differ from those found in *Gymnoscopelus* and in water. Low abundances of potentially light-emitting bacteria in light organs support the hypothesis of host production of light. This first description of myctophid-associated microbiota, and among the first on fish from the Southern Ocean, emphasizes the need to extend microbiome research beyond economically-important species, and start addressing ecologically-relevant species.

Gaskett, A. C., Bulman, C., He, X., & Goldsworthy, S. D. (2001). Diet composition and guild structure of mesopelagic and bathypelagic fishes near Macquarie Island, Australia. *New Zealand Journal of Marine and Freshwater Research*, 35(3), 469-476.
<https://doi.org/10.1080/00288330.2001.9517016>

Mesopelagic (200-1000 m) and bathypelagic (>1000 m) fish near Macquarie Island, Australia, are important in the diets of seals, seabirds, and Patagonian toothfish. They also form important links between the productivity at shallow and deeper water depths. Here we analyse the diets of 23 fish species, 13 of which are from the family Myctophidae from 254 stomach samples. Crustaceans (particularly copepods, amphipods, and euphausiids) were the dominant prey in 18 species. Fishes were the dominant prey in five species. Further analysis showed that five of the 13 myctophid fishes had a low level of similarity in diet composition between individuals of each species, whereas the other eight species had significantly high levels of similarity. Cluster analysis and randomisation procedures suggested the existence of five trophic guilds among the Myctophidae.

Gastauer, S., Scoulding, B., Fässler, S. M. M., Benden, D. P. L. D., & Parsons, M. (2016). Target strength estimates of red emperor (*Lutjanus sebae*) with Bayesian parameter calibration. *Aquatic Living Resources*, 29(3). <https://doi.org/10.1051/alar/2016024>

Red emperor (*Lutjanus sebae*) is a long-lived tropical demersal snapper which is widely distributed in the Western Pacific and Indian Ocean. Despite the commercial and recreational importance of the species for the Northern Demersal Scalefish Fishery off the Northwest coast of Western Australia, we still lack a thorough understanding of its distribution and abundance in the area. To better understand the acoustic scattering properties of red emperor its acoustic backscattering characteristics were modelled based on swimbladder and body morphology, determined using computed tomography scans. A Kirchhoff-ray mode approximation was coupled with empirical (ex situ) measurements of target strength (TS) obtained from a 38 and 120 kHz split-beam echosounder on board a fishing vessel. Bayesian methods were used for model parameter calibration, which provided uncertainty estimates for some of the TS-model parameters. The derived TS-length relationships were $19.7 \log 10(L) - 75.5$ (C.I. 5.9 dB) at 120 kHz and $14.6 \log 10(L) - 64.9$ (C.I. 5.8 dB) at 38 kHz. The study demonstrated that small commercial fishing vessels can be used to conduct ex situ experiments and target strength modelling can be effectively based on computer tomography scans. This relatively low cost approach could be applied to other species.

Gauthier, S., Oeffner, J., & O'Driscoll, R. L. (2014). Species composition and acoustic signatures of mesopelagic organisms in a subtropical convergence zone, the New Zealand Chatham Rise. *Marine Ecology Progress Series*, 503, 23-40. <https://doi.org/10.3354/meps10731>

The Chatham Rise is a submarine ridge east of New Zealand. The subtropical convergence occurs over this ridge and it is an area of high productivity, associated with important deepwater fisheries. Acoustic recordings suggest that there is a relatively high biomass of mesopelagic fish over the Chatham Rise, but little is known about the species composition, distribution, and spatio-temporal dynamics of the organisms responsible for the acoustic scattering layers. Two research trawl and acoustic surveys were carried out in May and June 2008 and November 2011 to assess the distribution and acoustic signatures of mesopelagic animals on the Chatham Rise. A total of 171 species or species groups were caught in 86 midwater trawls to a maximum depth of 1000 m. Seven species assemblages were described corresponding to different acoustic mark types. These 7 assemblages were dominated by euphausiids, *Maurolicus australis* (Stomii forms), *Lampanyctodes hectoris*, *Symbolophorus boops*, *Electrona carlsbergi*, *Diaphus danae* and *Gymnoscopelus piabilis* (all Myctophiformes). Euphausiids could be separated from mesopelagic fish species based on their multi-frequency acoustic response, but the 6 fish groups could not be separated based on their frequency response alone. These different fish assemblages were distinguished based on their unique acoustic mark characteristics (amplitude and dimension features of the volume backscatter), vertical distribution and ancillary information. Classification results were synthesised in a decision model. *M. australis* and *L. hectoris* were associated with shallower water on the central and western Chatham Rise, *D. danae* occurred mainly in deeper water on the north side of the Rise, and *E. carlsbergi* was associated with cooler water on the south Rise.

Geoffroy, M., Daase, M., Cusa, M., Darnis, G., Graeve, M., Hernandez, N. S., . . . Falk-Petersen, S. (2019). Mesopelagic Sound Scattering Layers of the High Arctic: Seasonal Variations in Biomass, Species Assemblage, and Trophic Relationships. *Frontiers in Marine Science*, 6. <https://doi.org/10.3389/fmars.2019.00364>

Mesopelagic sound scattering layers (SSL) are ubiquitous in all oceans. Pelagic organisms within the SSL play important roles as prey for higher trophic levels and in climate regulation through the biological carbon pump. Yet, the biomass and species composition of SSL in the Arctic Ocean remain poorly documented, particularly in winter. A multifrequency echosounder detected a SSL north of Svalbard, from 79.8 to 81.4 degrees N, in January 2016, August 2016, and January 2017. Midwater trawl sampling confirmed that the SSL comprised zooplankton and pelagic fish of boreal and Arctic origins. Arctic cod dominated the fish assemblage in August and juvenile beaked redfish in January. The macrozooplankton community mainly comprised the medusa *Cyanea capillata*, the amphipod *Themisto libellula*, and the euphausiids *Meganyctiphanes norvegica* in August and *Thysanoessa inermis* in January. The SSL was located in the Atlantic Water mass, between 200-700m in August and between 50-500m in January. In January, the SSL was shallower and weaker above the deeper basin, where less Atlantic Water penetrated. The energy content available in the form of lipids within the SSL was significantly higher in summer than winter. The biomass within the SSL was >12-fold higher in summer, and the diversity of fish was slightly higher than in winter (12 vs. 9 species). We suggest that these differences are mainly related to life history and ontogenetic changes resulting in a descent toward the seafloor, outside the mesopelagic layer, in winter. In addition, some fish species of boreal origin, such as the spotted barracudina, did not seem to survive the polar night when advected from the Atlantic into the Arctic. Others, mainly juvenile beaked redfish, were abundant in both summer and winter, implying that the species can survive the polar night and possibly extend its range into the high Arctic. Fatty-acid trophic

markers revealed that Arctic cod mainly fed on calanoid copepods while juvenile beaked redfish targeted krill (*Thysanoessa* spp.). The relatively high biomass of Arctic cod in August and of redfish in January thus suggests a shift within the SSL, from a Calanus-based food web in summer to a krill-based food web during winter.

Godo, O. R., Patel, R., & Pedersen, G. (2009). Diel migration and swimbladder resonance of small fish: some implications for analyses of multifrequency echo data. *ICES Journal of Marine Science*, 66(6), 1143-1148. <https://doi.org/10.1093/icesjms/fsp098>

Many fish with swimbladders exhibit diel vertical migrations (DVM). Ascents and descents of hundreds of metres occur, and altered swimbladder volume and buoyancy can result from incomplete secretion and resorption of gas. When acoustic observations are made near the resonance frequency of the swimbladder, the estimated fish biomass can be positively biased. When multiple-frequency echosounders are used, the frequency response of the backscatter might vary temporally and spatially and compromise the effectiveness of conventional target-identification methods. In this paper, variations in backscatter from mesopelagic fish are studied using data collected west of the British Isles with a five-frequency echosounder (Simrad EK60). Two acoustic layers, one dominated by pearlsides (*Maurolicus muelleri*) and the other by myctophids (Myctophidae), were monitored during their DVM. The frequency responses of the layers changed systematically, mainly characterized by increases in the nautical-area-backscattering coefficient ($s(A)$) values at 18 kHz relative to those at 38 kHz. This could have been caused by changes in the resonance frequencies of fish swimbladders, as they expanded and contracted during ascent and descent. Two $s(A)$ maxima in the myctophids layer suggest the presence of two types of target with different scattering characteristics. Models of sound scatter from myctophid swimbladders suggest that these peaks have resulted from resonance scattering. The $s(A)$ at 18 kHz attributed to *M. muelleri* also peaked, but at the maximum depth of their distribution. Spatial and temporal changes in the frequency responses of fish should be taken into account when pelagic fish communities are surveyed with multiple-frequency echosounders.

Greely, T. M., Gartner, J. V., & Torres, J. J. (1999). Age and growth of *Electrona antarctica* (Pisces : Myctophidae), the dominant mesopelagic fish of the Southern Ocean. *Marine Biology*, 133(1), 145-158. <https://doi.org/10.1007/s002270050453>

Numerically and in biomass, the lanternfish *Electrona antarctica* is the dominant fish in the vast pelagic region of the Southern Ocean bounded on the north by the Antarctic Convergence and in the south by the Antarctic continental shelf. It is an important krill predator, and in turn is important in the diets of flighted and swimming seabirds. Further, it is the southernmost and coldest-dwelling representative of the globally distributed fish family Myctophidae. The present study was undertaken to estimate the species' growth rate and average life span, to incorporate the information in a basic energy budget, and to compare the growth of *E. antarctica* with more northerly confamilials. Fishes were aged using primary growth increments that were resolved on sagittal otoliths using three sequential techniques: thin-section grinding and polishing, etching, and scanning electron microscopy (SEM). Based on increment width (0.8 to 1.2 μ m), continuity, and previous studies on confamilials, the microincrements were assumed to be deposited on a daily basis. Montages of SEM photomicrographs were constructed for each sagitta to allow the daily rings to be counted over the entire life span of 31 individuals representing the entire size range of the species. Results suggest a larval stage of 30 to 47 d and a maximum life span of 3.5 yr, with females growing faster than males in the last 1.5 yr of life and reaching a larger maximum

size. Construction of a simple energy budget using the best information available suggests that a surplus of energy is available to support the observed growth rates (0.05 to 0.07 mm d⁻¹). The results of the present study contrast markedly with previous estimates of an 8 to 11 yr maximum age for *E. antarctica*. These results provide important data addressing the ecology and population dynamics of the pelagic Antarctic ecosystem. *E. antarctica* is the end-member species in the continuum of vertically migrating myctophids that extend from the equator to the polar circle. Its growth rate is consonant with that of all other myctophid species examined using primary growth increments to determine age. The present study, in conjunction with earlier studies, suggests that growth rates of mesopelagic species are far higher than previously thought.

Ha, V. V. (2008). *Separating blue whiting (Micromesistius poutassou Risso, 1826) from myctophid targets using multi-frequency methods*. (Master thesis), University of Bergen, Bergen, Norway.
Retrieved from <http://hdl.handle.net/1956/3238>

Blue whiting (*Micromesistius poutassou* Risso, 1826) is a physoclists species, widely distributed in the Barents Sea, Norwegian Sea and Mediterranean Sea. They appear on the continental slope and shelf, in high concentration at 300-400 m depth. They play an important role in these ecosystems not only in term of abundance but also in the food chain. The abundance of the blue whiting stock is now estimated annually by acoustic methods. Traditionally, blue whiting was separated from other targets using catch information. Therefore, it often becomes problematic when only a few net samples are to be conducted. Multi-frequency method with an approach of measuring frequency response, *r(f)*, is a reliable method for distinguishing between species recorded in echograms. Acoustic data collected during blue whiting surveys in 2005 and 2006 were used to calculate *r(f)* of blue whiting and myctophids. The *r(f)* of blue whiting and myctophids were estimated for each “trawl-polygon” and for schools recorded along the survey tracks. The results showed significantly differences in *r(f)* for blue whiting and myctophid groups. It is evidently believed that *r(f)* are reliable variables used to discriminate between these species. Two approaches were deployed to separate blue whiting and myctophids; the discriminant function analysis and the classification tree. The *r(f)* at 18, 38 and 70 kHz, the echo strength at 38 kHz, *sA(38)*, and the depth of fish schools (school depth) were used as independent variables. Both discriminant function analysis and classification tree were successfully used to separate between species with a relatively high accuracy. *r(18)*, *r(70)* and *sA(38)* were the most important variables in the discriminant function analysis while *r(18)* and *r(38)* were the most powerful variables in the classification tree method. During the survey in 2006, target strength, TS, of blue whiting was measured in situ using the TS probe method. The TS were estimated to be from -37 dB to -34 dB for 38 kHz and from -39 dB to -38 dB for 120 kHz. The relationship between target strength and length of fish was $TS=20\log(L)-64.2$; $L=26.0$ cm. No significant relationship between TS and depth was found. The change in densities (tonnes/nmi²) of blue whiting in 2005 and 2006 were about +11.8%. Total biomass estimated for the 2005 survey was about 1.8 million tonnes within an area of 75,899 nmi². In the 2006 survey, it was estimated around 1.0 million tonnes for an area of 38,131 nmi².

Hernandez-Milian, G., Lusher, A., O'Brian, J., Fernandez, A., O'Connor, I., Berrow, S., & Rogan, E. (2017). New information on the diet of True's beaked whale (*Mesoplodon mirus*, Gray 1850), with insights into foraging ecology on mesopelagic prey. *Marine Mammal Science*, 33(4), 1245-1254. <https://doi.org/10.1111/mms.12430>

No abstract available.

Hersey, J. B., & Backus, R. H. (1954). New evidence that migrating gas bubbles, probably the swimbladders of fish, are largely responsible for scattering layers on the continental rise south of New England. *Deep Sea Research* (1953), 1(3), 190-191. [https://doi.org/10.1016/0146-6313\(54\)90050-7](https://doi.org/10.1016/0146-6313(54)90050-7)

No abstract available.

Horn, M. H., Grimes, P. W., Phleger, C. F., & McClanahan, L. L. (1978). Buoyancy function of the enlarged fluid-filled cranium in the deep-sea ophidiid fish *Acanthonus armatus*. *Marine Biology*, 46(4), 335-339. <https://doi.org/10.1007/BF00391405>

Acanthonus armatus Günther (family Ophidiidae) is a slightly negatively buoyant (mean weight in surface seawater = 0.58% of air weight) benthopelagic fish without a swimbladder that has reduced tissues and components (muscle, bone, brain, gills, lipids) and a massive head. This species has an enlarged cranial cavity (10% of head volume) filled, except for the very small brain, with a low-density (specific gravity 1.008) fluid. The fluid provided static lift of about 0.30 g each for 4 specimens whose weights in water ranged from 1.0 to 2.6 g. Osmotic concentrations of the cranial fluid averaged 294 mOsm 1-1 in 4 specimens and, in 2 specimens for which comparisons were possible, were 43 to 45% lower than the concentrations of the plasma and perivisceral fluid. Similarly, Na⁺ and K⁺ concentrations of the cranial fluid were lower than those of the plasma or perivisceral fluid. *A. armatus* has highly reduced heavy tissues and an increased content of dilute fluid, with a localization of even more highly dilute fluid in the enlarged cranium which partially offsets the relatively dense tissues of the head. Information on the morphology, behavior and ecology of the fish supports the interpretation of the buoyancy and chemical data. The conclusion is consistent with the hypothesis that obtaining and conserving energy and reducing predation are the important selective factors affecting the evolution of deep-sea fishes and that these factors have greatly influenced the chemical composition of the fishes.

Ito, Y., Yasuma, H., Masuda, R., Minami, K., Matsukura, R., Morioka, S., & Miyashita, K. (2011). Swimming angle and target strength of larval Japanese anchovy (*Engraulis japonicus*). *Fisheries Science*, 77(2), 161-167. <https://doi.org/10.1007/s12562-011-0323-1>

The swimming angle of larval Japanese anchovy (*Engraulis japonicus*) was measured in a tank, and target strength (TS) was calculated using a theoretical scattering model. The mean swimming angle was 12.8° (SD ± 22.1). Increased speeds of flow led to increased mean swimming angles. The mean swimming angle at flow of 5 cm s⁻¹ was higher than at other speeds. TS values were estimated using a distorted-wave Born approximation model for two cases. Average values were 1–3 cm s⁻¹ (11.5° ± 22.1) and 5 cm s⁻¹ (16.6° ± 21.7) for cases 1 and 2, respectively. For case 1, TS ranged from -92.0 to -74.7 dB with a mean of -79.4 dB at 120 kHz. For case 2, TS ranged from -92.2 to -75.2 dB with a mean of -79.9 dB. The mean TS in case 2 was lower than that in case 1, with the maximum difference being 1.0 dB at 120 kHz (standard length 22.0 mm). However, there were no significant differences between the regression lines of cases 1 and 2. Thus, changes in flow speed altered the swimming angle of larval Japanese anchovy, but had little influence on TS.

Jay, C. V. (1993). Structure and volume of the hoki, *Macruronus novaezelandiae* (Merlucciidae), swimbladder. *Journal of Fish Biology*, 43(4), 633-642. <https://doi.org/10.1111/j.1095-8649.1993.tb00446.x>

The structure of the hoki, *Macruronus novaezelandiae*, swimbladder is similar to well-developed swimbladders in other deep water fish that undergo extensive diel vertical migrations. The preponderance of a globular mass of submucosal tissue in the posterio-ventral floor of the swimbladder in large individuals is an unusual feature of unknown function, but has characteristics similar to regressed swimbladders that occur in some species of the Myctophidae. Two out of three different estimates of swimbladder volume were significantly lower than neutral buoyancy volume estimates, probably because the swimbladders were inflated artificially without accounting for their natural compliancy and internal pressure. Volume estimates from such swimbladders may reduce substantially the accuracy of target strength estimates from morphometry-based models of the swimbladder. However, this may be a trivial consideration in acoustic surveys compared to the probable occurrence of diel and seasonal variation in swimbladder shape and volume.

Johnson, R. K. (1979). *Gas bubble sizes for selected myctophids*. Oregon State University. School of Oceanography. Retrieved from <http://hdl.handle.net/1957/8086>

The mesopelagic animals which are most often detected acoustically are those which contain gas bubbles within their bodies. In the waters off the Oregon coast, the most abundant animals which contain gas bubbles are myctophids. Both the size and the shape of the bubble are important to acoustic measurements. This report summarizes the available information on the acoustically important characteristics of the most abundant myctophids: *Stenobrachius leucopsarus*, *Diaphis theta*, *Tarletonbeania crenularis*, and *Protomyctophum thompsoni* and *crockeri*.

Kaartvedt, S., Rostad, A., Klevjer, T. A., & Staby, A. (2009). Use of bottom-mounted echo sounders in exploring behavior of mesopelagic fishes. *Marine Ecology Progress Series*, 395, 109-118. <https://doi.org/10.3354/meps08174>

We deployed an upward-facing echo sounder mounted on the bottom and cabled to shore in a similar to 400 m fjord location for long-term studies of small mesopelagic fish and their potential predators. The population of the myctophid *Benthosema glaciale* displayed diverse diel vertical migration (DVM) behaviors, including normal DVM to surface waters at night, reverse DVM in the lower part of the water column in which fish ascended to similar to 200 m at day, as well as nonmigration of some individuals. The relative prevalence of these behavioral modes varied with season. Acoustic target tracking of individuals in deep water showed that *B. glaciale* was conspicuously inactive and drifted back and forth with weak tidal currents, essentially acting as plankton. Swimming was largely restricted to infrequent short bouts. More active swimming occasionally occurred in the vertical direction, and then in a stepwise pattern. Potential predators in deep water were swimming at speeds of <0.5 body length s⁻¹, with maximum speeds of similar to 1 body length s⁻¹. These results show that submerged echo sounders provide a means of non-intrusively studying both individual and population behavior of deep-living organisms.

Kaartvedt, S., Staby, A., & Aksnes, D. L. (2012). Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass. *Marine Ecology Progress Series*, 456, 1-6.
<https://doi.org/10.3354/meps09785>

Mesopelagic fishes occur in all the world's oceans, but their abundance and consequently their ecological significance remains uncertain. The current global estimate based on net sampling prior to 1980 suggests a global abundance of one gigatonne (10⁹ t) wet weight. Here we report novel evidence of efficient avoidance of such sampling by the most common myctophid fish in the Northern Atlantic, i.e. *Benthosema glaciale*. We reason that similar avoidance of nets may explain consistently higher acoustic abundance estimates of mesopelagic fish from different parts of the world's oceans. It appears that mesopelagic fish abundance may be underestimated by one order of magnitude, suggesting that the role of mesopelagic fish in the oceans might need to be revised.

Kaartvedt, S., Torgersen, T., Klevjer, T. A., Rostad, A., & Devine, J. A. (2008). Behavior of individual mesopelagic fish in acoustic scattering layers of Norwegian fjords. *Marine Ecology Progress Series*, 360, 201-209. <https://doi.org/10.3354/meps07364>

Mesopelagic acoustic scattering layers (SLs) in 2 fjords were studied from a stationary research vessel. Diel vertical movements of SLs were assessed by hull-mounted transducers, while in situ behavior of individuals constituting the SLs was resolved by a submerged echo sounder. The study focused on SLs made up of the lightfish *Maurolicus muelleri* and the lanternfish *Benthosema glaciale*. Individual fish migrated in a pronounced stepwise manner, alternating between vertical movements and stationary phases both during ascent and descent. Mean lengths of steps varied between 2.01 and 0.40 m, and mean duration of stationary phases between 69 and 36 s for fish in different SLs. Such travel-pause behavior concords with saltatory search, where fish scan the water for prey during the stationary phases, relocate and scan a new water parcel. Little activity was recorded among individuals in deep water, apart from infrequent, short shifts in vertical distribution. This study shows that stationary submerged echo sounders can provide detailed information on in situ behavior of mesopelagic fish.

Karpouzi, V. S., & Stergiou, K. I. (2003). The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. *Journal of Fish Biology*, 62(6), 1353-1365. <https://doi.org/10.1046/j.1095-8649.2003.00118.x>

In 18 marine fish species from the eastern Mediterranean, vertical mouth opening increased linearly with total length (L-T) for 10 species and log-linearly for eight species. Horizontal mouth opening was linearly related to L-T for 12 species and log-linearly for six species, whereas mouth area was a log-linear function of L-T for all fish species examined. Mouth shape varied greatly covering the whole spectrum from a full circle to an extended oval. In addition, the trophic level of the 18 species could be expressed as an asymptotic function of mouth area. The results are discussed within the context of the trophic ecology of the species examined in the study area.

Khodabandehloo, B., Agersted, M. D., Klevjer, T., Macaulay, G. J., & Melle, W. (2021). Estimating target strength and physical characteristics of gas-bearing mesopelagic fish from wideband in situ echoes using a viscous-elastic scattering model. *The Journal of the Acoustical Society of America*, 149(1), 673-691. <https://doi.org/10.1121/10.0003341>

Wideband (38 and 50–260 kHz) target strength of organisms were measured in situ using a towed platform in mesopelagic (200–1000 m depth) layers. Organisms with a gas-inclusion are strong scatterers of sound and acoustically distinct from organisms lacking one. In the mesopelagic zone, some of the fish species and physonect siphonophores have a gas-inclusion. Trawl and multinet biological sampling as well as photographic evidence indicate that in the study area (eastern mid-Atlantic Ocean) the majority of the gas-bearing organisms were fish. Subsequently, using a two-layer viscous-elastic spherical gas backscattering model, physical characteristics such as gas-bladder features and body flesh properties were deduced from the measured backscattering signal of individual gas-bearing fish. Acoustic techniques are non-extractive, can be used for the monitoring and quantification of marine organisms in a time- and cost-effective manner, and suit studies of the mesopelagic zone, which is logistically challenging. Vessel-mounted acoustics, widely used for epipelagic studies, has limitations for mesopelagic studies as the deep organisms are inaccessible to high-frequency (≥ 100 kHz) acoustic pulses transmitted from the surface due to absorption. Therefore, a towed platform equipped with wideband acoustics has several features that can be utilized for monitoring the mesopelagic dense scattering layers containing mixed species.

Klemmedson, A. D., Reiss, C. S., Goebel, M. E., Kaufmann, R. S., Dorval, E., Linkowski, T. B., & Borras-Chavez, R. (2020). Variability in age of a Southern Ocean myctophid (*Gymnoscopelus nicholsi*) derived from scat-recovered otoliths. *Marine Ecology Progress Series*, 633, 55-69. <https://doi.org/10.3354/meps13176>

Myctophids are ecologically important in the Southern Ocean, where they occupy a central trophic position and are a key energy resource for top predators. However, understanding their population dynamics is limited by a paucity of data due to sampling challenges. Antarctic fur seal *Arctocephalus gazella* scats provide large collections of otoliths and other prey remains that can be used to form time series for important mesopelagic taxa such as *Gymnoscopelus nicholsi* (Gn). Examination of otoliths from scats allowed for a reconstruction of Gn age and length structure from 8 selected sample years between 2000 and 2015. While mean reconstructed length did not change significantly over the time series, mean age declined. Older age classes were scarce in scat samples, and age-6 animals were not found after 2008. During the same time period, Gn otoliths in fur seal scats declined from approximately 2000 to fewer than 200. The decline in the number of otoliths in Antarctic fur seal scat samples coupled with the negative trend in mean age suggests declines in the availability of Gn on the South Shetland Island slope region between 2000 and 2015. This study demonstrates the utility of central-place foragers in assessing populations of unfished but ecologically important mesopelagic fishes, thus allowing evaluation of hypotheses about their population structure and dispersal.

Klevjer, T. A., Irigoien, X., Rostad, A., Fraile-Nuez, E., Benitez-Barrios, V. M., & Kaartvedt, S. (2016). Large scale patterns in vertical distribution and behaviour of mesopelagic scattering layers. *Scientific Reports*, 6, 11. <https://doi.org/10.1038/srep19873>

Recent studies suggest that previous estimates of mesopelagic biomasses are severely biased, with the new, higher estimates underlining the need to unveil behaviourally mediated coupling between shallow and deep ocean habitats. We analysed vertical distribution and diel vertical migration (DVM) of mesopelagic acoustic scattering layers (SLs) recorded at 38 kHz across oceanographic regimes encountered during the circumglobal Malaspina expedition. Mesopelagic SLs were observed in all areas covered, but vertical distributions and DVM patterns varied markedly. The distribution of mesopelagic backscatter was deepest in the southern Indian Ocean (weighted mean daytime depth: WMD 590 m) and shallowest at the oxygen minimum zone in the eastern Pacific (WMD 350 m). DVM was evident in all areas covered, on average similar to 50% of mesopelagic backscatter made daily excursions from mesopelagic depths to shallow waters. There were marked differences in migrating proportions between the regions, ranging from similar to 20% in the Indian Ocean to similar to 90% in the Eastern Pacific. Overall the data suggest strong spatial gradients in mesopelagic DVM patterns, with implied ecological and biogeochemical consequences. Our results suggest that parts of this spatial variability can be explained by horizontal patterns in physical-chemical properties of water masses, such as oxygen, temperature and turbidity.

Klevjer, T. A., Melle, W., Knutsen, T., & Aksnes, D. L. (2020). Vertical distribution and migration of mesopelagic scatterers in four north Atlantic basins. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 180. <https://doi.org/10.1016/j.dsr2.2020.104811>

We studied vertical distribution and diel vertical migration (DVM) behaviour of mesopelagic acoustic scattering layers in relation to environmental conditions in the Norwegian Sea, the Iceland Sea, the Irminger Sea, and the Labrador Sea. Distinct mesopelagic scattering layers were found in all basins, but the daytime depth of the layers varied between basins. The results suggested that daytime vertical distribution across the four basins are strongly influenced by optical conditions. DVM occurred in all basins, and since daytime vertical distribution was influenced by optical conditions, it affected the amplitude of vertical connectivity. We used the proportion of the acoustic backscatter that migrated vertically into the epipelagic zone as a proxy for active vertical flux to the mesopelagic. The proportion of micronekton backscatter participating in the vertical migrations varied between the basins, with the highest and lowest vertical connectivity in the Norwegian Sea and the Iceland Sea respectively. We conclude that a more than 8-fold reduction in backscatter flux in the Iceland Sea was primarily attributable to optical conditions there, as high nighttime light levels appeared to exclude the micronekton from the epipelagic zone.

Kloser, R. J., & Horne, J. K. (2003). Characterizing uncertainty in target-strength measurements of a deepwater fish: orange roughy (*Hoplostethus atlanticus*). *ICES Journal of Marine Science*, 60(3), 516-523. [https://doi.org/10.1016/S1054-3139\(03\)00048-1](https://doi.org/10.1016/S1054-3139(03)00048-1)

The variability of ensemble 38 kHz, target-strength (TS38) estimates for orange roughy (*Hoplostethus atlanticus*) (4.9 dB, factor of 3.1) in deep water (>600 m) limits the use of echo integration for absolute-biomass estimates. Orange roughy are high in oil content, have a wax-ester swimbladder, and show an active-avoidance response to sampling gear. The interpretations of ensemble, in situ target

strengths of orange roughy (range $\langle TS38 \rangle = -52.9$ to -51.0 dB for standard fish length $\langle SL \rangle = 35$ cm) are lower than previous model and surface-based measurements ($\langle TS38 \rangle = -48$ dB, $SL = 35$ cm). In situ TS measurements from individuals on the periphery of dense schools were processed to minimize uncertainties from single-target selection criteria, species composition, and active avoidance. Video and acoustic-tracking data quantified the variability in TS measurements arising from the variability in fish orientation. Multi-frequency acoustics and fish tracking are used to quantify in situ TS variability due to species identification and fish density. The Kirchhoff-ray-mode backscatter model was used to illustrate the sensitivity of species-specific backscatter to assumptions of tilt-angle and material properties (density and sound-speed contrasts). We conclude that a remaining source of uncertainty for in situ TS measurements is the assumption that dispersed targets are representative of the survey population.

Kloser, R. J., Ryan, T., Sakov, P., Williams, A., & Koslow, J. A. (2002). Species identification in deep water using multiple acoustic frequencies. *Canadian Journal of Fisheries and Aquatic Sciences*, 59(6), 1065-1077. <https://doi.org/10.1139/f02-076>

Multifrequency 12, 38, and 120 kHz acoustics were used to identify the dominant fish groups around a deepwater (>600 in) seamount (a known spawning site for orange roughy, *Hoplostethus atlanticus*) by amplitude mixing of the frequencies. This method showed three distinct acoustic groupings that corresponded to three groups of fishes based on size and swimbladder type: myctophids of total length less than 10 cm, morids and macrourids with lengths >30 cm, and orange roughy with a mean standard length of 36 cm. These three groups were the dominant groups caught in the demersal and pelagic trawls in the study area. A simple model of swimbladder resonance at depth of large and small gas-filled bladder fish groups is in agreement with our experimental observations. Traditionally, demersal and pelagic trawling is used to identify fish species in acoustic records. However, orange roughy are rarely caught in mid-water owing to net avoidance. Using three frequencies, these groups could be distinguished directly over their entire vertical extent from the acoustic records. This reduces a major source of positive bias uncertainty (factor range of 2.0-6.4) in the orange roughy biomass estimates.

Kloser, R. J., Ryan, T. E., Young, J. W., & Lewis, M. E. (2009). Acoustic observations of micronekton fish on the scale of an ocean basin: potential and challenges. *ICES Journal of Marine Science*, 66(6), 998-1006. <https://doi.org/10.1093/icesjms/fsp077>

Acoustic methods of characterizing micronekton communities (approximate to 2 to 20 cm length) on the scale of an ocean basin could provide valuable inputs to ecosystem-based fishery management, marine planning, and monitoring the effects of climate change. The micronekton fish are important forage for top predators (e.g. tunas), and information on their diversity, distribution, size-structure, and abundance is needed to increase accuracy of top-predator distribution and abundance predictions. At the scale of an ocean basin, four years of Tasman Sea transects using a fishing vessel provide fine-scale maps of acoustic backscatter at 38 kHz that reveal detailed spatial patterns and structure to depths of 1200 m. Research-vessel data provide detailed biodiversity, density, size structure, and acoustic-scattering information from depth-stratified net sampling and a lowered acoustic probe. Wet-weight biomass estimates of the micronekton fish in the region vary considerably by a factor of 5-58 between acoustics (16-29 g m⁻²), nets (1.6 g m⁻²), and large spatial-scale, ecological models (0.5-3 g m⁻²). We demonstrate the potential and challenges of an acoustic basin-scale, fishing-vessel monitoring programme, including optical and net sensing, which could assist in characterizing the biodiversity, distribution, and biomass of the micronekton fish.

Kloser, R. J., Williams, A., & Koslow, J. A. (1997). Problems with acoustic target strength measurements of a deepwater fish, orange roughy (*Hoplostethus atlanticus*, Collett). *ICES Journal of Marine Science*, 54(1), 60-71. <https://doi.org/10.1006/jmsc.1996.0171>

In situ target strength measurements of fish at 600 to 1200 m depth were made around a spawning aggregation of orange roughy off the east coast of Tasmania in 1992. The target strength data showed many modes, none of which could be definitely and uniquely attributed to orange roughy, partly because the orange roughy avoided the towed body housing the acoustics. Dominant modes at - 50 and - 55 dB were attributed to myctophid fishes with standard length modes at 8.2 and 5.3 cm; these fish have gas-filled swimbladders and were undisturbed by the towed body. Small modes at - 44 dB and - 31 dB were attributed to the macrourid *Coryphaenoides subserrulatus* and the morid *Halagyreus johnsonii*, respectively. The swimbladder of *H. johnsonii* is gas-filled, while that of *C. subserrulatus* contains a gas-filled spongy tissue matrix. No evidence was found of a separate mode at - 36 or - 41.3 dB, the previously reported target strength values of orange roughy. Modelling and tethered experiments on orange roughy suggested the target strength range for a 35 cm standard length fish was - 47.2 to - 53 dB. The modelling indicated values at the higher end of the range; measurements taken at depth of a tethered fish indicated the lower end. The dominant mode in the in situ data at - 50 dB (which ranges from about - 48 to - 52 dB) was probably associated with orange roughy as well as myctophids. We concluded that the in situ target strength for a 35 cm standard length orange roughy is between - 48 and - 52 dB. Such a low target strength (compared to other species from the same depth that have gas-filled swimbladders) makes acoustic assessment techniques using echo integration very sensitive to the number of fish with gas-filled swimbladders.

Kubilius, R. (2015). *Multi-frequency acoustic discrimination between gas bubble plumes and biological targets in the ocean*. (Doctoral thesis), University of Bergen, Bergen, Norway. Retrieved from <https://hdl.handle.net/1956/10076>

Seabed-originating gas bubble seeps have been observed worldwide from a variety of sources (e.g. Hovland and Judd, 1988) and are most frequently composed of methane and carbon dioxide. Some seabed gas leaks, such as "melting" methane hydrates, may intensify in the coming decades and are a subject of concern in the context of warming seas (Kvenvolden et al., 1993; Archer, 2007). The subsea gas extraction industry and proposed carbon dioxide storage in geological structures under the seabed are examples of potential manmade sources of gas bubble leaks (IPCC, 2005; DNV, 2010), and require swift and precise leak detection and identification. Active acoustic methods are well suited for rapid and cost effective monitoring of large water volumes. Scientific fisheries echo sounders provide calibrated, quantitative measures and are widely used in fish stock monitoring (Simmonds and MacLennan, 2005). As such, these were chosen within the umbrella R&D projects (AKUGAS and AALDOG), the needs of which shaped the scope and objectives of this doctoral study. Bottom-mounted echo sounders, observing laterally along the seabed are considered suitable for gas leak detection. Gas bubble plumes are easy to detect with echo sounders, but separating them from fish and plankton is not always straight forward, as some required information is lacking both for gas bubble plumes and biological targets. This lack is addressed here via selected case studies. In Paper I, the acoustic backscatter properties and natural body tilt orientation were investigated for a common schooling fish that lacks a swim bladder, lesser sandeel (*Ammodytes marinus*). Its natural orientation distribution was measured using optical measurement methods and is a crucial parameter affecting the acoustic backscattering from animals that are large enough to be directive targets at commonly used echo sounder frequencies. A more advanced stereo photogrammetric method was adapted and improved to

fit the needs of this doctoral study in Paper II. These were implemented to characterize the natural tilt orientation distribution of euphausiids (*Euphausia superba* and *Meganyctiphanes norvegica*) in several in situ and ex situ experiments (Paper II). Krill natural tilt orientation was measured to have a rather large variability (SD of up to 30-37°). This suggests, but does not prove, that dorsal and lateral aspect krill acoustic backscatter should not be drastically different due to the variable swimming behaviour and body postures adopted by these animals. Such knowledge will be useful for krill multi-frequency identification and target strength averaging either from models or from empirical data. The stereo photogrammetric measurement method (Paper II) was later applied to support fine scale acoustic backscatter measurements on gas bubble plumes (Paper IV) and saithe (*Pollachius virens*) (Paper III). In Paper III, the lateral aspect acoustic backscatter of saithe was characterised at 70, 120, 200 and 333 kHz. Saithe is a good representative of large, acoustically directive schooling fish that also possesses a gas-filled swim bladder. These can create strong and similar acoustic targets to plumes of free gas bubbles rising from the seabed. Saithe lateral aspect acoustic frequency response ($r(f)$) was measured based on both schools, single acoustic targets and single target tracks. It was found to have an opposite trend across the acoustic frequency band compared to dorsal aspect saithe $r(f)$ as reported in the literature. The reasons for such discrepancy are discussed along with the implications for acoustic target identification. Similarly, lateral aspect acoustic backscatter properties were characterised for induced methane, carbon dioxide and air bubble plumes at 70, 120, 200 and 333 kHz (Paper IV). A distinct gas plume frequency response was measured for gas bubbles of non-resonant size and is significantly different from the lateral aspect $r(f)$ of saithe. In synthesis, the similarity in acoustic backscattering between a gas bubble and biological targets possessing gas inclusions is discussed, both from a literature review and the investigations included here (Papers I-IV). The prospects of acoustic-based gas bubble plume detection and identification are discussed in the context of obscuring and confounding biological targets. Acoustic frequency response, routinely used to identify some fish and plankton for species or taxa (e.g. Korneliussen and Ona, 2002; 2003; Anon., 2005), is discussed for laterally observed seabed gas bubble plumes. Lateral aspect gas bubble plumes and swim bladder bearing fish frequency response was not available and hence was measured in Papers III and IV. Based on the available research and that defended here (Papers I-IV), it is suggested that behavioural and acoustic backscattering differences can be used to separate gas bubble plumes from the most common biological targets, plankton and fish. Gas-filled swim bladder bearing fish are the most similar biological acoustic targets to the gas bubble plumes. Schooling and swim bladder bearing fish that are quite directive acoustic targets can be separated using the acoustic frequency response information (indications in Paper III). Smaller, but abundant swim bladder bearing fish, such as members from Myctophidae and Sternopychidae, can be difficult to separate acoustically from a single gas bubble. However, the behaviour of such fish assemblages is substantially different from the gas bubble plumes. Using both backscattering frequency response and behaviour traits (at one time instance and over time) are likely to give the best chances for acoustic-based detection and identification of seabed gas bubble plumes.

Lourenco, S., Saunders, R. A., Collins, M., Shreeve, R., Assis, C. A., Belchier, M., . . . Xavier, J. C. (2017). Life cycle, distribution and trophodynamics of the lanternfish *Krefftichthys anderssoni* (Lonnberg, 1905) in the Scotia Sea. *Polar Biology*, 40(6), 1229-1245.
<https://doi.org/10.1007/s00300-016-2046-3>

Myctophid fish play an important role in the Southern Ocean pelagic food web. The lanternfish *Krefftichthys anderssoni* is one of the most common myctophids in the region, but its ecology is poorly known. This study examines spatial and temporal patterns in the species distribution of density, life cycle, population structure and diet using samples collected by mid-water trawl nets deployed in

different seasons across the Scotia Sea. Virtually absent from the sea-ice zone, the species was most abundant in the northern Scotia Sea around the Georgia Basin at depths below 400 m that are associated with the Circumpolar Deep Water. The species migrated during night from waters deeper than 700 m to waters above the 400 m following their main prey species: the copepods *Rhincalanus gigas* and *Calanoides acutus* and euphausiids of the *Thysanoessa* genus. Larvae length distribution and post-larvae length-frequency analyses suggested a life cycle of similar to 3 years with spawning and recruitment strongly connected with APF and the South Georgia shelf. Our results show that species spatial distribution, population structure and diet changed both seasonally and ontogenetically. This study is the most comprehensive examination of the ecology of *K. anderssoni* in the Southern Ocean to date and contributes to resolving how pelagic food webs and ecosystems operate in the region.

Love, R. H. (1978). Resonant acoustic scattering by swimbladder-bearing fish. *Journal of the Acoustical Society of America*, 64(2), 571-580. <https://doi.org/10.1121/1.382009>

A new model of swimbladder-bearing fish has been developed in order to provide improved predictions of the resonance frequency and acoustic cross section of such a fish. The model consists of a small spherical shell in water, enclosing an air cavity which supports a surface tension. The shell is a viscous, heat-conducting Newtonian fluid, with the physical properties of fish flesh. A comparison of the results obtained with the new model to experimental data indicates that the new model constitutes a definite improvement over previous models. The new model can predict the high values of damping and elevated resonance frequencies that previous models could not. The model appears to be most accurate for fish in which tension in the swimbladder wall has a minor effect on resonant scattering. This includes the fish which are of interest in studies of volume reverberation, and the new model should therefore be of considerable value in such studies.

Love, R. H. (2013). Comment on 'Resonant acoustic scattering by swimbladder-bearing fish" J. Acoust. Soc. Am, 64, 571-580 (1978) (L) Response. *Journal of the Acoustical Society of America*, 134(5), 3399-3402. <https://doi.org/10.1121/1.4823805>

In the 1970s a model of resonant scattering from a swimbladder-bearing fish was developed. The fish was modeled as an air bubble, representing a swimbladder, encased in a viscous spherical shell, representing the fish flesh. This model has been used successfully to correlate acoustic scattering data with fish information in a number of ocean locations. Recently, questions have arisen about viscous damping of the flesh and the thickness of the shell [K. Bait, J. Acoust. Soc. Am. 133. 5-8 (C) (2013)]. This Letter responds to those questions and provides practical insight into the model's use.

Love, R. H., Fisher, R. A., Wilson, M. A., & Nero, R. W. (2004). Unusual swimbladder behavior of fish in the Cariaco Trench. *Deep-Sea Research Part I-Oceanographic Research Papers*, 51(1), 1-16. <https://doi.org/10.1016/j.dsr.2003.09.004>

An extensive acoustic and biological experiment was conducted to examine the swimbladder behavior of fish in the Cariaco Trench, off Venezuela, whose deeper waters are anoxic. Forty-eight hours of broadband (1-20 kHz) acoustic scattering measurements determined volume scattering strengths as a function of depth, frequency, and time of day. Fifty-nine successful biological trawl deployments determined species composition and their depths as a function of time of day. A swimbladder scattering

model was used to correlate biological and acoustic results. The variations in swimbladder parameters required to match model results to the measured scattering strengths provide the basis of the explanation of swimbladder behavior. Adults of only two fish species, *Bregmacerous cantori* and *Steindachneria argentea*, were caught. Both species were in the upper 200 m at night and began a downward migration shortly before sunrise. *S. argentea* settled in the vicinity of the oxic-anoxic interface, at 300-440 m, and remained there until late afternoon. *B. cantori* migrated to depths greater than 800 m, deep into anoxic water. *B. cantori* dispersed in early afternoon and eventually congregated at depths of 360-550 m in late afternoon. Both species began an upward migration to their nighttime depths shortly before sunset. In the pre-dawn hours, scattering in the 3-8 kHz range increased dramatically. Swimbladder scattering modeling indicates that during this time swimbladder volumes expanded significantly, tension in the swimbladder walls increased, the properties of the flesh surrounding the swimbladders changed, and most importantly, the mass of gas in the swimbladders increased. The modeling further indicates that both species use the oxygen added before dawn to survive in their respective hostile environments during the day. Thus, the results of this experiment indicate that fish inhabiting the Cariaco Trench are able to live at hostile depths during the daytime because of changes they make to their swimbladders during the nighttime, before descending to those depths.

Maina, J. N., Wood, C. M., Narahara, A., Bergman, H. L., Laurent, P., & Walsh, P. (1996). Morphology of the Swim (Air) Bladder of a Cichlid Teleost: *Oreochromis alcalicus grahami* (Trewavas, 1983), A Fish Adapted to a Hyperosmotic, Alkaline, and Hypoxic Environment: A Brief Outline of the Structure and Function of the Swimbladder. In *Fish Morphology: Horizon of New Research*. H. M. Dutta & J. S. Datta-Mushi (Eds.), (pp. 179-192). Brookfield, VT: A. A. Balkema Retrieved from <https://www.taylorfrancis.com/chapters/edit/10.1201/9780203755990-11/morphology-swim-air-bladder-cichlid-teleost-oreochromis-alcalicus-grahami-trewavas-1983-fish-adapted-hyperosmotic-alkaline-hypoxic-environment-brief-outline-structure-function-swimbladder-maina-wood-narahara-bergman-laurent-walsh>

Oreochromis alcalicus grahami, a fish which lives in the shallow peripheral lagoons of the alkaline oxygen-deficient Lake Magadi, has a partly divided physostomous airbladder. This chapter describes the structural design of the airbladder in this group of fish and demonstrates the possible adaptive morphological changes the organ may have undergone to contribute to the survival of the fish in its unique habitat. It reviews knowledge of the structure of the airbladder while highlighting ideas on the plausible mode of function of this enigmatic organ. The airbladder was investigated by gross dissection and latex rubber casting to study its shape, size, and topographic anatomy and its basic structural components using transmission and scanning electron microscopy to establish its ultrastructural and spatial morphology. The ontogeny of the airbladder and its possible role as the progenitor of the lung has long been debated yet the circumstances and factors which induced the change are far from clear.

Marchal, E., & Lebourges, A. (1996). Acoustic evidence for unusual diel behaviour of a mesopelagic fish (*Vinciguerria nimbaria*) exploited by tuna. *ICES Journal of Marine Science*, 53(2), 443-447. <https://doi.org/10.1006/jmsc.1996.0062>

For 15 years, there has been a seasonal tuna fishery in the open equatorial Atlantic Ocean. There are no good reasons for explaining this concentration of fish, except the possible abundance of micronekton. However, micronekton are only found during the night in the upper layers, whereas tuna feed during

the day, according to current assumptions. An acoustic cruise carried out in November 1992 clearly showed the presence in this area of a large schooling biomass of a small mesopelagic fish, *Vinciguerria nimbaria* (Photichtyidae). Instead of diving to a great depth during the day as usual, they remained in the upper layers and tuna (*Katsuwonus pelamis* and *Thunnus albacares*) were found to feed on them. The atypical behaviour of *Vinciguerria* involved two processes: reverse phototaxis and a break in the diel vertical migrations. A review of the literature shows that this fish: (1) is a common item in tuna stomach contents; and (2) is never caught in the upper layers during the day. This apparent discrepancy has been resolved by our results: schooling behaviour during the day prevents *Vinciguerria* from being sampled adequately by the usual systematic net rows. The need to use acoustics for successful sampling is obvious. It is likely that this behaviour occurs in other areas and could explain the local concentration of tuna.

Marshall, N. B. (1965). Systematic and biological studies of the Macrourid fishes (Anacanthini-Teleostii). *Deep Sea Research and Oceanographic Abstracts*, 12(3), 299-322. [https://doi.org/10.1016/0011-7471\(65\)90004-5](https://doi.org/10.1016/0011-7471(65)90004-5)

There are over 300 species of Macrouridae of which 90 per cent or more live close to the continental slopes between depths of some 200 and 2000 m. In general organization, particularly that involving parts of the olfactory, gustatory and lateralis systems, the macrourids are closely similar to gadid and related groups of the order Anacanthini. There are correlations between the unpaired fin pattern, jaw position and gill raker structure in the two main subfamilies, Macrourinae and Bathygadinae. These correlations are evidently linked to ways of swimming and feeding (pp. 304-305). In size, macrourid eyes are inversely related to the depths of their living spaces. Slope-dwelling species have the largest and most elaborate eyes, while abyssal species have the smallest eyes. Judged by the pattern of nerves belonging to the ramus lateralis accessorius system, macrourids have an extensive gustatory surface over the body and fins. There is a highly developed lateralis system on the head, where very wide canals contain large neuromasts capped with prominent cupulae. The long axes of the latter are set across the canals. The functional significance of such orientation — and of other features of the lateralis system — is discussed. Whether slope or abyssal species, nearly all macrourids have a well developed swimbladder. The deeper their living space, the longer are the capillaries in the retia mirabilia. This is understandable considering the main functions of the retia : to keep gases within the swimbladder and to generate requisite gas tensions for secretion by the gas gland. Both functions become harder with increasing depth, but the efficiency of both directly depends—*inter alia*—on the length of the retial capillaries. The males of most macrourine species have a pair of large drumming muscles attached to the forward part of the swimbladder. These muscles are doubtless used to produce sounds. Abyssal macrourines and bathygadines do not have such muscles. These facts are considered in the light of present ideas concerning the very limited range in which fishes can home to sources of sound and water displacements. Unlike most benthic fishes of the deep-sea floor, numerous macrourids have a light organ which contains luminous bacteria and is housed along the mid-line of the underparts. The possible biological roles of luminescence are discussed. Limited evidence suggests that macrourids lay buoyant eggs close to the bottom. The youngest larvae are found in depths around 200 meters : older ones occur at deeper levels. The life-history pattern is discussed in relation to the problem facing slope species : the maintenance of populations that live over a relatively narrow strip of the deep-sea floor. The few bathypelagic macrourids seem to have wide distributions. The slope dwellers, and even most abyssal species, range much less widely. Most often, the former are confined to one side of an ocean. Though most species are found in tropical regions, the diversity of the group does not follow the rather regular pole-to-equator increase shown by bathypelagic fishes. Certain oceanic regions, such as the Sulu Sea,

the Gulf of Mexico and the Caribbean, and the Hawaiian Islands, have been centers for extensive speciation.

Marshall, N. B. (1970). *Swimbladder development and the life of deep-sea fishes*. Paper presented at the International Symposium on Biological Sound Scattering in the Ocean, Warrenton, VA. Retrieved from https://www.worldcat.org/title/proceedings-of-an-international-symposium-on-biological-sound-scattering-in-the-ocean/oclc/477878&referer=brief_results

No abstract available.

Marshall, N. B., & Staiger, J. C. (1975). Biological Results of the University of Miami Deep-Sea Expeditions. 110. Aspects of the Structure, Relationships, and Biology of the Deep-Sea Fish *Ipnops Murrayi* (Family Bathypteroidae). *Bulletin of Marine Science*, 25(1), 101-111. Retrieved from <https://www.ingentaconnect.com/content/umrsmas/bullmar/1975/00000025/00000001/art00009>

The accumulation of a large series (60 specimens) of the unusual benthic bathypteroid fish, *Ipnops murrayi* Günther, 1878, has prompted a comparison with material previously described. The few differences found are attributable to increased sample size. The lateral-line system is described in detail and compared with those of *Bathytyphlops* and *Bathypterois*. The family Bathypteroidae is recognized to contain the subfamilies Bathypteroinae, Ipnopinae, Bathymicropinae, and Bathytphlopinae. Relationships between the aulopoid, myctophid, synodontoid, and alepisauroid fishes are discussed.

McCartney, B. S., & Stubbs, A. R. (1971). Measurements of the acoustic target strengths of fish in dorsal aspect, including swimbladder resonance. *Journal of Sound and Vibration*, 15(3), 397-420. [https://doi.org/10.1016/0022-460X\(71\)90433-0](https://doi.org/10.1016/0022-460X(71)90433-0)

The need for measurements of the acoustic target strength of fish is discussed. The phenomenon of swimbladder resonance of small deep ocean fish is well known and is a useful means of estimating their sizes. For larger commercial fish in shallower seas the resonant frequency is much lower and resonance is very difficult to observe in the field. A method of observing and measuring the swimbladder resonance of a captive live fish in controlled conditions is described, and results on several gadoids are given. Reasons for the observed resonant frequencies being higher than predicted are given; the damping of resonance is high, which is expected. Application of these results to acoustic sizing at sea appears remote. They are relevant, however, to studies of low-frequency sound propagation, and the experimental technique is offered as a useful tool in physiological studies involving swim-bladder function. Measurements at higher frequencies in the diffraction and geometrical regions are also presented, resulting in an empirical equation for target strength as a function of length of the fish and wavelength. It is believed that this equation is useful for acoustic fish sizing using echo sounders at sea. The swimbladder is the major scatterer over the whole frequency range.

McClatchie, S., Macaulay, G. J., & Coombs, R. F. (2003). A requiem for the use of 20 log10 Length for acoustic target strength with special reference to deep-sea fishes. *ICES Journal of Marine Science*, 60(2), 419-428. [https://doi.org/10.1016/S1054-3139\(03\)00004-3](https://doi.org/10.1016/S1054-3139(03)00004-3)

Although it is well known that the slopes of target strength (TS) and length relationships vary widely, it is common in fisheries acoustics to force the TS-length regression through a slope of 20. Is it time to abandon this practice? The theoretical justification was that TS should be proportional to cross-sectional area, and that area should scale as the square of the linear dimension (fish length). There are now many species other than gadoids that are the subject of acoustic surveys, and many of them do not have the same morphology as the gadoid fishes. The slope of the TS-length regressions deviates significantly from 20. The empirical slope should be used wherever it can be shown to be more appropriate than the 20 log10 L model. Using the data from swimbladder models, it is shown that Macrourids, a merluccid hake and Oreosomatidae have a different relationship should between swimbladder size and fish size compared with that of gadoids. It is demonstrated that the 20 log10 L model is not appropriate for these deep-water fish and that deviations from the model arise, to a considerable degree, from variation in fish morphotypes. The TS of deep-water Macrourids, a merluccid hake and Oreosomatidae are lower than that of gadoids. This is related to the swimbladder size–fish size relationship in different morphotypes, although not much evidence can be found to support the concept that swimbladder sizes are generally smaller in deep-sea fishes.

McCune, A. R., & Carlson, R. L. (2004). Twenty ways to lose your bladder: common natural mutants in zebrafish and widespread convergence of swim bladder loss among teleost fishes. *Evolution & Development*, 6(4), 246-259. <https://doi.org/10.1111/j.1525-142X.2004.04030.x>

Summary: Convergence is an important evolutionary phenomenon often attributed solely to natural selection acting in similar environments. The frequency of mutation and number of ways a phenotypic trait can be generated genetically, however, may also affect the probability of convergence. Here we report both a high frequency of loss of gas bladder (swim bladder) mutations in zebrafish and widespread convergent loss of gas bladders among teleost fishes. The phenotypes of 22 of 27 recessive lethal mutations, carried by a sample of 26 wild-caught zebrafish, involve loss or noninflation of the gas bladder. Nine of these bladderless mutations showed no other obvious phenotypic abnormalities other than the lack of an inflated gas bladder. At least 19 of the 22 bladderless mutations are genetically distinct, as shown by unique morphology or complementation. Although we were not able to obtain eggs for all 21 required crosses to demonstrate definitively that the remaining three mutations are different from all other bladderless mutations, all available evidence suggests that these mutants are also distinct. At least 79 of 425 families of extant teleosts include one or more species lacking a gas bladder as adults. Analysis of the trait's phylogenetic distribution shows that the gas bladder has been lost at least 30-32 times independently. Although adaptive explanations for gas bladder loss are convincing, a developmental bias toward bladderless phenotypes may also have contributed to the widespread convergence of this trait among teleosts. If gas bladder development in teleosts is as vulnerable to genetic perturbation as it is in zebrafish, then perhaps a supply of bladderless phenotypes has been readily available to natural selection under conditions for which it is advantageous not to have a gas bladder. In this way, developmental bias and selection can work together to produce widespread convergence.

McGowan, D. W., Horne, J. K., & Parker-Stetter, S. L. (2019). Variability in species composition and distribution of forage fish in the Gulf of Alaska. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 165, 221-237. <https://doi.org/10.1016/j.dsr2.2016.11.019>

In the Gulf of Alaska (GOA), forage fish species, such as age-0 walleye pollock (*Gadus chalcogrammus*), capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*), and mesopelagic fishes (e.g. *Myctophidae*), are ecologically important as both consumers of zooplankton, and as prey for fish, seabirds, and marine mammals. As part of the Gulf of Alaska Integrated Ecosystem Research Program, an acoustic-trawl survey was conducted in the summer and fall of 2011 and 2013 to quantify variability in species composition, density, and distributions of forage fish over the continental shelf and slope in the central and eastern regions of the GOA. The forage fish community in 2011 was characterized by the absence of age-0 pollock and lower densities of capelin, herring, and mesopelagics compared to observations in 2013. Age-0 pollock were abundant across both regions in summer 2013, but were rarely observed in fall. In contrast, summer observations of herring were rare, while aggregations of herring were observed over the eastern GOA shelf in fall of both years. Seasonal changes in community composition are attributed to the transport of age-0 pollock from offshore waters in summer to nearshore waters in fall, and to immigration of herring to the eastern GOA shelf in fall. Forage fish spatial patterns varied within and between regions due to intra- and interspecific differences in horizontal and vertical distributions that were correlated with bottom depth. Observed spatial and temporal variability in community composition and distributions of forage fish species may potentially impact predator foraging in the GOA, as well as the effectiveness of monitoring to detect changes in forage fish biomass.

Mintenbeck, K., & Torres, J. J. (2017). Impact of Climate Change on the Antarctic Silverfish and Its Consequences for the Antarctic Ecosystem. In *Antarctic Silverfish: A Keystone Species in a Changing Ecosystem*. M. Vacchi, E. Pisano, & L. Ghigliotti (Eds.), (Vol. 3, pp. 253-286) https://doi.org/10.1007/978-3-319-55893-6_12

Pleuragramma antarctica is the dominant forage fish of the coastal Antarctic, exhibiting a circumantarctic distribution and a well documented abundance in all shelf environments, from the high Antarctic Weddell and Ross Sea systems, to the milder waters of the western Antarctic Peninsula (WAP) shelf. Rapid regional warming on the WAP has produced a dichotomy in annual weather patterns between the high Antarctic systems and the WAP, resulting in swiftly rising midwinter air temperatures and fewer sea ice days during the annual winter cycle on the WAP, and little change in the Ross and Weddell Seas. The WAP shelf thus provides a model system for examining the potential effects of climate warming on an important Antarctic species. *Pleuragramma*'s life history is characterized by slow growth, late maturity, a high reproductive investment and an association with coastal sea ice for spawning and larval development. All those features will allow the species to weather episodic annual failures in recruitment, but not long term change. Most effects of the increasing temperature associated with climate change will be indirect ones, as temperatures will not increase to the point where they are physiologically life-threatening in the short term. A recent survey of *Pleuragramma* distribution on the WAP shelf revealed a large break in its historical distribution in shelf waters, suggesting a collapse in the local population of silverfish there. The break occurred in the area that has been most heavily impacted by rapid regional warming: the northern mid-shelf including Anvers and Renaud Island. It may be that the multi-faceted effects of climate change are already at work in its local disappearance.

Miyashita, K. (2003). Diurnal changes in the acoustic-frequency characteristics of Japanese anchovy (*Engraulis japonicus*) post-larvae "shirasu" inferred from theoretical scattering models. *ICES Journal of Marine Science*, 60(3), 532-537. [https://doi.org/10.1016/S1054-3139\(03\)00066-3](https://doi.org/10.1016/S1054-3139(03)00066-3)

Diurnal changes in the acoustic-frequency characteristics of "shirasu", a post-larval stage of Japanese anchovy (*Engraulis japonicus*), were analysed based on theoretical scattering models. Since post-larval swimbladders contain gas at night but not during the day, the distorted-wave Born approximation (DWBA), based on the deformed-cylinder model, which assumes there is no gas in the swimbladder, was applied to daytime observations, and the fish-bladder resonance model, which assumes there is gas in the swimbladder, to those taken at night. The two sets of acoustic frequencies employed were 50 and 200 kHz, which are those used for shirasu commercial fishing, and 38 and 120 kHz, which are usually employed for acoustic surveys using a quantitative echosounder. During the daytime, differences in shirasu target strengths between the two frequencies were large, especially between 38 and 120 kHz, but at night there was little difference with frequency, suggesting that acoustic surveys for identifying and estimating the abundance of shirasu should be done during daytime, when differences occur between frequencies and the shirasu form dense schools.

Monti, J. M., & Hayek, C. S. (1993). Low Frequency Volume Scatter and Distant Reverberation: 200–1500 Hz. In *Ocean Reverberation*. D. D. Ellis, J. R. Preston, & H. G. Urban (Eds.), (pp. 263-270). Dordrecht: Springer Netherlands https://doi.org/10.1007/978-94-011-2078-4_36

Low frequency volume scatter and distant reverberation measurements have been made in the Icelandic Basin, Gulf of Alaska and the Ionian Sea. Volume scattering data showing effects of fish swimbladder resonance along with spatial and temporal dependencies have been obtained as a function of depth to 600 m and frequency from 200–1500 Hz using explosives and a vertical line array receiver. Distant reverberation results, obtained using controlled waveforms from a vertical line array of projectors and a horizontal line array receiver (i.e., a near-monostatic configuration), also show effects of biological scattering. Both ray and mode based distant reverberation model predictions, utilizing in situ volume scatter data, agree well with measurements.

Nafpaktitis, B. G., Backus, R. H., Craddock, J. E., Haedrich, R. L., Robison, B. H., & Karnella, C. (2018). Family Myctophidae - Swimbladder. In *Fishes of the Western North Atlantic: Order Inomi (Myctophiformes)*. (pp. 18). New Haven, CT: Yale University Press <https://doi.org/10.12987/9781933789309-003>

No abstract available.

Neighbors, M. A. (1992). Occurrence of inflated swimbladders in 5 species of lanternfishes (family Myctophidae) from waters off Southern California. *Marine Biology*, 114(3), 355-363. <https://doi.org/10.1007/bf00350026>

The swimbladders of three species of myctophid fishes (*Symbolophorus californiensis*, *Tarletonbeania crenularis* and *Diaphus theta*, collected in the Southern California Bight between 1963 and 1978), previously observed to have both inflated and noninflated swimbladders as adults, were examined to determine if the swimbladders either vary in their inflation on a diel basis or cease to be inflated and

possibly become nonfunctional in some individuals. The swimbladders of two lanternfishes reported to lack inflated swimbladders as adults (*Lampanyctus regalis* and *L. ritteri*) were included in the study for comparison. Only the swimbladder of *L. regalis* did not increase in size with increasing fish size. In the remaining four species, both the lengths and volumes of noninflated swimbladders were positively correlated with fish standard length (SL). Although the swimbladder continued to increase in size, inflated swimbladders were not found in *L. ritteri* > 23 mm SL. Inflated and noninflated swimbladders occurred in overlapping size ranges of *S. californiensis*, *T. crenularis*, and *D. theta*. Only 11 % of the *D. theta* swimbladders were inflated, and the occurrence of inflated swimbladders did not differ significantly with day vs night capture or fish size. Although the frequency of occurrence of inflated swimbladders decreased significantly in larger *S. californiensis*, both *S. californiensis* and *T. crenularis* caught at the surface at night with a neuston net had significantly higher proportions of inflated swimbladders than did those collected below the surface with either daytime or night-time trawls. The swimbladder does not appear to become nonfunctional in either species. Rather than maintaining either constant volumes or constant masses of gas in their swimbladders during their vertical migrations, both species may inflate their swimbladders only while in the surface waters at night, and have noninflated swimbladders while at other depths of their vertical ranges.

Neighbors, M. A., & Nafpaktitis, B. G. (1982). Lipid compositions, water contents, swimbladder morphologies and buoyancies of nineteen species of midwater fishes (18 myctophids and 1 neoscopelid). *Marine Biology*, 66(3), 207-215. <https://doi.org/10.1007/bf00397024>

Lipid compositions, water contents, swimbladder morphologies and specific gravities were studied for 19 species of oceanic midwater fishes, chiefly myctophids (lanternfishes) collected offshore from Oregon and California from 1975–1979. Three groups of species were recognizable. The first group had bodies low in both lipid and water content; they were denser than seawater, regardless of swimbladder morphology, which varied from absent through non-inflated to inflated. The second group had bodies low in lipid but high in water content; they were neutrally buoyant, evidently because of their high content of water, although their swimbladders were never inflated. The majority of the members of the aforementioned groups contained higher proportions of triglycerides than wax esters. The third group had bodies with high lipid but low water content; those with high triglyceride content had swimbladders ranging from non-inflated to (less commonly) inflated, were denser than seawater, and the lipid percentage of their body weights varied both with size and season, indicating that triglycerides function mainly as an energy store. The adults of species in the third group with a higher content of wax esters than triglycerides lacked inflated swimbladders, were neutrally buoyant, and the lipid percentage of their body weights was relatively constant with size and season, indicating that wax esters permit these fishes to attain neutral buoyancy in seawater.

Nero, R. W., Thompson, C. H., & Love, R. H. (1997). Abyssopelagic grenadiers: the probable cause of low frequency sound scattering at great depths off the Oregon and California coasts. *Deep Sea Research Part I: Oceanographic Research Papers*, 44(4), 627-645. [https://doi.org/10.1016/S0967-0637\(96\)00098-2](https://doi.org/10.1016/S0967-0637(96)00098-2)

Volume reverberation measurements from the slope base and abyssal plain along the coasts of Oregon and northern California show an unexpected scattering layer peaking around 2000 Hz at depths greater than 1000 m. A model of swimbladder resonance applied to published records of bottom-dwelling grenadier size and abundance provided a good fit to the data, suggesting the widespread pelagic

occurrence of grenadiers, *Coryphaenoides* spp., of 20–68 cm length at densities near 0.004 ind. m⁻² over the slope base and abyssal plain.

Nielsen, J. G., & Munk, O. L. E. (1964). A Hadal Fish (*Bassogigas profundissimus*) with a Functional Swimbladder. *Nature*, 204(4958), 594-595. <https://doi.org/10.1038/204594a0>

During the Danish Galathea Expedition (1950–52) a specimen of the brotulid fish, *Bassogigas profundissimus* (Roule, 1913), was caught in the Sunda trench (Station No. 466, depth 7,160 m); it measured 157 mm in standard length. The gear used was a herring otter trawl, which was operated at the bottom for a period of 2 h. The bottom material consisted of bluish mud, and the bottom temperature was 1.5° C. The uphaul of the trawl took 4 h.

Ohshima, S., Yasuda, T., Tanaka, H., & Sassa, C. (2012). Biomass fluctuation of two dominant lanternfish *Diaphusgarmani* and *D. chrysorhynchus* with environmental changes in the East China Sea. *Fisheries Science*, 78(1), 33-39. <https://doi.org/10.1007/s12562-011-0424-x>

Acoustic surveys have been conducted for estimating the biomass of commercially important fish (e.g., anchovy, jack mackerel), lanternfish (*Diaphusgarmani* and *D. chrysorhynchus*), and pearlside (*Maurolicus japonicus*) in summer in the East China Sea (ECS) since 1997. The biomass of lanternfish and pearlside was 2.26–19.16 times that of commercially important fish, and these species represented substantial biomass in the ECS. Though there were no correlations between biomass of pearlside and environmental indices, significant correlations between biomass of lanternfish and southern oscillation index (SOI) in March (positive correlation), arctic oscillation (AO) in March (negative) and October (positive), monsoon index (MOI) in February (positive), and Kuroshio flow mass in winter (positive) were observed. Weak AO and strong MOI would cool down the sea temperature and would lead to increased primary and secondary production in the ECS, thereby enhancing larval survival of lanternfish. The SOI would affect the Kuroshio meander in the ECS, and strong SOI and Kuroshio flow mass would transport larvae of lanternfish to the present survey area. This is the first report on the lanternfish standing stock and its fluctuation in the ECS.

Ok, M., & Gucu, A. C. (2019). A study on European anchovy (*Engraulis encrasicolus*) swimbladder with some considerations on conventionally used target strength. *Turkish Journal of Zoology*, 43(2), 203-214. <https://doi.org/10.3906/zoo-1809-21>

Hydroacoustic surveys are one of the prime methods to assess the commercially top-ranked small pelagic stocks. The method relies on acoustic scattering from a fish, which is largely controlled by the size and morphology of the swimbladder. In this study, the changes in the size of the European anchovy swimbladder sampled in the Black Sea were investigated. Ventral cross-sectional area (by photographing the ventrally dissected fish) and volume (by dorsal and lateral X-raying) of the swimbladders were estimated. Comparison of areas showed that the stomach fill and presence of viscera did not have a statistically significant impact on the swimbladder size while the hepatosomatic index showed significant impact. Although the vertical distribution of the anchovy is naturally not very wide due to absence of sufficient oxygen below 100 m, sampling depth showed significant impact on the volume of the swimbladder. However, it was also observed during X-ray imaging that a considerable number of fish (87%) had deflated swimbladders. The reasons for this variability, which may have significant implication

on the acoustic estimations and stock assessment, were also discussed. The importance of acclimatization of the fish at surface conditions in studies addressing changes in swimbladder morphometry was underlined.

Olivar, M. P., Bernal, A., Molí, B., Peña, M., Balbín, R., Castellón, A., . . . Massutí, E. (2012). Vertical distribution, diversity and assemblages of mesopelagic fishes in the western Mediterranean. *Deep Sea Research Part I: Oceanographic Research Papers*, 62, 53-69.
<https://doi.org/10.1016/j.dsr.2011.12.014>

The mesopelagic fish community of the western Mediterranean was studied during two cruises carried out in December 2009 and July 2010 in the shelf and slope zones around the Balearic Islands. Much of what was previously known about this deep water group of fishes in the Mediterranean Sea came from studies performed using planktonic and small midwater nets. This study was the first attempt to use large pelagic trawls and small nets combined with information about the main sound scattering layers to analyse mesopelagic fish composition, diversity and species assemblages. This community is characterised by a relatively low diversity compared to other oceanic regions of the world, with Myctophiformes and Stomiiformes being the main contributors. Bathymetry and the level of the water column were the most important factors structuring the investigated fish assemblages, and similar vertical patterns were observed for the different species collected during the two study periods. A shelf assemblage composed of a few species of myctophids, with *Notoscopelus elongatus* being the main contributor, was distinguished. The slope assemblage included both Myctophiformes and Stomiiformes that showed differences in their day-night main location along the water column. In terms of species behaviour, two important groups were detected. The first was non-migrant or weakly migrant species, with the paradigmatic example being the gonostomatid *Cyclothona braueri*, which occurred at a depth of 400–600m; this species is partly responsible for the permanent acoustic (38kHz) response at this depth. The second group, near-surface migrants at night, was represented by most of the juvenile and adult myctophids, exemplified by *Ceratoscopelus maderensis*, with the exception of just a few of the largest size classes of some species, such as *Lampanyctus crocodilus* and *N. elongatus* that remain near the bottom.

Paig-Tran, E. W. M., Barrios, A. S., & Ferry, L. A. (2016). Presence of repeating hyperostotic bones in dorsal pterygiophores of the oarfish, *Regalecus russellii*. *Journal of Anatomy*, 229(4), 560-567.
<https://doi.org/10.1111/joa.12503>

Hyperostosis, excessive bone growth along bone that stems from bone, periosteum or articular or epiphyseal cartilage, occurs in at least 22 families of fishes most of which are tropical or subtropical marine species. While the presence of hyperostosis is well documented in fishes, the mechanism driving the development of the excessive bone growth is unclear. This study documented hyperostosis along the dorsal pterygiophores in both sexes of oarfish, *Regalecus russellii*; however, it was not present in all specimens examined. This is the second lampridiform fish with hyperostoses and the first case documented in a deeper-water, epi-mesopelagic fish. In oarfish, the majority of the dorsal pterygiophores tissues are poorly mineralized, anosteocytic bones with some fish displaying localized stiffened, hyperostotic growths near the distal edge. Oarfish lack a swim bladder so they must continuously beat their bi-directional dorsal fin to maintain position within the water column while engaged in locomotory behavior. These fishes have areas of localized, hyperostotic skeletal elements along the dorsal pterygiophores that, presumably, function as a stiffened lever system to support fin

undulation. It was noted that hyperossification was not present in all fish examined and was only documented in fish with total lengths greater than 3m.

Pelster, B. (2015). Swimbladder function and the spawning migration of the European eel *Anguilla anguilla*. *Frontiers in Physiology*, 5(486). <https://doi.org/10.3389/fphys.2014.00486>

The spawning migration of the European eel is an extensive journey over 5000 to 7000 km from the European coast to the Sargasso Sea. Eels do not feed during this journey and on-board fuels must be sufficient to support the journey of 3.5 to 6 month, as well as sexual maturation and the spawning activity. Swimming of eels appears to be quite energy efficient compared to other fish species, and elevated hydrostatic pressure has been shown to even reduce the costs of transport. Recent studies revealed, however, that during traveling eels perform extensive diurnal migrations and swim at a depth of about 100–300 m at night time, but go down to 600–1000 m at day time. At a depth of 200 m eels are exposed to a hydrostatic pressure of 21 atmospheres (2.13 MPa), while at 800 m hydrostatic pressure increases to 81 atmospheres (8.21 MPa). Accordingly, without any compensation at a depth of 800 m swimbladder volume will be reduced to about 25% of the volume established with neutral buoyancy at 200 m. Consequently, these diurnal changes in depth must be taken into consideration for a calculation of the energy requirements of the spawning migration. Without compensation a compression of the swimbladder will result in a status of negative buoyancy, which makes swimming more costly. Trying to keep the status of neutral buoyancy during descent by gas secretion into the swimbladder in turn requires metabolic activity to enhance swimbladder perfusion and for acid production of the gas gland cells to stimulate gas secretion. During ascent gas is passively removed from the swimbladder in the resorbing section and in the blood transported to the gills, where it is lost into the water. Accordingly, the swimbladder appears to be a crucial organ for the spawning migration. It can be assumed that an impairment of swimbladder function for example due to an infection with the nematode *Anguillicola crassus* significantly threatens the success of the spawning migration.

Pena, H., & Foote, K. G. (2008). Modelling the target strength of *Trachurus symmetricus murphyi* based on high-resolution swimbladder morphometry using an MRI scanner. *ICES Journal of Marine Science*, 65(9), 1751-1761. <https://doi.org/10.1093/icesjms/fsn190>

The acoustic target strength (TS) of Chilean jack mackerel (*Trachurus symmetricus murphyi*) was computed from three-dimensional reconstructions of the swimbladder form. The primary morphometric data were derived from high-resolution images made with a clinical whole-body 3-tesla magnetic resonance imaging (MRI) scanner. The fish were obtained from a commercial purse-seiner operating off Chile during 2003. Transverse MRI sequences of 18 fish were performed with a volumetric pixel 0.5×0.5 mm in cross section and 0.7 mm in the axial direction. From each transverse section, the swimbladder contour was traced manually using a digital pen tablet and smoothed using an automatic interpolation routine. The digital contours were used to build a triangular mesh spanning the swimbladder surface. The high-resolution swimbladder models revealed details such as undulations in the dorsal surface of the swimbladder caused by the backbone, and holes where the haemal spines penetrate the posterior end of the swimbladder. The Kirchhoff approximation was used to compute TS as a function of fish orientation at 38 kHz. The mean dorsal-aspect TS was computed for several orientation patterns and regressed on the logarithm of total fish length to derive operationally simple formulae.

Pena, M. (2019). Mesopelagic fish avoidance from the vessel dynamic positioning system. *ICES Journal of Marine Science*, 76(3), 734-742. <https://doi.org/10.1093/icesjms/fsy157>

The study of marine organism behaviour and vertical distribution requires the use of techniques that do not disturb their natural state. This study analyses the mesopelagic fishes behaviour influenced by the presence of a research vessel. Acoustic data recorded on board the RV "Angeles Alvarino" during the RAPROCAN 2017 survey showed a clear pattern of mesopelagic fishes migrating deeper in the water column at night when the DP system was connected. Details on how the scatterers changed their trajectory when migrating to the surface at night and the progressive increase in avoidance depth when dawn approached is shown. An experiment was carried out to discern fish reaction to vessel lights and to the DP system. While a dispersed diving was detected when the lights were switched on, a more acute reaction to the DP system was registered with not only vertical displacement, but also an increment in scattering produced by an aggregating behaviour. Both vessel DP-noise and light modify the mesopelagic fish behaviour, which needs to be accounted for when studying mesopelagic layers close to the surface. Surveys aiming at estimating abundance and biomass from these species are encouraged to do so at day time.

Peña, M., & Calise, L. (2016). Use of SDWBA predictions for acoustic volume backscattering and the Self-Organizing Map to discern frequencies identifying *Meganyctiphanes norvegica* from mesopelagic fish species. *Deep Sea Research Part I: Oceanographic Research Papers*, 110, 50-64. <https://doi.org/10.1016/j.dsr.2016.01.006>

To acoustically assess the biomass of multiple species or taxa within a survey region, the volume backscatter data should be apportioned to the constituent sound scatterers. Typically, measured backscatter is attributed to certain species using predictions at different frequencies, mostly based on the difference in scattering at the frequencies of 38 and 120kHz (dual frequency method). We used the full version of the stochastic distortedwave Born approximation (SDWBA) model to predict backscatter spectra for *Meganyctiphanes norvegica* and to explore the sensitivities of Δ MVBS to the model parameters, e.g. acoustic frequency and incidence angle, and animal density and sound speed contrast, length, and shape. The orientation is almost the unique parameter responsible for variation, with flatness affecting longer lengths. We present a summary of Δ MVBS that can serve as the basis for identification algorithms. Next, we simulate the scenario encountered in the Balearic Sea (western Mediterranean) where Northern krill are mixed with mesopelagic fish species (bristlemouths and lanternfishes), which are modeled with a prolate spheroid model. Simulated numerical data are employed to emulate the discrimination process with the most common identification techniques and typical survey frequencies. The importance of using density-independent techniques for acoustic classification is highlighted. Finally, an unsupervised neural network, the Self-Organizing Map (SOM), is used to cluster these theoretical data and identify the frequencies that provide, in this case, the most classification potential. The simulation results confirm that pairs of frequencies spanning the Rayleigh and geometric scattering regimes of the targets are the most useful for clustering; a minimum of four frequencies are necessary to separate the three species, while three frequencies are able to differentiate krill from mesopelagic fish species.

Pena, M., Olivar, M. P., Balbin, R., Lopez-Jurado, J. L., Iglesias, M., & Miquel, J. (2014). Acoustic detection of mesopelagic fishes in scattering layers of the Balearic Sea (western Mediterranean). *Canadian Journal of Fisheries and Aquatic Sciences*, 71(8), 1186-1197. <https://doi.org/10.1139/cjfas-2013-0331>

The distributions of micronekton layers in the Balearic Sea (western Mediterranean) were investigated by acoustic methods. Two multidisciplinary surveys were carried out in late autumn 2009 and summer 2010, recording acoustic, biological, and hydrographic data. We described acoustic layers, migratory behavior, sampled species, and water masses processes. Acoustic modeling of gas-bearing organisms was employed to explain differences between acoustic estimates and sampled abundances. The influence of environmental variables on the vertical distribution and migration pattern of these organisms was analyzed. The thermocline depth was related to the preferred depth for migrating myctophids, while nonmigrant species dwelled in the oxygen minimum zone of the water column both in late autumn and summer periods.

Pena, M., Villanueva, R., Escanez, A., & Ariza, A. (2018). Opportunistic acoustic recordings of (potential) orangeback flying squid *Sthenoteuthis pteropus* in the Central Eastern Atlantic. *Journal of Marine Systems*, 179, 31-37. <https://doi.org/10.1016/j.jmarsys.2017.11.003>

Squids are fast swimmers that are difficult to catch by nets and to record with echosounders in the open ocean. A rare detection of orangeback flying squid *Sthenoteuthis pteropus* in the Central Eastern Atlantic Ocean off the coast of Senegal was accomplished during the MAFIA oceanographic survey carried out between Brazil and the Canary Islands in April 2015. Although net sampling did not yield any subadult or adult individuals, dozens were visually detected from the vessel jumping out of the water at night and displaying their characteristic dorsal photophore patch. A few squids were caught with fishing lines and identified at the species level. The acoustic echograms revealed distinctive previously unobserved acoustic echotraces that seemed to be caused by those squids, which were the only new species detected at that station (over a bottom depth ranging from 4010 to 5215 m, between 10 degrees 45'N 22 degrees 41'W and 10 degrees 53'N 22 degrees 40'W). The acoustic response and swimming behaviour shown by those echotraces reinforced this hypothesis. The (potentially) squid recordings dove rapidly (0.19 m/s to 0.48 m/s) from around 10 m below the mesopelagic fish layer, which had migrated to the subsurface at night (35 m depth), to depths of 70-95 m, and swam upward, apparently attacking fish from below. The morning squid migration to deeper waters (250-300 m) was also recorded acoustically. Downward movements of squid swimming at speeds of 0.22 m/s were calculated from the echogram, while the mesopelagic migrating fish swam at 0.27 m/s reaching 250 m depth. S-v120 - S-v38 averaged 2.7 +/- 3.2 dB for the squid echotraces while the mesopelagic layer showed values of -8.8 +/- 0.9 dB. These ranges agreed with values in the literature and from theoretical models. This study provides more insight into the migrating behaviour of oceanic squids, a species group that is poorly represented in the acoustic literature due to challenges in studying them.

Perelman, J. N., Firing, E., van der Grient, J. M. A., Jones, B. A., & Drazen, J. C. (2021). Mesopelagic Scattering Layer Behaviors Across the Clarion-Clipperton Zone: Implications for Deep-Sea Mining. *Frontiers in Marine Science*, 8(492). <https://doi.org/10.3389/fmars.2021.632764>

The Clarion-Clipperton Zone (CCZ) is a 4 million km² area in the eastern Central Pacific Ocean exhibiting large variability in environmental parameters, particularly oxygen and primary production, that is being

targeted for deep-sea polymetallic nodule mining. This remote region's pelagic biology is very poorly sampled, including for micronekton and zooplankton that provide essential ecosystem services such as carbon flux and support for commercial fisheries. We built a baseline of deep scattering layer (DSL) depths and vertical migration behaviors, proxies for mesopelagic micronekton and zooplankton communities, using shipboard acoustic Doppler current profiler datasets. Acoustic data (38 kHz, 75 kHz) were compiled from research cruises passing near or through the CCZ (2004–2019), and environmental data (mean midwater oxygen partial pressure, surface chlorophyll-a, and sea surface height anomaly) were assembled from the World Ocean Atlas and satellite oceanographic datasets. Our results suggest that midwater oxygen, associated with the Eastern Tropical Pacific Oxygen Minimum Zone (OMZ), is the strongest predictor of daytime DSL depths and the proportions of midwater populations that undergo vertical migration in this region. We used these relationships to predict micronekton and zooplankton behaviors across the CCZ, including licensed mining exploration areas and no-mining reserves. While the OMZ encompasses most licensed exploration areas, the current network of reserves lies outside of the core OMZ and ultimately may not represent or protect the pelagic OMZ fauna at highest risk from mining impacts. This research will further assist in developing resource exploitation regulations by the International Seabed Authority, and will provide mesopelagic baseline information for monitoring changes that may occur in the CCZ once industrial-scale mining begins.

Pérez-Arjona, I., Godinho, L., & Espinosa, V. (2020). Influence of fish backbone model geometrical features on the numerical target strength of swimbladdered fish. *ICES Journal of Marine Science*, 77(7-8), 2870-2881. <https://doi.org/10.1093/icesjms/fsaa160>

The method of fundamental solutions has been applied to evaluate the influence of fish models geometrical features on the target strength (TS) directivity and TS frequency response of swimbladdered fish. Simplified models were considered for two fish species: gilt-head sea bream (*Sparus aurata*, Linnaeus 1758) and Atlantic salmon (*Salmo salar*, Linnaeus 1758), and different geometrical details of their morphology were studied, such as backbone presence, and its curvature or the inclusion of vertebrae modulation. Swimbladder shape and tilt, together with the inclusion of backbone (and its realistic curvature) for dorsal measurements were the most important features for proper estimation of mean TS. The estimation of mean TS is considered including the effect of fish tilt, the echosounder frequency, and the fish-to-transducer distance.

Phleger, C. F. (1998). Buoyancy in marine fishes: Direct and indirect role of lipids. *American Zoologist*, 38(2), 321-330. <https://doi.org/10.1093/icb/38.2.321>

The major lipids that have a direct role in buoyancy of marine fish are wax esters, squalene, and alkyldiacylglycerols. Wax esters are stored extracellularly in certain fishes, such as the orange roughy (*Hoplostethus atlanticus*), and therefore buoyancy appears to be their sole function. Some myctophid fishes have wax-invested swimbladders, where the non-compressible wax esters may aid in diurnal vertical migration, by replacing compressible swimbladder gases. Squalene is metabolically inert in the livers of certain sharks, and therefore probably has buoyancy as its only function. Alkyldiacylglycerols (DAGE) are abundant components of liver oil of certain deep sea sharks and holocephalans, where they may have an important role in buoyancy. Triacylglycerols and cholesterol are lipids that have an indirect role in buoyancy of marine fish. Many fishes in the ocean have oil-filled bones (mostly triacylglycerols). Although this oil aids buoyancy, its major function is as an energy storage lipid which can be utilized during starvation. Cholesterol, which is found in high amounts in the lipid-rich membranes of the

swimbladder of deep sea fishes, may aid buoyancy by combining with oxygen gas in the swimbladder membranes to facilitate gas secretion in fish at great depths in the ocean. Further research is needed to understand the physical state of lipids, such as wax esters at deep sea temperatures and pressures, and more evidence is needed to clarify the role of cholesterol-rich membranes in swimbladders of deep sea fishes.

Phleger, C. F., Holtz, R. B., & Grimes, P. W. (1977). Membrane biosynthesis in swimbladders of deep sea fishes *Coryphaenoides acrolepis* and *Antimora rostrata*. *Comparative Biochemistry and Physiology Part B: Comparative Biochemistry*, 56(1), 25-30. [https://doi.org/10.1016/0305-0491\(77\)90217-6](https://doi.org/10.1016/0305-0491(77)90217-6)

1. Excised tunica interna from the swimbladder of an abyssal fish (*Coryphaenoides acrolepis*) incorporated acetate-1-14C and squalene-4-3H into membrane lipids, cholesterol, phosphatidyl ethanolamine, phosphatidylcholine, cardiolipin, and to a lesser extent sphingomyelin.
2. Ultrastructural study of the tunica interna of the swimbladder of another abyssal fish (*Antimora rostrata*) revealed large cytoplasmic vacuoles lined and filled with “bilayer” membrane.
3. The membrane-lined vacuoles in the tunica interna cells may be an assembly point for the biosynthesis of the gram quantities of pure “bilayer” membrane found on the interior of the swimbladder.

Planque, B., Kristinsson, K., Astakhov, A., Bernreuther, M., Bethke, E., Drevetnyak, K., . . . Stransky, C. (2013). Monitoring beaked redfish (*Sebastes mentella*) in the North Atlantic, current challenges and future prospects. *Aquat. Living Resour.*, 26(4), 293-306. Retrieved from <https://doi.org/10.1051/alr/2013062>

Beaked redfish inhabits North Atlantic waters in the depth range 100–950 m, over the continental shelf, slope and the open ocean. Individuals can live demersal or pelagic, at various stages of their life cycle. The geographical distribution of the species extends to most of the Atlantic waters from Newfoundland and the Labrador basin in the west to the Barents Sea in the east. Monitoring beaked redfish is challenging because of the species wide geographical distribution and large scale migrations; deep distribution, which complicates trawling and hydroacoustic surveys; difficulties with tagging; and persistent difficulties in taxonomic identification. These challenges make it a particularly problematic species to observe with conventional research methods. We review these key challenges and provide recommendations for the coordinated observation of *Sebastes mentella* in the North Atlantic that would best contribute to the assessment and ecological research on this species.

Proud, R., Handegard, N. O., Kloster, R. J., Cox, M. J., & Brierley, A. S. (2019). From siphonophores to deep scattering layers: uncertainty ranges for the estimation of global mesopelagic fish biomass. *ICES Journal of Marine Science*, 76(3), 718-733. <https://doi.org/10.1093/icesjms/fsy037>

The mesopelagic community is important for downward oceanic carbon transportation and is a potential food source for humans. Estimates of global mesopelagic fish biomass vary substantially (between 1 and 20 Gt). Here, we develop a global mesopelagic fish biomass model using daytime 38 kHz acoustic backscatter from deep scattering layers. Model backscatter arises predominantly from fish and siphonophores but the relative proportions of siphonophores and fish, and several of the parameters in

the model, are uncertain. We use simulations to estimate biomass and the variance of biomass determined across three different scenarios; S1, where all fish have gas-filled swimbladders, and S2 and S3, where a proportion of fish do not. Our estimates of biomass ranged from 1.8 to 16 Gt (25-75% quartile ranges), and median values of S1 to S3 were 3.8, 4.6, and 8.3 Gt, respectively. A sensitivity analysis shows that for any given quantity of fish backscatter, the fish swimbladder volume, its size distribution and its aspect ratio are the parameters that cause most variation (i.e. lead to greatest uncertainty) in the biomass estimate. Determination of these parameters should be prioritized in future studies, as should determining the proportion of backscatter due to siphonophores.

Pusch, C., Hulley, P. A., & Kock, K. H. (2004). Community structure and feeding ecology of mesopelagic fishes in the slope waters of King George Island (South Shetland Islands, Antarctica). *Deep-Sea Research Part I-Oceanographic Research Papers*, 51(11), 1685-1708.
<https://doi.org/10.1016/j.dsr.2004.06.008>

The role of mesopelagic fishes in the Southern Ocean ecosystem and more particular their trophic effect on the standing stock of mesozooplankton is at present poorly understood. To get a deeper insight in the Antarctic mid-water ecosystem the mesopelagic fish community of the King George Island slope (South Shetland Islands) was sampled with a pelagic trawl in 1996. The community structure was analysed and the feeding ecology was studied of the five most abundant species. A total of 18 mesopelagic fish species in 10 families was identified. Of these, the Nlyctophidae was the most important family by species number (9 species), individual number (98.5% of all individuals) and fish wet weight (87.3% of the total weight). The assemblage was numerically dominated by four myctophids (*Electrona antarctica*, *Gymnoscopelus braueri*, *Gymnoscopelus nicholsi*, *Protomyctophum bolini*) and one gempilid (*Paradiplospinus gracilis*). Multivariate statistical analysis of the mesopelagic fish data reveals two major groups of stations according to the sampled depth: a shallow group of stations (295-450 m depth) and a deeper group of stations (440-825 m depth). The change in relative abundance of mesopelagic fish species at 440-450 m coincides with the presence of warmer and denser Circumpolar Deep Water at and below these depths. Deeper stations were characterized by a higher density and increased diversity of mesopelagic fish species. The community patterns identified correlated well with the vertical depth distribution of the most abundant species. Dietary analysis reveals that myctophids are mostly zooplanktivorous, while the gempilid *P. gracilis* is classified as a piscivorous predator. The small *P. bolini* feed mainly on copepods of the species *Metridia gerlachei*, while the most important prey item of the larger myctophids *E antarctica*, *G. braueri*, and *G. nicholsi* were various species of euphausiids. Investigation of feeding chronology showed that *G. nicholsi* and *P. bolini* were feeding day and night. Daily ration estimates for myctophid species ranged from 0.28% to 3.3% of dry body weight (0.5-5.94% of wet body weight). Krill (*Euphausia superba*) were the most important food of *E antarctica* and *G. nicholsi*, accounting for 53.1% and 58.3% of the total food weight, respectively. The annual removal from the krill stock by both species was estimated to amount to 11.1-26.7% in the South Shetland Islands region. This estimate emphasizes the important role of mesopelagic fish in the Antarctic ecosystem as a prevalent consumer of krill.

Receveur, A., Kestenare, E., Allain, V., Menard, F., Cravatte, S., Lebourges-Dhaussy, A., . . . Menkes, C. (2020). Micronekton distribution in the southwest Pacific (New Caledonia) inferred from shipboard-ADCP backscatter data. *Deep-Sea Research Part I-Oceanographic Research Papers*, 159. <https://doi.org/10.1016/j.dsr.2020.103237>

Acoustic data are invaluable information sources for characterizing the distribution and abundance of mid-trophic-level organisms (micronekton). These organisms play a pivotal role in the ecosystem as prey of top predators and as predators of low-trophic-level organisms. Although shipboard-ADCP (acoustic Doppler current profiler) acoustic backscatter signal intensity cannot provide an absolute biomass estimate, it may be a useful proxy to investigate variability in the distribution and relative density of micro-nekton. This study used acoustic recordings data spread across 19 years (1999-2017) from 54 ADCP cruises in New Caledonia's subtropical EEZ (exclusive economic zone) to assess seasonal and interannual variabilities and spatial distribution of micro-nekton. The dataset was composed of two different ADCPs: 150 kHz for the first period, followed by 75 kHz for more recent years. We examined the 20-120 m averaged scattering layer. Using the few cruises with concurrent EK60 measurements, we proposed that the backscatter from the ADCPs and 70 kHz EK60 were sufficiently closely linked to allow the use of the backscatter signal from the ADCPs in a combined dataset over the full time series. We then designed a GAMM (generalized additive mixed model) model that takes into account the two ADCP devices as well as temporal variability. After accounting for the effect of the devices, we showed that the acoustic signal was mainly driven by diel vertical migration, season, year, and ENSO (El Nino-Southern Oscillation). In a second step, a consensus model between two statistical approaches (GAMM and SVM) (support vector machine) was constructed, linking the nighttime 20-120 m backscatter to the oceanographic and geographic environment. This model showed that sea surface temperature was the main factor driving backscatter variability in the EEZ, with intensified backscatter during the austral summer (December to May) in the northern part of the EEZ. We showed that acoustic density differed significantly, spatially and temporally from micronekton biomass predicted for the same period by the SEAPODYM-MTL (mid-trophic level) ecosystem model. The seasonal cycle given by ADCP data lagged behind the SEAPODYM-MTL seasonal cycle by around three months. Reasons to explain these differences and further needs in observation and modeling were explored in the discussion. In addition to providing new insights for micronekton dynamics in this EEZ (i.e., the science needed for ecosystem-based fisheries management), the data should help improve our ability to model this key trophic component.

Rees, D. J., Byrkjedal, I., & Sutton, T. T. (2017). Pruning the Pearlsides: Reconciling morphology and molecules in mesopelagic fishes (Maurolicus: Sternopychidae). *Deep-Sea Research Part II-Topical Studies in Oceanography*, 137, 246-257. <https://doi.org/10.1016/j.dsr2.2016.04.024>

The genus *Maurolicus* comprises extremely abundant vertically-migrating fishes that have considerable biomass in a number of regions worldwide. The genus was generally considered monotypic, with a single species, *M. muelleri* (Gmelin, 1789), inhabiting all world oceans. Based on differences in combinations of a limited number of morphometric characters, 15 separate species have been proposed, mostly associated with different ocean basins and seamounts. However, due to similarities in external morphology and overlap in ranges of morphometric characteristics, there remains a need for further validation of these species. Here, we present results of a multi-gene analysis, together with morphological data, for five putative *Maurolicus* species from multiple locations in the northern and southern hemispheres. Sampling encompasses described species from the North and South Atlantic, Mediterranean Sea, south-east Indian Ocean and the western South Pacific. Mitochondrial (16S and COI)

and nuclear (ITS-2) gene sequences for 120 specimens were used in Maximum Parsimony and Bayesian Inference analyses as well as creation of haplotype networks. Morphological character analyses were based on data from 279 adult individuals. Several clear groupings emerge, conflicting with previously recognised species: (1) a 'northern' Glade comprising *Maurolicus muelleri* and *M. amethystinopunctatus*, (2) a 'southern' Glade comprising *M. australis*, *M. walvisensis* (also *M. japonicus*) and (3) eastern, Equatorial and western North Atlantic *M. weitzmani*. The southern clade taxa are genetically indistinguishable and not well defined morphologically and present a clear case for synonymisation as *M. australis*. Synonymisation is also proposed for *M. muelleri* and *M. amethystinopunctatus*, with limited morphological variation likely to reflect physical and biological differences experienced north / south of the sub-polar front. *Maurolicus weitzmani* is clearly differentiated from all other *Maurolicus* species on both a molecular and morphological basis. Studies of genetic and morphological diversity in *Maurolicus* will further contribute to the question of 'what constitutes a species in the open ocean?', where a complex picture is emerging of both unexpected variation, as well as the unexpectedly absent genetic variation, in cosmopolitan taxa.

Riaz, J., Walters, A., Trebilco, R., Bestley, S., & Lea, M. A. (2020). Stomach content analysis of mesopelagic fish from the southern Kerguelen Axis. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 174. <https://doi.org/10.1016/j.dsr2.2019.104659>

Mesopelagic fish represent an important trophic link between zooplankton and higher order predators in Southern Ocean food webs. Information on their feeding habits is still sparse, representing a key area of uncertainty in efforts to understand and model Southern Ocean food web dynamics. We used visual assessment of stomach contents to characterise the diets of three myctophids (*Electrona antarctica*, *Gymnoscopelus braueri*, *Krefftichthys anderssoni*) and one bathylagid (*Bathylagus antarcticus*) over the southern extension of the Kerguelen Plateau ('southern Kerguelen Axis'), a highly productive area of both biological and economic importance in the Indian sector of the Southern Ocean. Diets of all four species were dominated by euphausiids, amphipods, copepods and fish. *Bathylagus antarcticus* also preyed upon a high proportion of soft-bodied organisms. There was strong evidence for dietary variability both within and between species, and this variability was driven by latitudinal variation in zooplankton assemblages. Size-based shifts in diet were apparent, with larger individuals of myctophid and bathylagid species consuming larger prey. Linear mixed effects models also demonstrated that the weight of prey consumed increased in relation to predator weight. Dietary information presented here advances our understanding of the mesopelagic components of Southern Ocean food webs, which will improve the development of food web models for the region.

Ross, L. G. (1976). The permeability to oxygen of the swimbladder of the mesopelagic fish *Ceratoscopelus maderensis*. *Marine Biology*, 37(1), 83-87. <https://doi.org/10.1007/bf00386782>

The permeability to oxygen of the swimbladder of physoclistous fish is important because of the usually high oxygen content of the bladder. The oxygen permeability and guanine content of the swimbladder wall of the mesopelagic myctophid *Ceratoscopelus maderensis* (Lowe) were measured. The oxygen permeability was $0.0672 \text{ cm}^3 \mu\text{m/atm min cm}^2$ and the guanine content was $73 \mu\text{g/cm}^2$. Attention is drawn to the high rates of gas loss which would occur from a swimbladder with these characteristics and the problems of maintaining the gas content, especially at depth.

Saenger, R. A. (1988). Swimbladder size variability in mesopelagic fish and bioacoustic modeling. *Journal of the Acoustical Society of America*, 84(3), 1007-1017. <https://doi.org/10.1121/1.396737>

Bioacoustic predictions of volume scattering strength $Sv(z, f)$ below 20 kHz due to mesopelagic swimbladdered fish contain errors arising from biological sampling limitations and uncertainties in swimbladder target strength. These predictions all utilize allometric equations relating, say, swimbladder equivalent spherical radius R to fish standard length l . Since the equations take no account of swimbladder size variability that is acoustically significant, the predictions contain "swimbladder variability error" (SVE) as well. New modeling procedures are presented to reduce SVE in Sv predictions for arbitrary size-depth distributions of swimbladdered fish with gas-filled swimbladders. It is assumed that the swimbladder size allometry properties of these fish, either as individual species or as a species class, can be described by appropriate bivariate normal density distributions $p(x,y)$, where $x=\ln l$ and $y=\ln R$, as suggested by recent results of Saenger (submitted to Can. J. Fish. Aquat. Sci.). SVE in predictions using allometric equations is estimated by comparing theoretical predictions made, respectively, with a bivariate normal model and its associated simple allometric law regression equation. Results suggest that SVE is generally appreciable for naturally occurring fish size distributions and, in particular, is partly responsible for discrepancies commonly observed between predicted and measured values of Sv at low-kHz frequencies for nighttime near-surface scattering layers.

Saenger, R. A. (1989). Bivariate Normal Swimbladder Size Allometry Models and Allometric Exponents for 38 Mesopelagic Swimbladdered Fish Species Commonly Found in the North Sargasso Sea.

Canadian Journal of Fisheries and Aquatic Sciences, 46(11), 1986-2002.

<https://doi.org/10.1139/f89-249>

With x and y log-transformed fish standard length/and equivalent swimbladder radius R , respectively, probability density distributions $p(x,y)$ for mesopelagic swimbladdered fish species are assumed to be bivariate normal. From archival measurements, models are developed for 36 nonregressive species, 2 regressive species, and selected species groups found off Bermuda. Statistical tests suggest the hypothesis is valid for many of these species, and that failures are due largely to small sample variability and bias in the available data. Marked differences between regression, major axis, and reduced major axis allometric exponents, which sometimes occur when x,y correlation is low, are explained. A dimensionless allometric law $R^* = k^* (l^*)^m$ involving structural variables l^* and R^* scaled to l_{max} is used to compare specific swimbladder growth trends. Major axis estimates of m^* and k^* for the nonregressive species group are each lognormally distributed with respective means and . A structural relation model for this group based on the hypothesis that swimbladder wall area grows approximately as the first power of fish volume or mass is verified. Last, detailed buoyancy properties are calculated for 6 nonregressive species with bivariate normal (x,w^*) -distributions, where w^* is the logarithm of percentage swimbladder volume.

Saunders, R. A., Collins, M. A., Foster, E., Shreeve, R., Stowasser, G., Ward, P., & Tarling, G. A. (2014). The trophodynamics of Southern Ocean Electrona (Myctophidae) in the Scotia Sea. *Polar Biology*, 37(6), 789-807. <https://doi.org/10.1007/s00300-014-1480-3>

The Scotia Sea is one of the most productive regions of the Southern Ocean, but its surface waters are experiencing a rapid increase in temperature, which may be changing the behaviour and distribution of many myctophids and their prey species. *Electrona antarctica* and *Electrona carlsbergi* are two of the

most abundant myctophids in the region, but their ecology is poorly understood and their response to ongoing environmental change is difficult to determine. This study investigated spatial and temporal patterns in their abundance, population structure and diets using mid-water trawl nets deployed across the Scotia Sea during spring, summer and autumn. *E. antarctica* was the most numerically abundant species (0.09-0.21 ind. 1,000 m(-3)), with greatest concentrations occurring in the sea-ice sectors. *E. carlsbergi* occurred in more northern regions, comprising densities of 0.02-0.11 ind. 1,000 m(-3). There was evidence of seasonal variation in depth distribution, size-related sexual dimorphism and size-specific vertical stratification for both species. Latitudinal trends in sex ratio and female body size were apparent for *E. antarctica*. Its diet varied between regions, seasons and size classes, but overall, *Euphausia superba*, *Metridia* spp. and *Themisto gaudichaudii* were the dominant prey items. *E. carlsbergi* appeared not to recruit in the Scotia Sea. Its diet was dominated by copepods, particularly *Rhincalanus gigas* and *Metridia* spp., but regional, seasonal and ontogenetic variations were evident. This study contributes to our understanding of how mid-water food webs are structured in the Southern Ocean and their sensitivity to ongoing environmental change.

Saunders, R. A., Collins, M. A., Shreeve, R., Ward, P., Stowasser, G., Hill, S. L., & Tarling, G. A. (2018).

Seasonal variation in the predatory impact of myctophids on zooplankton in the Scotia Sea (Southern Ocean). *Progress in Oceanography*, 168, 123-144.

<https://doi.org/10.1016/j.pocean.2018.09.017>

Myctophids are the biomass-dominant mesopelagic fishes in the Southern Ocean, but their trophic role within the pelagic food web south of the Antarctic Polar Front is poorly resolved from a seasonal perspective at the ocean-basin scale. In this study, the predatory impact of the predominant Southern Ocean myctophid community (*Electrona antarctica*, *Electrona carlsbergi*, *Gymnoscopelus braueri*, *Gymnoscopelus fraseri*, *Gymnoscopelus nicholsi*, *Protomyctophum bolini*, *Protomyctophum tenisoni*, *Protomyctophum choriodon*, *Krefftichthys anderssoni* and *Nannobrachium achirus*) on their zooplankton prey was examined during austral spring, summer and autumn in the Scotia Sea, one of the most productive regions of the Southern Ocean. Seasonal variations in diet and predation rates were apparent for all species. Based on the percentage index of relative importance, myctophids had high overlap in their diets, with all species mostly consuming copepods, small euphausiids and amphipods. Myctophid size was a key determinant of diet in the region, with larger species and intra-specific size classes consuming larger prey. Cluster analyses revealed myctophid feeding guilds that appeared to change seasonally, although there was little evidence of dietary specialisation. Myctophid predation on the daily productivity of most copepod species was relatively low across seasons (< 7%), except for *Calanus simillimus* that was predated upon highly in summer (similar to 26%). From the macrozooplankton component of the prey field, the myctophid community consumed substantial proportions of the euphausiid *Thysanoessa* spp. in each season (similar to 7 to 76% daily productivity), particularly in summer. Relatively high proportions of the daily Antarctic krill (*Euphausia superba*) productivity (similar to 8-58%) were also consumed by the larger myctophid species, particularly in summer by *Electrona antarctica*, suggesting increased competition for krill resources during the higher predator breeding season and possible reductions in food web stability during periods of reduced krill availability at this time. The amphipod *Themisto gaudichaudii* formed an important part of the larger myctophid species' diet in all seasons, with between 10 and 38% of its daily productivity being consumed. Myctophid predation on the daily productivity of salps was up to 4%, whilst their impact on ostracods and pteropods was negligible (< 0.1% of daily productivity) in all seasons. This study demonstrates that Southern Ocean myctophids link secondary productivity to higher predators through

both krill-independent and krill-dependent trophic pathways across seasons, with myctophids comprising a more krill-dependent pathway during austral summer.

Saunders, R. A., Collins, M. A., Stowasser, G., & Tarling, G. A. (2017). Southern Ocean mesopelagic fish communities in the Scotia Sea are sustained by mass immigration. *Marine Ecology Progress Series*, 569, 173-185. <https://doi.org/10.3354/meps12093>

The biomass of mesopelagic fish in the Southern Ocean is one of the largest of any ocean region and is dominated (both in terms of diversity and biomass) by myctophids (lantern-fish). Despite their high ecological importance both in this region and globally, our understanding of the life cycles and distribution of myctophids remains limited. We examined length-frequency data from trawl nets collected across a major sector of the Southern Ocean (the Scotia-Weddell sector) in different seasons to determine patterns of recruitment and growth. There was an absence of larval myctophids, of any species, in net catches, while larger, older individuals became increasingly dominant with increasing latitude. Very few specimens were found to contain mature gonads, indicating that individuals do not reach reproductive condition in this region. Most myctophid species that occurred within the survey regions neither recruited locally nor were self-supporting. Myctophids are prey to a large number of higher predators (penguins, seals and cetaceans) in the Scotia Sea, and are a major predator of zooplankton and krill. We show that this vital part of the Southern Ocean food-web is dependent on mass immigration from lower latitudes in the region. By implication, the sensitivities of this system depend not only on local conditions but also on levels of connectivity to other oceanic regions.

Saunders, R. A., Collins, M. A., Ward, P., Stowasser, G., Hill, S. L., Shreeve, R., & Tarling, G. A. (2015). Predatory impact of the myctophid fish community on zooplankton in the Scotia Sea (Southern Ocean). *Marine Ecology Progress Series*, 541, 45-64. <https://doi.org/10.3354/meps11527>

Myctophids are the most abundant mesopelagic fishes in the Southern Ocean, although their trophic role within the predominantly krill-based food web in regions south of the Antarctic Polar Front (APF) is poorly resolved. This study therefore examined the diets of 10 species of myctophid fishes: *Electrona antarctica*, *E. carlsbergi*, *Gymnoscopelus braueri*, *G. fraseri*, *G. nicholsi*, *Krefftichthys anderssoni*, *Proto myctophum bolini*, *P. tenisoni*, *P. choriodon* and *Nannobrachium achirus*, in the Scotia Sea, together with their predatory impact on the underlying zooplankton community. Myctophids and their prey were sampled in different seasons by scientific nets deployed across the Scotia Sea from the sea-ice zone to the APF. Based on the percentage index of relative importance, myctophids had high overlap in their diets, although the data indicate dietary specialisation in some species. There was also a distinct switch in diet, from copepods to euphausiids and amphipods, with increasing myctophid size. Myctophid predation impacted daily copepod production by between 0.01 and 5%, with *Calanus simillimus* being most impacted. Total annual consumption of copepods was around 1.5 million t (Mt) per year. All myctophids preyed upon the euphausiid *Thysanoessa* spp., consuming similar to 12% of its daily productivity and around 4 Mt per year. However, only larger myctophid species preyed upon Antarctic krill *Euphausia superba*, consuming 2% of its daily productivity, which could amount to as much as 17 Mt per year. *Themisto gaudichaudii* was also an important dietary component, with 4% of its daily productivity being consumed, amounting to around 2 Mt per year. This study demonstrates that myctophids link secondary productivity to higher predators both through krill-dependent and krill-independent trophic pathways.

Saunders, R. A., Collins, M. A., Ward, P., Stowasser, G., Shreeve, R., & Tarling, G. A. (2015). Distribution, population structure and trophodynamics of Southern Ocean *Gymnoscopelus* (Myctophidae) in the Scotia Sea. *Polar Biology*, 38(3), 287-308. <https://doi.org/10.1007/s00300-014-1584-9>

Gymnoscopelus braueri, *Gymnoscopelus fraseri* and *Gymnoscopelus nicholsi* are common in the Southern Ocean mesopelagic fish community. However, their ecology is poorly understood in the region. This study investigated spatial and temporal patterns in their abundance, population structure and diets at different times of year within the Scotia Sea to ascertain their functional role in the pelagic food web. *G. braueri* was the most abundant species (0.07-0.17 ind. 1,000 m(-3)) throughout the Scotia Sea. *G. fraseri* was absent from the sea-ice sectors and occurred mostly around the Antarctic Polar Front (APF), comprising densities of 0.01-0.04 ind. 1,000 m(-3). *G. nicholsi* occurred in low abundance (< 0.01 ind. 1,000 m(-3)) throughout the region. *G. braueri* and *G. fraseri* had a lifespan of 4 and 3 years, respectively, but spatial variation in their population structures was evident and recruitment appeared to occur only around the APF. *G. nicholsi* had a lifespan of > 4 years. There was evidence of seasonal variation in depth distribution, size-related sexual dimorphism and vertical segregation in size classes for each species. Overall, diets were dominated by copepods (*Metridia* spp., *Rhincalanus gigas*, *Pleuromamma robusta*) and euphausiids (*Thysanoessa* spp. and *Euphausia superba*), although *G. fraseri* did not predate *E. superba*. Regional, seasonal and ontogenetic patterns in diet were evident for all species. This study provides new insight into the ecology of these *Gymnoscopelus* species in the Scotia Sea. Such details contribute towards resolving how pelagic food webs are structured in the Southern Ocean and their sensitivity to ongoing environmental change.

Saunders, R. A., Collins, M. A., Ward, P., Stowasser, G., Shreeve, R., & Tarling, G. A. (2015). Trophodynamics of *Protomyctophum* (Myctophidae) in the Scotia Sea (Southern Ocean). *Journal of Fish Biology*, 87(4), 1031-1058. <https://doi.org/10.1111/jfb.12776>

This study investigated spatial and temporal patterns in distribution, population structure and diet of Bolin's lanternfish *Protomyctophum bolini*, Tenison's lanternfish *Protomyctophum tenisoni* and gaptooth lanternfish *Protomyctophum choriodon* in the Scotia Sea using data collected by midwater trawl during spring, summer and autumn. *Protomyctophum bolini* was the most abundant species of the genus encountered throughout the Scotia Sea with the greatest concentrations occurring around the Antarctic Polar Front (APF). This species had a life cycle of 2+years, but spatial differences in population structure were apparent as the I-group was absent from all regions south of the APF, suggesting that the species does not recruit in the Scotia Sea. *Protomyctophum tenisoni* occurred mostly in waters characteristic of the APF and was absent from the southern Scotia Sea. It had a limited size range, but there was clear size-related sexual dimorphism with males significantly larger than females. The species had a life cycle of c. 2years, but the I-group (c. 1year old, 1 November to 31 October the next year) occurred only in regions close to the APF suggesting that recruitment is restricted to these waters. A seasonal southward migration for *P. choriodon* is likely as the species occurred mostly to the south-west of South Georgia in summer, but extended to the sea-ice sectors in autumn. *Protomyctophum choriodon* had a life cycle of 4+years in the Scotia Sea and the population was dominated by age classes >3years old. Larval stages were absent during the surveys for all species. Diurnal variations in vertical distribution were apparent for all three species. Interspecific variations in diet were evident, but all species were primarily copepod feeders, with *Metridia* spp., *Rhincalanus gigas* and *Calanus simillimus* generally dominating their diet. Small euphausiids, principally *Thysanoessa* spp., were also an important component of their diets, particularly for *P. choriodon* which had the largest body size. The spatial and

temporal variations in diet for both *P. bolini* and *P. tenisoni* were broadly consistent with underlying abundance patterns within the mesozooplankton community.

Saunders, R. A., Fielding, S., Thorpe, S. E., & Tarling, G. A. (2013). School characteristics of mesopelagic fish at South Georgia. *Deep-Sea Research Part I-Oceanographic Research Papers*, 81, 62-77. <https://doi.org/10.1016/j.dsr.2013.07.007>

In this paper, we describe the variation in myctophid schools characteristics at South Georgia using multifrequency acoustic data collected annually between November 2007 and January 2012. We studied the relationship between the proximity of land and the distribution and schooling characteristics of myctophid fish. We also examined patterns in schooling behaviour in relation to oceanographic data. Fish schools were identified using a dual-frequency dB identification method (Sv120-38 kHz), where negative Sv120-38 kHz is indicative of gas-bearing organisms, such as swimbladdered fish. Available net data were used to provide information on the mesopelagic fish community in the region. School morphometrics (e.g. length, thickness, area) data were extracted and pooled according to their distance from the shore (0-30 km, 30-60 km, 60-90 km, 90-120 km). A total of 578 schools were detected in the survey region and there was high variation in school backscattering strength (NASC), length, height, perimeter, depth and horizontal distribution between surveys, including distinct inter-annual variation in these parameters when surveys were conducted in the same season (2009-2012). Schools were distributed predominantly on-shelf (0-500 m isobaths) during some summer surveys (2007 and 2012) and predominantly off-shelf on others (> 500 m isobaths; 2009, 2010 and 2011). There was also evidence of bathymetric separation in the horizontal distribution of schools. Schools observed in the late-season in 2008 had the greatest NASC, largest height and the deepest depth distribution. Most schools occurred at depths between similar to 60 and 300 m, but they did not occupy the same water masses during each survey. Schools became progressively thinner, shallower and acoustically weaker with increasing distance to land, whilst school length and perimeter increased correspondingly. The change in fish schooling behaviour between environments could be a response to a combination of local predatory threats over short spatial/temporal scales and differences in oceanographic conditions, such as current velocity. The trend could also be evidence of spatial habitat partitioning of myctophids, with different schooling species, or different life-stages, orientating along a bathymetric gradient at South Georgia.

Saunders, R. A., Hill, S. L., Tailing, G. A., & Murphy, E. J. (2019). Myctophid Fish (Family Myctophidae) Are Central Consumers in the Food Web of the Scotia Sea (Southern Ocean). *Frontiers in Marine Science*, 6. <https://doi.org/10.3389/fmars.2019.00530>

Myctophids are the most abundant and diverse mesopelagic fishes in the Southern Ocean. They are a conduit of energy between primary consumers and higher marine predators, and between the surface layers and the mesopelagic depths. However, there remain major uncertainties about their ecology, particularly regarding their role in Southern Ocean food webs in waters south of the Antarctic Polar Front, which are often regarded as dominated by Antarctic krill. Limited data on the feeding ecology of myctophids has made it difficult to assess the importance of myctophids as consumers of krill and how they fit in the traditional view of a krill-dominated system (diatom-krill-higher predator). We provide a new assessment of the role of myctophids in Southern Ocean food webs using information from recent trophodynamic studies of myctophids conducted in the Scotia Sea, one of the most productive regions of the Southern Ocean and a region that sustains both major populations of higher predators (sea birds,

seals, whales) and important commercial fisheries (krill, toothfish, and mackerel icefish). Collectively, these data show that myctophids have a central role in Southern Ocean food webs as both predators and prey. Large myctophid species are prevalent consumers of krill throughout their distributional range and in different seasons in the Scotia Sea. Moreover, best estimates of both myctophid and higher predator consumption of krill to date indicate that large myctophids are the greatest predators of krill in this region, consuming almost as much krill as do all other vertebrates. Nevertheless, there are several smaller myctophid species that do not eat krill, instead consuming copepods and other small euphausiids. Myctophids therefore link primary producers to higher predators through both krill-dependent and krill-independent trophic pathways, emphasizing their importance in regional food webs. Consequently, trophic pathways involving large myctophids are unlikely to be exempt from the direct consequences of projected redistribution and/or reduction in krill population biomass under scenarios of ocean-warming, whilst trophic pathways involving small myctophids may be more resilient to such effects and become increasingly important to higher trophic levels. Further studies are required to determine the extent to which myctophids can maintain food web stability and sustain higher predator populations during periods of prolonged reductions in krill abundance. Including knowledge of the role of myctophids in Southern Ocean food webs will be important for developing robust projections of the impacts of future change to inform decision making for conservation and management.

Saunders, R. A., Ingvarsdottir, A., Rasmussen, J., Hay, S. J., & Brierley, A. S. (2007). Regional variation in distribution pattern, population structure and growth rates of *Meganyctiphanes norvegica* and *Thysanoessa longicaudata* in the Irminger Sea, North Atlantic. *Progress in Oceanography*, 72(4), 313-342. <https://doi.org/10.1016/j.pocean.2006.09.005>

Euphausiids are a key component of the northern North Atlantic marine ecosystem and *Meganyctiphanes norvegica* and *Thysanoessa longicaudata* are dominant both numerically and in terms of biomass. The Irminger Sea is remote and experiences often-hostile weather conditions. Consequently, few studies have been conducted there, and detailed information on the seasonal distribution, abundance and growth of euphausiids is limited. Here we explore patterns of abundance and spatial and temporal variation in length-frequency distribution in order to determine regional growth rates for both species in the Irminger Basin. Regional composite length-frequency distributions for spring, summer and winter were devised by aggregating discrete net haul data according to the results of a multivariate cluster analysis of length conducted on spring and summer net sample data. Three biologically distinct regions within the Irminger basin were apparent (Central Irminger Sea, Northern Irminger Sea and East of Greenland Shelf). These regions corresponded broadly with distinct physical zones within the basin. Modes in the composite length-frequency distributions were determined by fitting multiple normal distributions, and regional differences in growth were investigated by tracking modes between seasons. The results provide some evidence for regional variability in growth and population dynamics. The population structure and growth of *M. norvegica* was similar in the open ocean regions of the Northern and Central Irminger Basin, but different in the region around the East Greenland Shelf. There was a distinct absence of larger individuals (+1-group) in the open ocean regions compared to East Greenland Coast region, and growth rates were marginally higher. A similar pattern in population structure was also observed for *T. longicaudata*. Variability in growth and abundance are discussed in relation to prevailing environmental characteristics such as temperature and food availability.

Saunders, R. A., Lourenco, S., Vieira, R. P., Collins, M. A., Assis, C. A., & Xavier, J. C. (2020). Age and growth of Brauer's lanternfish *Gymnoscopelus braueri* and rhombic lanternfish *Krefftichthys anderssoni* (Family Myctophidae) in the Scotia Sea, Southern Ocean. *Journal of Fish Biology*, 96(2). <https://doi.org/10.1111/jfb.14206>

This study examines age and growth of Brauer's lanternfish *Gymnoscopelus braueri* and rhombic lanternfish *Krefftichthys anderssoni* from the Scotia Sea in the Southern Ocean, through the analysis of annual growth increments deposited on sagittal otoliths. Otolith pairs from 177 *G. braueri* and 118 *K. anderssoni* were collected in different seasons from the region between 2004 and 2009. Otolith-edge analysis suggested a seasonal change in opaque and hyaline depositions, indicative of an annual growth pattern, although variation within the populations of both species was apparent. Age estimates varied from 1 to 6 years for *G. braueri* (40 to 139 mm standard length; L-S) and from 0 to 2 years for *K. anderssoni* (26 to 70 mm L-S). Length-at-age data were broadly consistent with population cohort parameters identified in concurrent length-frequency data from the region for both species. The estimated values of von Bertalanffy growth curves for *G. braueri* were $L_{\infty} = 133.22$ mm, $k = 0.29$ year⁻¹ and $t(0) = -0.21$ year and the values for *K. anderssoni* were $L_{\infty} = 68.60$ mm, $k = 0.71$ year⁻¹ and $t(0) = -0.49$ year. There were no significant ($P > 0.05$) differences in growth between sexes for either species, suggesting that males and females have similar growth and development trajectories in the Scotia Sea. A positive allometric relationship between L-S and wet mass was found for each species, as well as a significant ($P < 0.0001$) linear relationship between otolith size and L-S. Growth performance (CYRILLIC CAPITAL LETTER EF ') was similar between the two species and congruent with other myctophid species across the Southern Ocean. This study provides important parameters for future Southern Ocean ecosystem studies in a resource management context.

Saunders, R. A., & Tarling, G. A. (2018). Southern Ocean Mesopelagic Fish Comply with Bergmann's Rule. *American Naturalist*, 191(3), 343-351. <https://doi.org/10.1086/695767>

The applicability of macroecological rules to patterns in body size varies between taxa. One of the most examined is Bergmann's rule, which states that body size increases with decreasing temperature and increasing latitude, although the rule is not universal and the proposed mechanisms underpinning it are multifarious and lack congruence. This study considers the degree to which Bergmann's rule applies to the Southern Ocean mesopelagic fish community. We studied patterns in body size, temperature, and latitude across a 127 latitudinal gradient within the Scotia-Weddell sector. Intraspecific Bergmann's rule was found to apply to 8 of the 11 biomass-dominant species in the family Myctophidae. The rule was also apparent at an interspecific level. Our study suggests that greater attainable body size in this community is a necessary attribute to reach colder regions further south. The adherence of these taxa to Bergmann's rule enables such species to act as sentinels for identifying the drivers and consequences of ocean warming for the Southern Ocean ecosystem.

Sawada, K., Uchikawa, K., Matsuura, T., Sugisaki, H., Amakasu, K., & Abe, K. (2011). In situ and ex situ target strength measurement of mesopelagic lanternfish, *Diaphus theta* (family Myctophidae). *Journal of Marine Science and Technology-Taiwan*, 19(3), 302-311. Retrieved from <https://jmst.ntou.edu.tw/marine/19-3/302-311.pdf>

Acoustic target strengths (TS) of myctophid fish *Diaphus theta* were measured in situ at 70 kHz off the east coast of Hokkaido by tethering an acoustic-optical system (the Japanese Quantitative Echosounder

and Stereo-video Camera System or J-QUEST chi) at a depth of 150 m from a research vessel. Fish length distributions were obtained from daytime hauls taken with a frame trawl after the TS measurement. Measured average TS ($\langle TS \rangle$) and a standard length (SL) in cm gave the empirical length - average TS relationship, $\langle TS \rangle = 20\log SL - 70.6$, assuming that the linear TS is proportional to the square of the SL. A laboratory TS measurement and theoretical modeling of D. theta support the estimated length - average TS relationship.

Shreeve, R. S., Collins, M. A., Tarling, G. A., Main, C. E., Ward, P., & Johnston, N. M. (2009). Feeding ecology of myctophid fishes in the northern Scotia Sea. *Marine Ecology Progress Series*, 386, 221-236. <https://doi.org/10.3354/meps08064>

The diets of 9 species of myctophid fishes, *Electrona carlsbergi*, *E. antarctica*, *Gymnoscopelus fraseri*, *G. nicholsi*, *G. braueri*, *Protomyctophum bolini*, *P. choriodon*, *Krefftichthys anderssoni* and *Nannobrachium achirus*, were investigated during austral autumn in the northern Scotia Sea. Based on the percent index of relative importance (%IRI), the data suggest dietary specialisation in some species, which may permit resource partitioning. Hierarchical agglomerative cluster analysis of Bray-Curtis similarity (60% threshold) separated the myctophid community into distinct feeding guilds. One group (*G. braueri* and *E. antarctica*) fed principally on *Themisto gaudichaudii*, another (*P. choriodon* and *G. fraseri*) primarily on copepods (*Metridia* spp. and *Rhincalanus gigas*), and a third group (*G. nicholsi* and *F. bolini*) consumed copepods and euphausiids (mostly *Metridia* spp. and *Euphausia frigida*). The diets of *E. carlsbergi* and *K. anderssoni* differed from the other species, with *E. carlsbergi* being the only species that consumed salps. There was a general switch in diet from copepods to euphausiids and amphipods as the myctophid predator size increased. Dietary specialisation is likely the result of a combination of predator size, gape size, filtering capacity of the gill rakers and the vertical distribution of predators and prey. Antarctic krill were only consumed by the larger myctophids, which represented a numerically minor part of the myctophid community, supporting the concept that myctophids can provide a krill-independent link between secondary production and higher trophic levels. However, the northern Scotia Sea is dominated by adult krill, which are only suitable as prey for larger fish. In the northern Scotia Sea, myctophid predation had a very small impact on copepod production but a higher impact on macrozooplankton, with a best-estimate of 4% of the daily production of *Themisto gaudichaudii* and 6% of that of *Euphausia superba* being consumed.

Smoker, W., & Pearcy, W. G. (1970). Growth and Reproduction of the Lanternfish *Stenobrachius leucopsarus*. *Journal of the Fisheries Research Board of Canada*, 27(7), 1265-8. <https://doi.org/10.1139/f70-148>

Growth and reproductive patterns of the common lanternfish *Stenobrachius leucopsarus* (Eigenmann and Eigenmann) are described by length-frequency analysis, otolith analysis, and examination of ovaries. Length-frequency analysis showed that growth is approximately linear, 1.59 mm standard length per month, during the 2nd, 3rd, and part of the 4th year of life. Yearling fish average 23 mm long, 2-year-olds 41 mm, and 3-year-olds 59 mm. Otolith analyses indicate that some fish may live to be 8 years old, but confidence in this method is limited to fish 5 years old or younger. Fitting mean lengths of age-groups defined by otolith analyses with the von Bertalanffy equation gave $L_\infty = 85$ mm, $k = 0.34$. Back calculation of lengths at the times of formation of otolith annuli gave another set of estimated mean lengths of age-groups, which, fitted by the von Bertalanffy equation, describes a growth curve similar to the one described by otolith analyses. The inflection in growth in weight occurs at about 4

years of age. Time of spawning, determined from egg measurements, occurs from December to March. Reproductively mature individuals are 4 years old and older. Recruitment of young size groups is also seasonal, 20- to 25-mm individuals appearing in largest proportions in trawl samples in the winter, presumably about 8 months after spawning. Comparison with other studies indicates that spawning may occur earlier in Monterey Bay, California, than off Oregon, but growth rates and sizes of age-groups I–V are similar. Comparisons with published results of otolith analyses show similar age determinations for the smaller size groups.

Sobradillo, B., Boyra, G., Martinez, U., Carrera, P., Pena, M., & Irigoien, X. (2019). Target Strength and swimbladder morphology of Mueller's pearlside (*Maurolicus muelleri*). *Scientific Reports*, 9. <https://doi.org/10.1038/s41598-019-53819-6>

In the last few years, there has been increasing interest in the commercial exploitation of mesopelagic fish and a trawl-acoustic methodology has been recommended to make estimates of abundance of these resources. This study provides relevant information on the scattering properties of a key mesopelagic fish species in the Bay of Biscay, Mueller's pearlside (*Maurolicus muelleri*), necessary to convert the acoustic density into numerical abundance. The target strength (TS) of pearlside was estimated for the first time at five frequencies commonly used in acoustic surveys. A high-density filter was applied to reduce the bias derived from overlapping echoes erroneously assigned to single targets. Its relationship with fish length ($b(20)$) was also determined (-65.9 +/- 2, -69.2 +/- 3, -69.2 +/- 2, -69.5 +/- 2.5 and -71.5 +/- 2.5 dB at 18, 38, 70, 120 and 200 kHz, respectively). Biomass estimates of pearlside in the Bay of Biscay during the four years of study (2014–2017) are given using the 38 kHz frequency. Morphological measurements of the swimbladder were obtained from soft X-ray images and used in the backscattering simulation of a gas-filled ellipsoid. Pearlside is a physoclist species, which means that they can compensate the swimbadder volume against pressure changes. However, the best fit between the model and the experimental data showed that they lose that capacity during the trawling process, when the swimbladder volume is affected by Boyle's law.

Stanton, T. K., Sellers, C. J., & Jech, J. M. (2012). Resonance classification of mixed assemblages of fish with swimbladders using a modified commercial broadband acoustic echosounder at 1–6 kHz. *Canadian Journal of Fisheries and Aquatic Sciences*, 69(5), 854–868. <https://doi.org/10.1139/f2012-013>

Recently developed broadband acoustic methods were used to study mixed assemblages of fish spanning a wide range of lengths and species. Through a combination of resonance classification and pulse-compression signal processing, which provides for high-range resolution, a modified commercial broadband echosounder was demonstrated to provide quantitative information on the spatial distribution of the individual size classes within an assemblage. In essence, this system spectrally resolves the different size classes of fish that are otherwise not resolved spatially. This method reveals new insights into biological processes, such as predator-prey interactions, that are not obtainable through the use of a conventional narrowband high-frequency echosounder or previous broadband systems. A recent study at sea with this system revealed aggregations containing bladdered fish 15–30 cm in length (Atlantic herring (*Clupea harengus*) and silver hake (*Merluccius bilinearis*)) and a variety of species of smaller fish 2–5 cm in length. These observations infer that the smaller 2–5 cm fish can be colocated in the same aggregations as their predator, the larger silver hake, as well as pre-spawning herring. While this technological advancement provides more information, there remain challenges in

interpreting the echo spectra in terms of meaningful biological quantities such as size distribution and species composition.

Suetsugu, K., & Ohta, S. (2004). Functional change in the swimbladder with fish size in *Coryphaenoides acrolepis*. *Deep Sea Research Part I: Oceanographic Research Papers*, 51(9), 1275-1282.
<https://doi.org/10.1016/j.dsr.2004.05.004>

One common macrourid fish, *Coryphaenoides acrolepis*, was analyzed to examine the relationship between the length of the rete mirabile (RmL) and water depth with fish size. The relationships differed when specimens were divided into two size classes based on pre-anal fin length (PAF). The RmL in specimens with PAF >15cm became longer with greater depth, while in specimens with PAF <15cm it was not affected by depth. On the other hand, the RmL became longer with fish size in the small-size class, while in the large-size class it was not affected by fish size. These differences suggest that the function of the swimbladder in *C. acrolepis* changes with fish size. The swimbladder of larger specimens would provide more buoyancy than that of smaller ones, and the RmL of *C. acrolepis* would become longer with growth when PAF is <15cm. This functional change in the swimbladder at a PAF of 15cm was in agreement with results on both changes in feeding habits and the start of reproduction. Our findings suggest that *C. acrolepis* experiences a decisive life cycle change when PAF reaches 15cm. This study also suggests the possibility that a functional change in the swimbladder might be widespread among deep-sea demersal species in which the diet changes with fish size.

Taylor, F. H. C. (1968). The Relationship of Midwater Trawl Catches to Sound Scattering Layers off the Coast of Northern British Columbia. *Journal of the Fisheries Research Board of Canada*, 25(3), 457-472. <https://doi.org/10.1139/f68-040>

In 1964 and 1965 three midwater trawl cruises off the continental slope near the Queen Charlotte Islands were made to study the relationship of the catches to sound scattering layers. During the daytime four layers were distinguished, not all necessarily present at one time. In summer the most intense and persistent layer lay at 220-230m; others were at 330-400, 185, and 90m. In fall the main and deep layers were shallower. Vertical migration occurred at dusk and dawn. The main layer frequently split into three parts with different vertical migration patterns. At dawn a layer gradually appeared at about 90m, intensified rapidly, and descended to the daytime level. Catches show fishes are associated with the sound scattering layers. The largest day catches were from the main layer. At night fish did not appear to be concentrated to the same extent relative to the layers. The largest night catches were usually smaller than the largest day catches and shallower. Myctophids of eight species, four common, made up 80% of the catch, chauliodontids 6%, argentinids 4%, melamphids, rockfish, and larval flatfish 2% each. The remaining 2% comprised 27 species in 21 families. Depth distribution and vertical migration varied considerably with the species. Myctophids with gas-filled swim bladders were apparently dominant in the main layers whereas species without swim bladders - stomiatoids, argentinids, and melamphids - or myctophids with fat-filled swim bladders were dominant below the main layer and in the deep layer. Fish with no swim bladders or with fat-filled ones may make longer vertical migrations than those with gas-filled bladders.

Thorvaldsen, K. G. (2018). *Improved density measurements of mesopelagic fish and the presence of physonect siphonophores in sound scattering layers, measured with multifrequency acoustics and a stereo camera mounted on a lowered probe*. (Master of Science), University of Bergen, Bergen, Norway. Retrieved from <https://hdl.handle.net/1956/18753>

The mesopelagic layer is a massive layer of biomass which stretches from 200-1000 meters depth in almost all locations of the world oceans. These layers are inhabited by many groups of animals, from small zooplankton to larger fishes. While studied since the 1960s, the mesopelagic layer has gained recent scientific and industrial interest due to its potentially large unexploited biomass. These layers are populated by small fishes, which may be ensonified and detected by echo sounders, creating a layer of reverberation called the deep scattering layer. In Norwegian waters, two of the most abundant mesopelagic fishes are the Glacier Lanternfish (*Benthosema. Glaciale*), and the Muellers pearlside (*Maurolicus Muelleri*). Recent estimates using echo sounders, suggest that their potential biomass could be as high as 10 billion tonnes worldwide. There are however several challenges with respect to quantifying mesopelagic fishes in an accurate manner. Unwanted swimbladder resonance, other animals with similar echoes, and fishes without or changing swimbladder may potentially create large biases in these investigations. Very low catchability in modern trawls may also complicate the measurements. In this study mesopelagic fishes were measured both with traditional survey methods using vessel mounted transducers, and a lowered acoustic probe where the fishes were measured at short range at their natural depths. It was discovered that the biomass measured were lower with the lowered probe than with the traditional method, but in the same order of magnitude, from 0.01-0.09 fish/m³. The difference was found was mainly due to the difference between target strength taken from literature, and the directly measured target strength from the probe. Camera observations of physonect siphonophores in the observation volume, may suggest that the biomass of fish measured is even lower. Observation and comparison of the difference in backscattering between 38 and 70 kHz, with higher backscattering at 70 kHz, may suggest that siphonophores are close to resonant at 70 kHz in our data. This gives hope for future classification of this group, especially if wideband are used. In this manner, this study shed light on some of these possible shortcomings and challenges for traditional ways to measure these fishes, but also suggest new methods for solving some of the more important questions.

Torgersen, T., & Kaartvedt, S. (2001). In situ swimming behaviour of individual mesopelagic fish studied by split-beam echo target tracking. *ICES Journal of Marine Science*, 58(1), 346-354.
<https://doi.org/10.1006/jmsc.2000.1016>

The mesopelagic fishes Muller's pearlside (*Maurolicus muelleri*) and northern lantern-fish (*Benthosema glaciale*) were studied in near-surface waters during their diel vertical migrations. The fish apparently alternated between swimming predominantly vertically and horizontally, although many fish were descending slowly (similar to 1 cm s⁻¹) during horizontal swimming. Vertical swimming speeds during rapid ascents and descents were typically 10-30 cm s⁻¹, corresponding to several body lengths s⁻¹. Horizontal swimming paths varied extensively, some fish following a rather straight track, others displaying pronounced smooth or sharp turns. Horizontal swimming speeds appeared to be in the same range: as the vertical swimming speeds during ascents and descents, but were less reliably estimated as this component was more affected by noise than the vertical component. Both the advantages and limitations of the split-beam tracking technique in behavioural studies are discussed in light of these observations.

Trenkel, V. M., & Berger, L. (2010). *What information can acoustic data provide on marine biodiversity?* Paper presented at the ICES Annual Science Conference, Nantes, France. Retrieved from <https://www.ices.dk/sites/pub/CM%20Documents/CM-2010/Q/Q0110.pdf>

Acoustics derived indicators have primarily been used in the context of single species management in the form of species biomass or abundance indices, often disaggregated by age class. Very little use has been made of acoustics to derive other indicators, despite the fact that these methods have huge potentials, both in terms of simultaneously sampling across several trophic levels as well as at a range of spatial and temporal scales, which are not paralleled by any bottom trawl sampling program. In this presentation we make proposals on how acoustic data might be used to estimate diversity indices, making use of multi-frequency information which broadly reflect trophic levels. The proposed diversity indices are evaluated using simulated data and data from the Bay of Biscay.

Valkirs, A. (1978). Lactate dehydrogenase activity in the swimbladder gas gland of *Symbolophorus evermanni* (myctophidae)—A diurnally migrating fish. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology*, 59(1), 125-126. [https://doi.org/10.1016/0300-9629\(78\)90318-3](https://doi.org/10.1016/0300-9629(78)90318-3)

1. Lactate dehydrogenase (LDH) affinity for pyruvate increases considerably at pH 7.0 and 7.4 with decreasing temperature.
2. At pH 8.0 the enzyme-substrate (E-S) affinity is decreased with decreasing temperature.
3. The maximal reaction velocity (Vmax) decreases with decreasing pH and temperature.
4. Adjustment of E-S affinity with changing temperature seems to be adaptive to the behavior of these fish.

Van Noord, J. E., Olson, R. J., Redfern, J. V., Duffy, L. M., & Kaufmann, R. S. (2016). Oceanographic influences on the diet of 3 surface-migrating myctophids in the eastern tropical Pacific Ocean. *Fishery Bulletin*, 114(3), 274-287. <https://doi.org/10.7755/fb.114.3.2>

We examined the stomach contents of 3 vertically migrating myctophid fish species from the eastern tropical Pacific (ETP) Ocean and used a classification tree to examine the influence of spatial, biological, and oceanographic predictor variables on diet. *Myctophum nitidulum* (n = 299), *Symbolophorus reversus* (n = 199), and *Gonichthys tenuiculus*, (n = 82) were collected with dip nets from surface waters, and prey taxa were quantified from bongo net tows from August through November 2006. A classification tree produced splits with longitude and sea surface salinity (SSS), thereby separating 3 geographically and oceanographically distinct regions of the ETP (offshore, nearshore, and intermediate), where diet was similar among the 3 species. Myctophids consumed, primarily, ostracods offshore (76.4% mean percentage by number [MNI]), euphausiids nearshore (45.0%), and copepods (66.6%) in the intermediate region. The offshore region was characterized by a greater abundance of ostracods in the zooplankton community (17.5% by number) and within a deep mixed-layer depth (MLD) (mean 52.6 m, max 93.0 m). SSS was low in the nearshore region (< 32.9 psu) and the MLD was shallow. The intermediate region represented a transition zone between the oceanographic condition of the offshore and nearshore regions. Our results indicate that these 3 myctophid species share a similar regional diet that is strongly influenced by longitude, ostracod availability, SSS, and MLD.

Verma, A., Kloser, R. J., & Duncan, A. J. (2017). Potential Use of Broadband Acoustic Methods for Micronekton Classification. *Acoustics Australia*, 45(2), 353-361. <https://doi.org/10.1007/s40857-017-0105-8>

Broadband acoustic methods are an emerging technology with potential use in identification and classification of marine organisms. The application of broadband methods to scientific surveys of mesopelagic micronekton (animals of 2-20 cm length found at depths of 200-1000 m) is described. The principles of the broadband system are briefly outlined with particular emphasis on its use for micronekton detection and identification employing the TS-frequency curve of single targets. The use of acoustic scattering models to determine characteristics of the marine organism such as size and material properties is also discussed. As an example of the application of this technique, broadband echosounders mounted on a depth-profiling platform were used to collect high-frequency (55-160 kHz) acoustic data from mesopelagic depths (up to 600-1000 m) of the Great Australian Bight region. Some example results from narrowband and broadband echosounders are compared. The resulting frequency-dependent target strength curves of selected targets enabled classification into different acoustic groups, demonstrating the significant advantage provided by the broadband system. There is still a large gap between the achievable acoustic classification and the ultimate aim of species level classification, and to this end some limitations of broadband echosounder systems in identifying targets are discussed along with the use of video and still cameras to assist in the interpretation of acoustic data.

Wang, X., Zhang, J., Zhao, X., Chen, Z., Ying, Y., Li, Z., . . . Zhou, M. (2019). Vertical distribution and diel migration of mesopelagic fishes on the northern slope of the South China sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, 167, 128-141. <https://doi.org/10.1016/j.dsr2.2019.05.009>

Mesopelagic fishes are major components contributing to deep-sea scattering layers in the open ocean. They have the potential to support a substantial higher trophic level harvest, but knowledge about this possible resource is still rudimentary. Some of the mesopelagic fishes undertake diel vertical migration (DVM) over large depths by feeding in shallow water during darkness and migrating to depth to avoid visual predators during daylight. The vertical distribution and diel migration pattern of the mesopelagic fishes on the northern slope of the South China Sea were investigated during two multidisciplinary surveys carried out in October 2014 and June 2015. Based on acoustic and biological sampling, a distinct deep scattering layer (DSL) consisting mainly of mesopelagic fishes was identified in deep water (>300 m). Extensive diel vertical migration for hundreds of meters to form dense aggregations in the epipelagic zone (0-150 m) at night was observed in both seasons, but the migration was highly species dependent. While most of the Myctophiformes and the Perciformes undertook DVM, most of the Salmoniformes and Beryciformes remained in deep water both day and night. Based on paired day-night differences of acoustic density in the DSL, the migrating proportion of mesopelagic backscatter varied markedly in different locations, ranging from 28% to 63%, with a mean of 48% in two seasons. The extensive vertical migration occurred in separate groups at different periods during sunset and sunrise hours. Additional analysis showed that the center of gravity of the mesopelagic backscatters (200-1000 m) and their night distribution in the subsurface layer (10-150 m) were positively correlated with the mean temperature in respective zones. Moreover, some of the mesopelagic communities on the slope were found to undertake pronounced diel horizontal migration in a pattern of towards the shore in the evening and away from the shore after midnight. The horizontal migrant species were mainly Myctophidae, in particular Diaphus chrysorhynchus and Diaphus garmani. Simultaneous analysis on typical tidal currents indicated that the horizontal migration, over a large distance with high speed and

biomass, could not be explained by passive transport due to tidal currents alone, and the active swimming of the mesopelagic fishes may also play an important role.

Wheeler, E. H. (1971). *Swimbladder Studies*. Naval Underwater Systems Center New London, CT.
Retrieved from <https://apps.dtic.mil/sti/citations/ADA066650>

The objectives of this study were as follows to describe the condition of the swimbladder in the abundant species of the collection, including measurements where feasible, and to determine the effect of formaldehyde preservation on the swimbladder.

Yancey, P. H., Lawrence-Berrey, R., & Douglas, M. D. (1989). Adaptations in mesopelagic fishes. *Marine Biology*, 103(4), 453-459. <https://doi.org/10.1007/BF00399577>

Mesopelagic fishes were collected from depths of 400 to 900 m off Oregon (USA) in September 1983, October 1985 and June 1989. Species of mesopelagic fish without diel vertical migrations (non-migrators) are known to have high body-and muscle-water contents relative to epipelagic and vertically migrating mesopelagic species. This characteristic is reported to correlate with low food availability. Through histology, we show that four species of swimbladderless non-migrators (*Bathylagus pacificus*, *B. milleri*, *Tactostoma macropus* and *Chauliodus macouni*) have large deposits of gelatinous material which stain positively for acidic glycosaminoglycans (GAGs) and negatively for lipid and protein. GAGs are highly hygroscopic and are thus responsible in part for the high body-water content of these species. The material is located between myotomal (swimming) muscle cells, along the dorsal midline and surrounding the spine in all four species, and the two *Bathylagus* species have an additional subcutaneous layer. The subcutaneous layer of *B. pacificus* has very high (96%) water, low protein (3%) and low ion contents and is positively buoyant, unlike myotomal muscle (89% water, 6.7% protein, negatively buoyant). In contrast, four species of vertical migrators (*B. ochotensis*, *Stenobrachius leucopsarus*, *Tarletonbeania crenularis* and *Diaphus theta*) have no such deposits. The role of this gelatinous material as a possible buoyancy mechanism in an energy-poor habitat is discussed.

Yasuma, H., Miyashita, K., Sawada, K., & Aoki, I. (2006). Swimbladder morphology and target strength of myctophid fish of the northwestern Pacific. *The Journal of the Acoustical Society of America*, 120(5), 3107-3107. <https://doi.org/10.1121/1.4787575>

Swimbladder shapes of fish from 14 myctophid species captured around Japan were measured using an x-ray method to estimate the theoretical target strength. Using those x-ray images, the fish were classified into bladder species and nonbladder species according to the presence of the gas. Five species had no swimbladder in any body size range examined. Others contained bladder and nonbladder fishes in relation to growth. The growth of swimbladder length was not proportional to that of body length (allometric growth) in some bladder fishes. Based on morphological parameters of the body and swimbladder, the relationships between body length and target strength from 38 to 200 kHz were estimated using theoretical acoustical backscattering models. Estimated values of target strength showed greater than 10-dB differences between bladder and nonbladder fishes, even when the fish were of equivalent size. Because of the allometric growth of the swimbladder, values of the target strength were not proportional to the square of the body length in most bladder species. In addition, larger fishes (over 60 mm) of *Myctophum asperum* showed regressive growth of the swimbladder (or

target strength), suggesting that the use of the $20\log$ relationship is inappropriate for bladder species of myctophid.

Yasuma, H., Miyashita, K., & Yamamura, O. (2006). Acoustic identification and density estimate of *Diaphus theta* (myctophidae) off Hokkaido, Japan. *The Journal of the Acoustical Society of America*, 120(5), 3019-3019. <https://doi.org/10.1121/1.4787087>

Diaphus theta is the most abundant micronektonic fish in the northwestern Pacific. Field acoustic data and biological samples were obtained both day and night off of eastern Hokkaido, Japan in September 2006 to estimate the fish density and diel changes of its vertical distribution. Differences of acoustical target strength (TS) values between at 38 and 120 kHz were applied to identify *D. theta* echos using field echo data. Theoretical estimation using swimbladder acoustic scattering models showed that the TS difference (TS 120-38 kHz) of larger fishes (over 60 mm) was between -4 and 1 dB; that for smaller fishes (less 60 mm) was less than .4 dB. These values differed from those of other major component species of the deep-scattering layer, such as krill and pollock, suggesting that the echo from *D. theta* is acoustically identifiable. Diel vertical distributions of *D. theta* were estimated after identification. Relatively dense schools were observed at around 400-m depth during daytime, although the schools were scattered widely above 100-m depth during nighttime. These results matched those obtained by biological sampling. In the surface layer (above 100 m), the estimated fish densities were about tenfold higher at nighttime than in daytime.

Yasuma, H., Ohshima, S., Yasuda, T., Fukuwaka, M.-a., & Abe, K. (2016). Intraspecific variation in the swimbladder occurrence and possibility of acoustic discrimination of the dominant mesopelagic fish *Diaphus garmani* off western Kyushu, Japan. *The Journal of the Acoustical Society of America*, 140(4), 3303-3303. <https://doi.org/10.1121/1.4970515>

No abstract available.

Yasuma, H., Sawada, K., Olishima, T., Miyashita, K., & Aoki, I. (2003). Target strength of mesopelagic lanternfishes (family Myctophidae) based on swimbladder morphology. *ICES Journal of Marine Science*, 60(3), 584-591. [https://doi.org/10.1016/s1054-3139\(03\)00058-4](https://doi.org/10.1016/s1054-3139(03)00058-4)

This article reports theoretical values of target strength (TS) for mesopelagic lanternfishes based on morphological measurements of their swimbladders. Three species of lanternfishes, *Diaphus theta* (26.9-77.4 mm standard length (SL)), *Symbolophorus californiensis* (85.0-108.4 mm SL), and *Notoscopelus japonicus* (126.0-133.2 mm SL), were examined. After external morphological measurement of the fish body, a specialized "soft X-ray" imaging system was used to map the swimbladders and obtain their morphological parameters. The swimbladder was inflated in *D. theta*, uninflated in *S. californiensis*, and was absent in *N. japonicus*. For *D. theta*, the swimbladder length does not increase in proportion to the body length, suggesting that the contribution of the swimbladder to acoustic reflection is reduced with growth in this fish. Based on the morphological measurements, the theoretical TS of the fish at 38 kHz was calculated using the approximate deformed-cylinder model (DCM) and the general prolate-spheroid model (PSM). For all three species, the calculations showed about 3 dB difference between the TS indicated by the DCM and PSM. Given that the description of body shape is poor in PSM, the DCM results were adopted for fish without a swimbladder or an empty

one. The intercept $b(20)$ in the standard formula $TS = 20 \log SL + b(20)$ was -85.7 dB (DCM) for *S. californiensis* and -86.7 dB (DCM) for *N. japonicus*. On the other hand, the PSM model was adopted for *D. theta* since its swimbladder has too small an aspect ratio to apply the DCM. For *D. theta*, the relationship between SL and TS is best expressed by $TS = 11.8 \log SL - 63.5$, which implies that its scattering cross-section is not proportional to the square of the body length.

Yasuma, H., Takao, Y., Sawada, K., Miyashita, K., & Aoki, I. (2006). Target strength of the lanternfish, *Stenobrachius leucopsarus* (family Myctophidae), a fish without an airbladder, measured in the Bering Sea. *ICES Journal of Marine Science*, 63(4), 683-692.
<https://doi.org/10.1016/j.icesjms.2005.02.016>

This paper reports theoretical values of target strength (TS) for the lanternfish *Stenobrachius leucopsarus*, a fish without an airbladder, which dominates the Subarctic marine mesopelagic fish community. Two models for liquid-like slender bodies, the general prolate-spheroid model (PSM) and the deformed-cylinder model (DCM), were used to compute the TS of the fish relative to its orientation. The relative mass density g and the sound speed h in sea-water were measured and used in both models. To confirm the appropriateness of the models, tethered experimental measurements were carried out at 38 kHz for five specimens. The value of g measured by the density-bottle method was very low (1.002-1.009) compared with that of marine fish in general. The value of h measured by the time-average approach was 1.032-1.039 at the water temperature at which *S. leucopsarus* is found. TS-fluctuation patterns against fish orientation (the TS pattern) estimated from the DCM and PSM were in good agreement in the area of their main lobes. Both models reproduced the main lobes of the measured TS patterns in near-horizontal orientation ($<+/- 20$ degrees), and they were considered to be effective in measuring the TS of *S. leucopsarus* in a horizontal (swimming) position. After these comparative experiments, we computed the TS of 57 fish (27.8-106.9 mm) at 38, 70, 120, and 200 kHz, using the DCM. A plot of body length (in log scale) against TS showed a non-linear relationship at all frequencies. *S. leucopsarus* had a very low TS (<-85 dB, TS_{cm}), suggesting that acoustic assessment would be highly sensitive, especially when the proportion of small fish is high (e.g. $L/\lambda < 2$), and an appropriate frequency should be considered that takes into account both the length composition and the depth of occurrence.

Ye, Z., & Farmer, D. M. (1994). Acoustic scattering from swim-bladder fish at low frequencies. *The Journal of the Acoustical Society of America*, 96(2), 951-956. <https://doi.org/10.1121/1.410269>

Models of acoustic resonant scattering from swim-bladder fish are sensitive to the choice of damping coefficient and resonance frequency. Existing theory does not provide a consistent representation of the role played by tissue surrounding the swim bladder in determining this coefficient and empirical fits are therefore often used to adjust model parameters for specific examples. In an attempt to provide a firmer theoretical basis for the interpretation of experimental results, it is shown how the elastic properties of the tissue can be combined with the swim bladder in a consistent way. Although the analysis must eventually be extended to swim bladders of arbitrary shape, for simplicity the essential features are illustrated with a spherical geometry. The results emphasize the need for accurate measurement of the bulk elastic properties of tissue, specifically the complex shear modulus.

Zhang, J., Wang, X. L., Jiang, Y. N., Chen, Z. Z., Zhao, X. Y., Gong, Y. Y., . . . Zhou, M. (2019). Species composition and biomass density of mesopelagic nekton of the South China Sea continental slope. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 167, 105-120.
<https://doi.org/10.1016/j.dsr2.2018.06.008>

Two surveys using a combination of midwater trawl and acoustics were undertaken in October 2014 and June 2015 to investigate species composition and biomass density of mesopelagic nekton over the continental slope of the South China Sea (CSSCS). In two surveys, diversity and dominant species of nekton (Chondrichthyes, Osteichthyes and Cephalopoda) showed obviously diel and depth-dependent difference. In 2014, in general species richness and diversity of nekton in the 0-100 m at night were greater than that in the 350-650 m during the day and 350-650 m at night. In Jun. 2015, species richness and diversity of nekton in the 350-650 m during the day were much greater than that in the 350-650 m at night and 0-100 m at night. Myctophidae and Diaphus are the most common fishes in the CSSCS mesopelagic zone. Jellyfishes could cause the nautical area scattering coefficient (NASC) to increase, but the effect of jellyfishes on NASC could vary over the light-night cycle and trawl depth. Catch rates of different nektonic categories varied by time of day and depth. Night-time catch rate at trawl depths 0-100 m were greatest, with Myctophidae the most abundant category. In 2014, from 350 to 650 m, day and night mean catch rates of myctophids were similar, however, in 2015, mean day catch rates were 64.1% night values. Cephalopoda are an important component of mesopelagic nekton. At escape rates of 0.95 and 0.99, daytime trawl-based biomass densities in the 350-650 m depth range in 2015 were 0.339 g m(-2) and 1.693 g m(-2), respectively. Mean daytime NASC from 200 to 1000 was 3163 +/- 1223 m(-2) nmi(-2) (2014) and 2503 +/- 698 m(-2) nmi(-2) (2015); corresponding acoustic and trawling data produced mesopelagic nekton biomass density estimates of 9.80 gm(-2) (2014) and 28.45 g m(-2) (2015). More fishes with swimbladders (mainly small sized lanternfishes of light weight) dominated catch in 2014 than in 2015.