Behavior and habitat selection of deep-sea fishes: a methodological perspective

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Abstract

The behavior and habitat selection of deep-sea fishes has been studied with various methods. Five of the most promising approaches to investigate the behavioral ecology are reviewed: (1) functional morphology, (2) field sampling, (3) acoustic tracking, (4) *in-situ* surveillance, and (5) *ex-situ* experimentation. Functional morphology, often a "by-product" of taxonomic and systematic studies, is strongly comparative and correlative, and serves to examine hypotheses on behavioral strategies. Field sampling with towed gear identifies vertical and horizontal distribution in the water column and deployments of stationary gear document aggregation and diversity patterns on or close to the seafloor. With acoustic instruments vertical migrations and segregation patterns can be tracked. *In-situ* observations with cameras and attraction devices or from underwater vehicles focus studies on behavior and habitat selection over small to large-scale intervals and distances, both vertically and horizontally. *Ex-situ* behavioral studies of deep-sea fishes brought to the surface have been conducted to a limited extent, mainly in unpressurized aquaria. An integrated approach which combines various methods would provide a more complete understanding of behavioral diversity and adaptations to environmental factors.

Introduction

The deep sea, i.e. the vast area of the oceans below 200 m water depth, is largely unexplored and basic questions related to the evolution of deep-sea organisms are unresolved, e.g., how many species live there and what are their behavioral habits? Although fishes are among the best studied fauna at greater depth, their systematics, ecology, and evolution still requires intensified research.

About 2700 deep-sea fish species have been described. Koslow et al. (1997) estimated that at least another 1000 species exist. Some taxa can be regarded as "ancient" deep-sea dwellers, e.g., those species that possess light organs like anglerfishes (Ceratoidei) or lanternfishes (Myctophidae). Other fishes are morphologically less differentiated and more closely related to shallow-water species (= secondary deep-sea fishes; Andriashev, 1953). Ecologically, deep-sea fishes have been grouped into open-water, pelagic, and bottom-associated, demersal species. Further depth-related subdivision considers also light penetration (to ca. 1000 m maximally) and bottom topography: mesopelagic (200 -1000 m), bathypelagic (1000 to ca. 3500 m), and abyssopelagic (>3500 m) species in the open water, bathyal (200 to ca. 3500 m; upper, mid- and lower slope) and abyssal (> 3500 m) species on the bottom. The greatest depth from which a fish has been collected is 8370 m (Nielsen, 1977).

In recent years novel technologies have provided more frequent access and more detailed records in the light-reduced and hyperbaric regime of the deep sea, making it possible to answer fundamental questions about adaptations to extreme conditions. An amazing array of sampling, analyzing, and exploratory methods can now be used to study deep-sea fish behavior. We provide here an overview of the five most significant approaches: (1) functional morphology, (2) field sampling, (3) acoustic tracking, (4) *in-situ* surveillance, and (5) *ex-situ* experimentation. As we hope, this review will stimulate more research in this field.

(1) Functional morphology

Functional morphology arises often as a "by-product" of taxonomic and systematic studies. The approach is strongly comparative and correlative emphasizing the testing of hypotheses about behavioral strategies by investigating the adaptive significance of organism structures in relation to distinct environmental features.

Functional morphological studies of deep-sea fishes have commonly focused on non-visual perception and communication modalities based on the comparative examination of chemo-tactile organs on head, body, fins, or barbels, and the structure of sound-producing organs (e.g., in grenadiers, Macrouridae, and cuskeels, Ophidiidae; see Marshall, 1979; Carter and Musick 1985; Merrett and Haedrich, 1997). Chemo-tactile sensing facilitates detection of food, predators, or conspecifics in the immediate surroundings or allows predators to track prey via currents (e.g., Wilson and Smith, 1984; Baird & Jumper, 1995).

Many deep-sea fishes have large otoliths (calcium carbonate structures in the inner ear) that may have a selective sound-perception function (Paxton, 2000). Differences in otolith form among closely related species strongly suggest that they permit intraspecific communication. For instance, the two sister species of the genus *Spectrunculus* (Ophidiidae), *S. crassus* and *S. grandis,* co-occur in the northern Atlantic at bathyal and abyssal depths (Uiblein et al., 2008). Recent morphological comparisons leading to the resurrection of *S. crassus* as a valid species have shown that they clearly differ in otolith shape (Uiblein et al., 2008). Members of this family have the capability to produce sounds based on "drumming" muscles

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that connect the swimbladder with modified ribs and the otic capsule (Merrett and Headrich, 1997). Species differences in hearing capacity and selectivity may relate to the production of species-specific sound signals and social communication in deep-sea fishes much like has been observed in shallow water species (e.g., Mann et al., 1997; Cruz and Lombarte, 2004; Rountree et al., 2006).
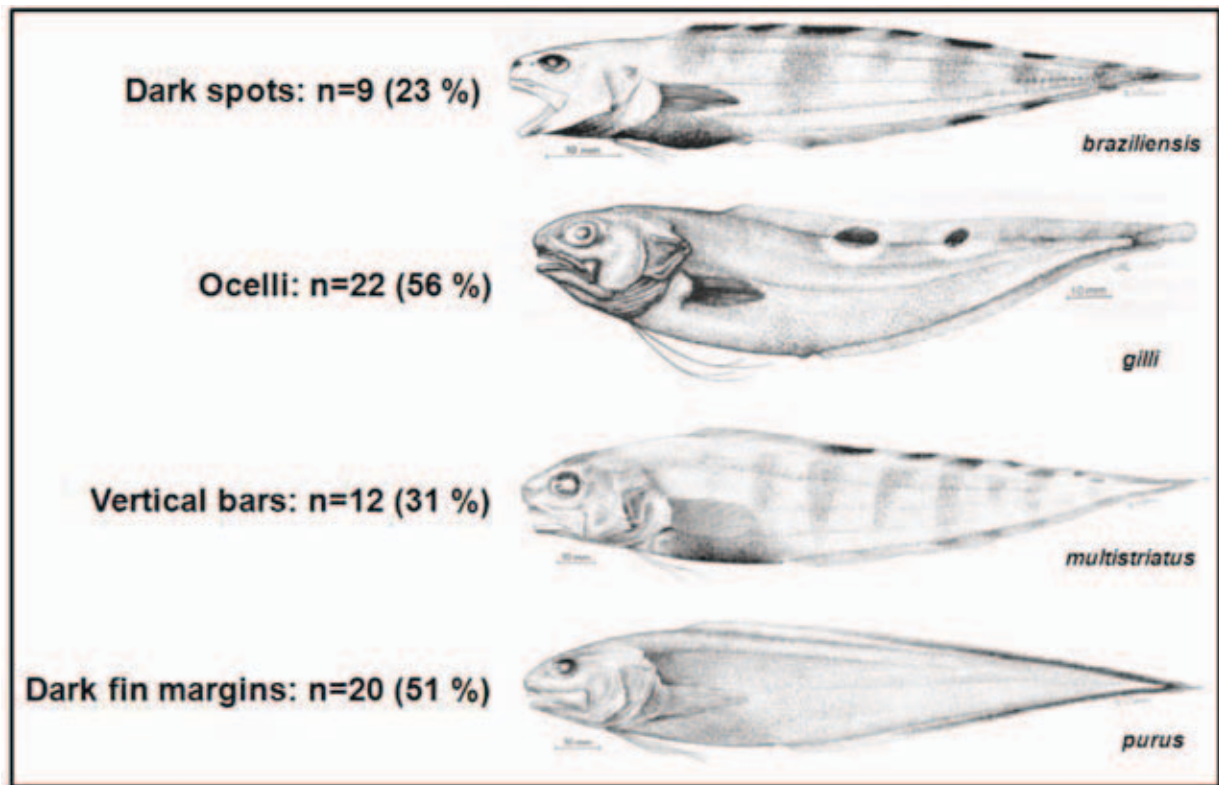

Fig. 1. Among 50 species of the cuskeel genus *Neobythites*, family Ophidiidae, 39 (= 78 %) show coloration patterns. For each of the four different coloration types one species is shown as an example. The number of species showing the respective color pattern and percentages referring to the total number of colored species is also provided (after Uiblein and Nielsen, 2005).

The shallowest part of the deep sea is still weakly illuminated by downwelling light. Well-developed eyes should be able to perceive sunlight until a depth of around 1000 m and distinction of contrasting colors should be possible to ca. 500-600 m depending on water clarity (Clark and Denton 1961). The latter prediction has been supported by investigations of eyespot (=ocellus) development and ontogenetic niche shifts in the ophidiid *Neobythites stefanovi* (Uiblein et al., 1994; Uiblein and Nielsen, 2005). This species shows typical circular to elliptical dark spots surrounded by a contrasting pale ring on the dorsal fin (Nielsen and Uiblein 1993; Fig. 1). Various functions have been ascribed to ocelli. They may reduce predation risk by, for instance, deterring visually hunting predators or deflecting their attacks to less vital parts of the body. Alternatively, they may enhance social communication and species recognition or they may serve several functions simultaneously (Uiblein and Nielsen, 2005).

Neobythites stefanovi occurs on the upper slope of the Northwestern Indian Ocean and the Red Sea and has one ocellus on the dorsal fin positioned at about mid-body (Nielsen and Uiblein, 1993). In the Red Sea population, an upward-directed ontogenetic migration from about 800m to less than 600m was detected that

development of the ocellus (Uiblein et al., 1994; Uiblein, 1996). This observation was interpreted as an indication for ocellus antipredator function, as risk from visually hunting predators should increase in shallower and more illuminated habitats.

A morphological comparison of the *N. stefanovi* specimens collected in the Gulf of Aden, Indian Ocean, with the generally deeper-occurring population from the adjacent Red Sea revealed a significantly higher ocellus diameter in the latter. The enlarged ocellus should intensify the signaling effect and enhance its visibility to predators at larger, less illuminated depths (Uiblein, 1995). While this observation fits well with the assumed antipredator function of the ocellus, a posterior shift in the position of this color structure found in the Gulf of Aden population required alternative interpretations. In a subsequent study of coloration patterns 50 *Neobythites* species, 22 species were found to have well-developed ocelli (Uiblein and Nielsen, 2005, Fig. 1). Among co-occurring species considerable variation in ocellus position and number occurred which suggests a social communication function that would limit interspecific interactions and hybridization (Uiblein and Nielsen, 2005).

Thus, ocelli in *Neobythites* may serve two different functions, minimization of predation risk and social communication for enhancement of species recognition. Direct evidence from *in-situ* or *ex-situ* behavioral observations is however still lacking and further sampling, especially in the Indo-West Pacific, is needed to improve the understanding of both the ecological function of the coloration and the systematics of this genus.

(2) Field sampling

Field sampling of deep-sea fishes can also reveal important information on behavior. Sampling can be conducted either with towed gear, such as various types of trawls, or with static gear such as longlines, baited traps, or gillnets. Sampling with towed pelagic gear generally allows investigating vertical or horizontal distribution and migration at larger scale, whereas static gear can be applied in studies of smaller scale habitat selection and aggregation formation.

Sampling with towed gear has helped to define migration patterns as exemplified by studies of the diversity and distribution of pelagic fishes in the area of the Canary Islands (CE Atlantic). The Canary Islands are typical oceanic islands of volcanic origin with a narrow shelf and a steep slope that enhance spatial interactions among deep-sea and adjacent shallow-water habitats (Uiblein and Bordes, 1999). A total of 103 pelagic trawl tows during seven cruises from above the island shelf and the slope and from the surface down to depths of ca. 1000 m resulted in the collection of more than 68000 adult or juvenile fishes belonging to 19 orders, 51 families, 126 genera, and 220 species (Wienerroither 2005, Wienerroither et al., 2009).

By multivariate classification and ordination methods (hierarchical agglomerative clustering and non-metric multidimensional scaling) four ecologically separable groups could be distinguished with the lanternfish *Lepidophanes gaussi* being the indicator species for vertically migrating mesopelagic fishes and *Diaphus dumerilii* for the group of horizontal migrators between oceanic waters and the island shelf (Wienerroither 2005, Wienerroither et al., submitted). Other lanternfishes like *Hygophum hygomii* formed aggregations close to the shelf at night. High densities occurred particularly in areas of high productivity and
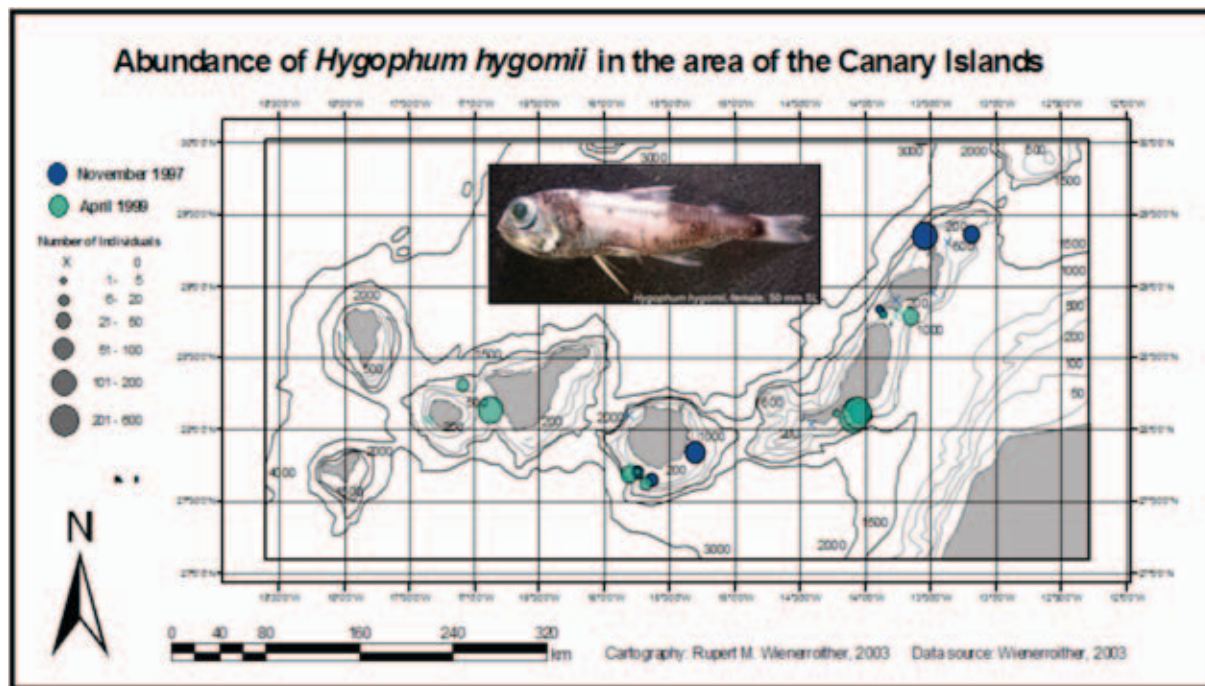
Fig. 2. Number of individuals of the lanternfish *Hygophum hygomii* collected during two cruises in the Canary Islands, Eastern Central Atlantic (after Wienerroither, 2003).

specific hydrological conditions, like eddies and upwellings (Fig. 2; Wienerroither, 2003). Among the group of typically shelf-associated fishes also some epipelagic species like chub mackerel *Scomber colias* occurred that were observed to migrate from the shelf into the oceanic water in opposed direction to the mesopelagic fishes. Such horizontal migrations can be seen in the context of both foraging and predation-risk avoidance.

Migrations of deep-sea fishes may also serve reproduction. For instance, long-distance horizontal movements of the lanternfish *Diaphus theta* in the western North Pacific were tracked by towed bongo-net and midwater collections of larvae, juveniles, and adults during different seasons (Moku et al., 2003). The peak abundance of larvae was observed in July in the transition waters between the Oyashio and Kuroshio fronts. Larvae and juveniles were distributed in transition waters, whereas larger individuals were collected in the Oyashio and the Western Subarctic waters. These results indicate that this species performs a spawning migration from the Oyashio and Western Subarctic waters into the transition waters crossing the Oyashio front.

Stationary gear, such as longlines, baited traps, or gillnets, provide insights about small-scale habitat selection and aggregation formation. For example, during long-line cruises in the area of Lanzarote and Furteventura, Canary Islands, operations at depths between 18 and 1208 m collected a total of 1885 fishes belonging to 73 species and 38 families (Uiblein et al., 1996, 1998; Lorance et al., 2002). Among different depth zones clear variations in fish total weight and number, species richness and diversity, and the relative abundance of single species were found. These results reflect to some extent the particular topography of the Canary Islands and associated hydrological variability. During two periods, in October 1995 and November 1997, an unusually high number of deep-sea cod, *Mora moro* (Moridae), with advanced gonadal maturity was collected off eastern Fuerteventura, one of the two islands studied, at around 1000 m depth

(Uiblein et al., 1996, 1998). At lesser depths and during other seasons, only a few individuals of this species were caught in the same area. These data strongly suggest the formation of a spatially and seasonally restricted spawning aggregation. Males arrived earlier than females at the spawning grounds and there appeared to be distinct microhabitat preferences related to a specific depth and sites close to a canyon with local upwelling activity (Fig. 3).
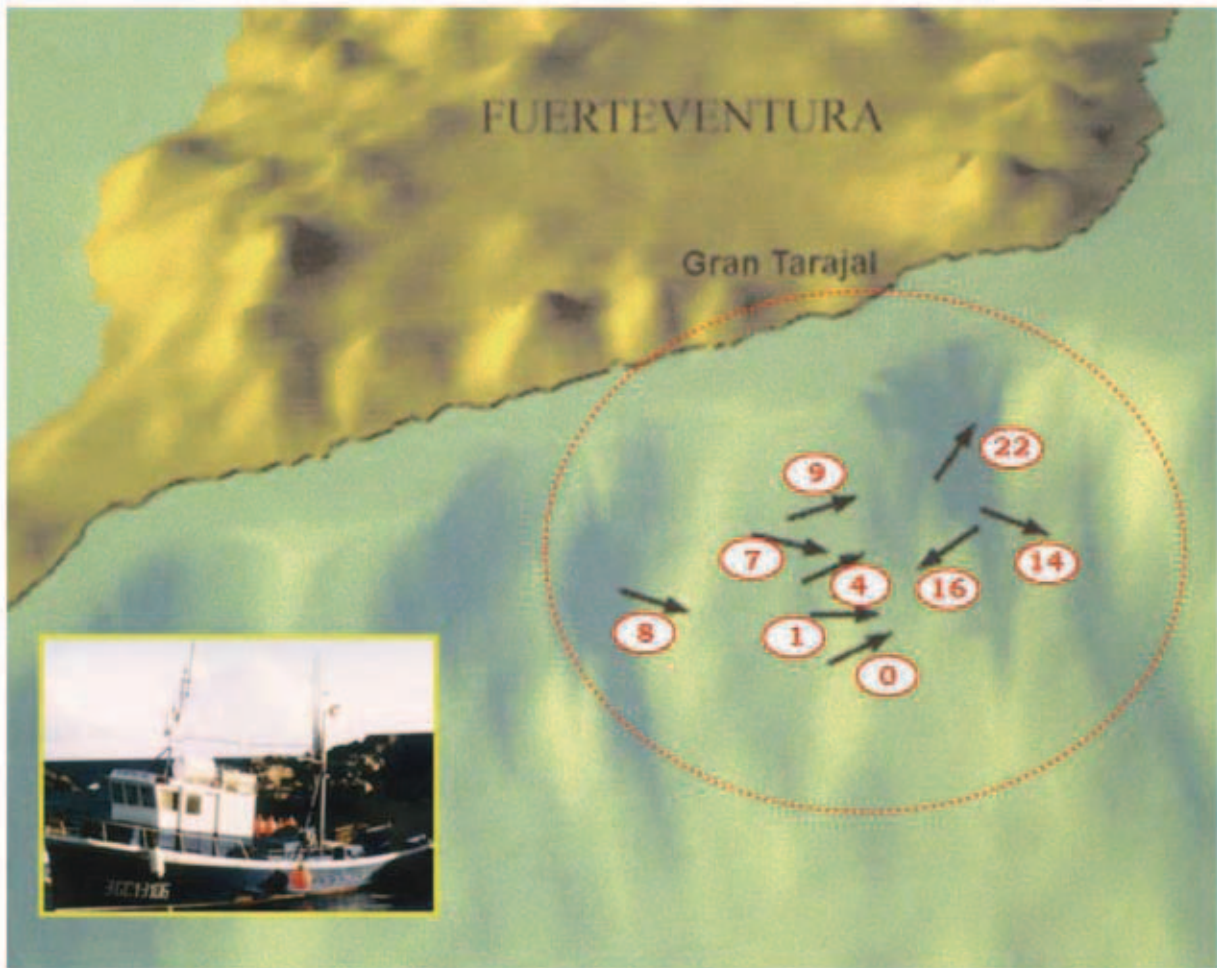

Fig. 3. Number of deep-sea cod, *Mora moro,* collected at bottom longline stations at between 800 and 1200 m depth, SE Fuerteventura, Canary Islands, Eastern Central Atlantic. Note the high numbers close to the entrance of a canyon-like steep topographic structure (after Uiblein et al., 1998).

(3) Acoustic tracking

Acoustic methods including echosounders, sonar, and acoustic tagging allow investigation of deep-sea fish vertical/horizontal migrations, spatial distribution, and aggregation formation. Acoustic tagging has been successfully adopted to track migrations of demersal fishes at great depth (e.g., Bagley et al., 1994; Priede and Bagley, 2000). Acoustics has enhanced the understanding of vertical migration patterns over large depth ranges and deep scattering layer formation (e.g., Opdal et al., 2008).

During the pelagic cruises in the Canary Islands (see also above) acoustics was employed to study the deep scattering layer formed at ca. 400 to 700 m depths off various islands and the diurnal vertical migration of organisms related to this layer. In parallel, pelagic trawl samples from both the deep scattering layer and
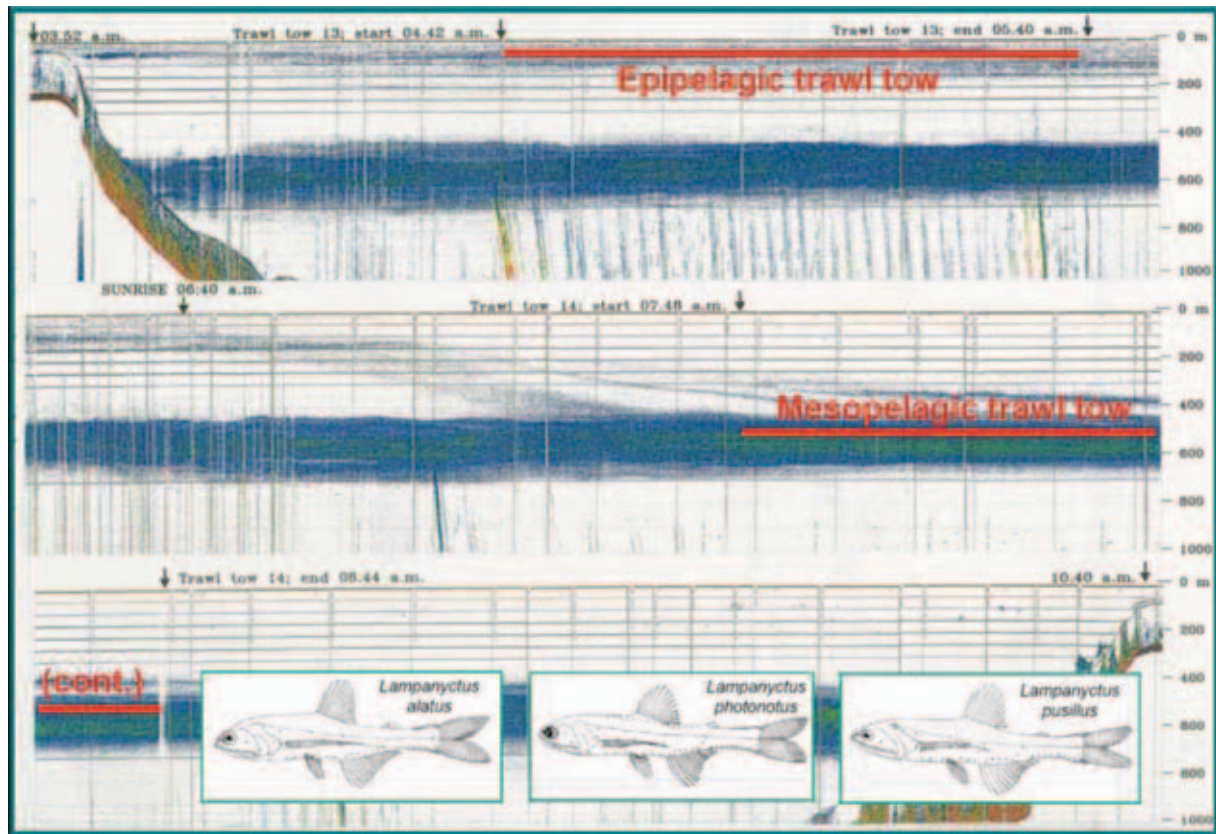
Fig. 4. Echogram taken off SE Fuerteventura, Canary Islands, during late night and morning of 12th April 1997, with vertical position of pelagic trawl tows and drawings of three myctophid species (genus *Lampanyctus*) inserted that were collected by both tows (after Bordes et al., 1999; Wienerroither 2003, Bordes et al., 2009).

the surface were taken to track and identify the species undergoing those migrations (Bordes et al., 1999). For instance, off Fuerteventura, trawl hauls were performed close to the surface late at night and at a depth overlapping with the continuously formed deep scattering layer after sunrise on 12 April 1997 (Fig. 4; for a description of acoustic methods used see Bordes et al., 1999). The echogram taken during this period clearly shows the initially formed shallow scattering layer that after sunrise moves downwards and, subsequently, later unites with the deep scattering layer. Lanternfishes like the three *Lampanyctus* species, *L. alatus, L. photonotus,* and *L. pusillus* were collected by both trawl tows, and hence their vertical migration activity in this area and during this particular time period is defined.

Acoustics can also assist to track horizontal migrations of deep-sea fauna, especially when the shallow scattering layer and the fishes therein reside close to the surface at night, as shown in recent studies off Oahu, Hawaii (Benoit-Bird and Au, 2006). In this case a towed camera was used to identify the faunal components, but this method did not provide taxonomic resolution like the pelagic trawl-supported study in the Canaries. The Hawaiian study indicated a horizontal mass migration onto the shelf by mesopelagic fishes which remained at the surface during the night. Like the Canary Islands, the Hawaiian archipelago is of volcanic origin with narrow platforms and steep slopes thus enhancing the spatial exchange and interaction between the neritic and oceanic fauna. The forces inciting such horizontal migrations are still

unknown, but predation, food, or competition may be among the most influential factors. Abrupt topography around oceanic islands and shallow seamounts may enhance trapping of oceanic zooplankton like copepods which may be used as a locally aggregating food resource by shelf-dwelling and mesopelagic fishes (Bordes et al., 1999; see also chapter 2).

(4) *In-situ* surveillance

In-situ studies of deep-sea fish behavior can be performed from both stationary and mobile platforms that allow direct observation or recording of behavior. Stationary platforms include landers that are submerged from ships and equipped with cameras and bait to attract and record scavenging fishes. This method allows observation of elements of foraging behavior such as search, detection, or handling of food items (Isaacs and Schwartzlose, 1975, Guennegan and Rannou, 1979, Wilson & Smith, 1984) and estimating species composition and density (Priede, 1994; Collins et al., 1999; Henriques et al., 2002; King et al., 2007).

Mobile platforms such as underwater vehicles allow tracking fishes and investigating their behavior over a larger area during vertical or horizontal transects (e.g., Yoklavich et al., 1999; Lorance et al., 2002; Drazen et al., 2003; Uiblein et al., 2002, 2003, 2006; Lorance et al., 2006; Stein et al., 2006; Uiblein, 2009; Fig. 5). Prolonged observation of single individuals can be achieved by stopping the vehicle at selected sites or following individuals during forward locomotion. This method can be used, for instance, to investigate specific movement patterns (Janssen et al., 1986; Moore, 2002), changes in body coloration (e.g., from
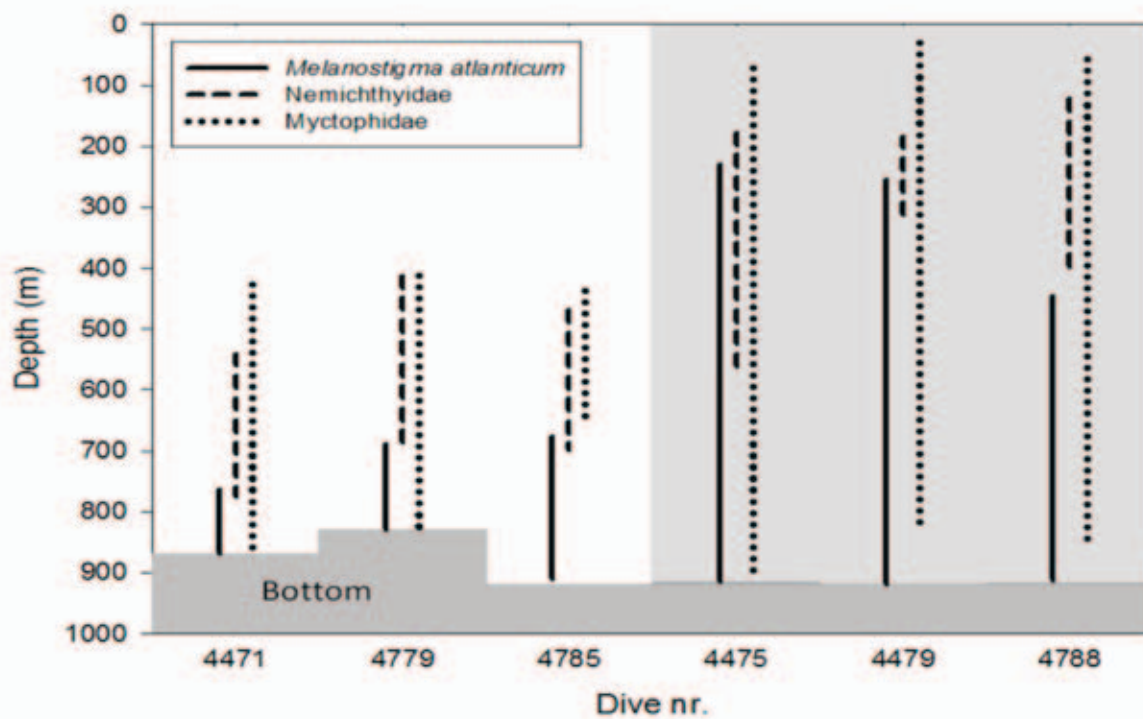

Fig. 5. Vertical distribution of three fish taxa observed during manned submersible dives in Oceanographer canyon, Gulf of Maine, NW Atlantic, in September 2002 (dives nr. 4471, 4475, 4479) and September 2004 (dive 4779, 4785, 4788). The dark-shadowed horizontal layer indicates the bottom, the light-shadowed vertical layer designates dives during night-time as compared to daytime (white background) (in part after Uiblein et al., 2006).

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Table 1. Overview of the categories of behavior and other characteristics of deep-sea fishes based on video recordings during dives with the manned submersible *Nautile* in the Bay of Biscay, NE Atlantic.

Behavior/Characteristics (taxa)	Category
Activity level (all)	Inactive - Active - Arriving disturbed
Locomotion behavior (all)	No locomotion - Station holding - Drifting - Forward movement
Position in water column (all)	Attached to bottom - Slightly above bottom - Well above bottom (> 1 total length) - High above bottom (> 3 total lengths)
Disturbance response (all)	No disturbance - At short distance - At far distance
Swimming speed (*Synaphobranchus kaupi*)	Body undulations s^{-1} - Body lengths moved s^{-1}
Coloration (*Hoplostethus atlanticus*)	Entire body whitish - Head whitish, body with red colour patches - Body and head in "typical" red color

white to red in orange roughy, *Hoplostethus atlanticus,* see Lorance et al., 2002 and Table 1), or the response to bait (Widder et al., 2005).

In-situ observations with the manned submersible *Nautile* in the Bay of Biscay, NE Atlantic (Uiblein et al., 2003) have revealed novel insights into the behavioral ecology of deep-sea fishes, their natural habitat use at small spatial scale, and interspecific variation. Differences between adjacent habitats in activity level, vertical position above bottom, and locomotion mode (e.g., forward movement, station holding, and drifting, see Table 1) have been also found as, for instance, in cutthroat eel, *Synaphobranchus kaupi,* roundnose grenadier, *Coryphaenoides rupestris,* and orange roughy, *Hoplostethus atlanticus* (Fig. 6). In northern cutthroat eel differences in swimming speed (measured as body undulations s^{-1} and body lengths moved s^{-1}) among sites were
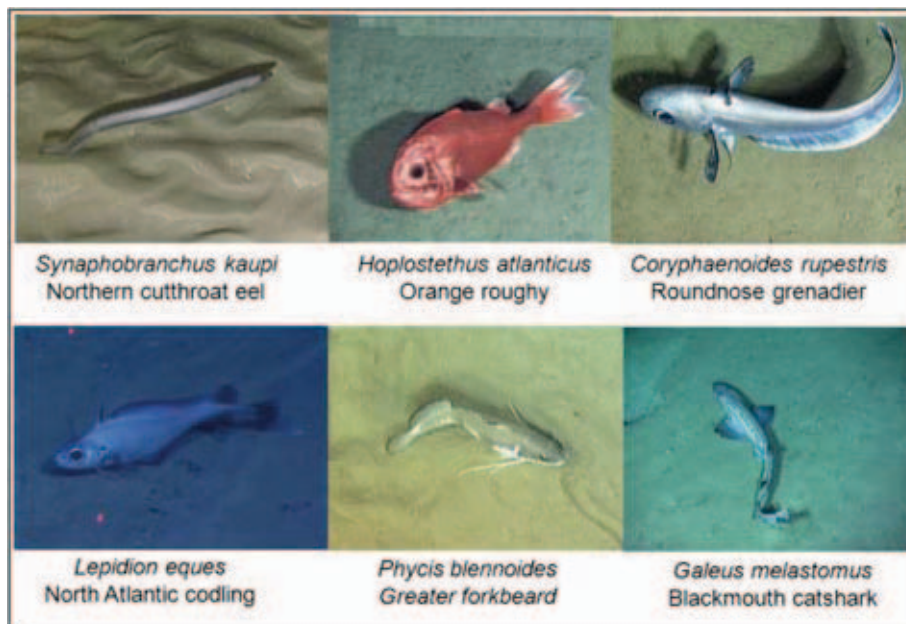

Fig. 6. Images of selected fish species videotaped for behavioral studies (Uiblein et al., 2003) during submersible dives in the Bay of Biscay, NE Atlantic .

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discovered, too (Uiblein et al., 2002). These results strongly suggest a high degree of behavioral plasticity in deep-sea fishes allowing adjustment to small-scale spatial or temporal fluctuations in hydrography and food availability.

All *in-situ* methods, even deployed cameras without bait (Koslow et al., 1995), create disturbance that needs to be carefully investigated in order to document whether they alter naturally occurring behavior (Uiblein et al., 2002; 2003). Interestingly, the detailed analysis of disturbance behavior itself can also provide information on perceptual and reaction capabilities of deep-sea fishes as well as on non-human induced environmental influences on behavior (Uiblein & Lorance, 2007; Uiblein, 2009).

(5) *Ex-situ* experimentation

Experiments under controlled conditions are necessary in order to relate the differential influences of environmental and organism-related factors on fish foraging, predator avoidance, learning, cognition, communication, or social behavior (e.g., Uiblein, 1992; Amorim et al., 2004; Wong et al., 2005). For this purpose one may study deep-sea fishes either in captivity in the ocean or "*ex-situ*" after collection on board of a vessel or on land. Both normal and pressurized tanks have been used to maintain deep-sea fishes. Unpressurized tanks are useful for species that occur in shallow water such as vertically migrating mesopelagic fishes (e.g., lanternfishes) or bottom-associated fishes (e.g., snailfishes, Liparidae, or eelpouts, Zoarcidae) that extend from the shelf into the deep sea (e.g., Robison, 1973; McCosker and Anderson, 1976; Sakurai and Kido, 1992).

There is growing evidence from scientific laboratories as well as from public aquaria that deep-sea fishes can be kept alive for longer periods (e.g., McCosker and Anderson, 1976; Miwa et al., this volume). Reports of detailed behavioral observations and successful experimentation are however scarce. Often acclimatizing was not sufficiently accomplished and virtually no or only few behavioral elements could be studied.

For example, during recent cruises off the Gulf of Maine (e.g., http://at-sea.org/missions/maineevent6 /synopsis.html; Uiblein et al., 2006) several fish species were collected with the manned submersible *Johnson Sealink* and kept alive in tanks, among them the hatchetfish *Argyropelecus aculeatus,* the sawtoothed eel *Serrivomer beanii,* and the eelpout *Melanostigma atlanticum*. One specimen of the latter was collected on 5 October 2005 in Oceanographer canyon at 2293 ft, kept in a small glass tank on the RV *Seward Johnson I* and transferred to the Woods Hole Aquarium a few days later where it was kept alive and survived for three months (until 16 January 2006). However, the specimen was not observed feeding over the entire period (John Galbraith, personal communication) and most probably died of starvation. Another short-lived specimen collected during the same cruise was kept just several days on board in a kreisel (Fig. 7). In this container the fish showed typical curling-up behavior (Fig. 7) that has been observed in nature. This posture may be interpreted as an antipredator strategy, as it could serve to mimic the form of a medusa (Robison, 2004) or make detection and / or attacking more difficult for predators. Alternatively, it might be also a biomechanical phenomenon allowing the fish to float more easily, or may simply reflect sleeping or resting and drifting.

Another species of the genus *Melanostigma, M. pammelas,* was kept in captivity for more than a year (McCosker and Anderson, 1976) and was one of the first deep-sea fish species in which feeding behavior was

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observed (Belman and Anderson, 1979). Feeding behavior was also observed in the snailfish, *Careproctus rastrinus* (Liparidae) (Sakurai and Kido, 1992), and in the robust bathypelagic fangtooth, *Anoplogaster cornuta* (Anoplogasteridae), which was kept successfully in tanks for several days (Robison, 1973) and fed with shrimps (Childress and Meek, 1973). In the latter study the fangtooth were kept in large containers in a cold room after transfer from the ship on land. Using dim red light for illumination the fish were stimulated at various body parts to elicit chemically and/or mechanically mediated feeding responses. Many important parameters like predator search and prey detection at distance or type, size and behavioral activity of the prey were not investigated.

There have been also successful trials to keep fishes in pressurized tanks after previous decompression or *in-situ* transfer (e.g., Smiley and Drawbridge, 2007, Miwa et al., this volume). Many of these systems are still under development (e.g., Damasceno-Oliveira et al., 2004) and often the space provided in the tanks is too small for fish to show much of their behavioral repertoire. Pressurized experimental chambers have also the disadvantage of restricted access for manipulations of environmental factors. Decompression over a longer period with stepwise transfer to decreasing pressure may allow acclimatizing of deep-sea fishes to surface conditions (St. John, 2003).

Examples of experimental approaches that may be applicable to studies of deep-sea fish behavior come from work on cave animals (e.g., Uiblein et al., 1992; Uiblein and Parzefall, 1993; Uiblein 1996a, b, c; Parzefall 1996, 2000). Caves provide light-reduced conditions similar to the deep sea, and some groups of fishes like the cuskeels (order Ophidiiformes) live in both habitats (e.g., Parzefall, 1996, Uiblein, 1996a, b). Experimental studies of cave animal behavior and habitat selection are very much advanced compared to those of deep-sea fishes. Particularly interesting are comparisons between so-called secondary and the more adapted primary cave dwellers which provide insights into evolutionary steps animals undergo when adapting to lightless conditions (Uiblein et al., 1992) and choosing between illuminated and dark habitats (Uiblein et al., 1996). That cave biology has also some relevance for considering ecological and evolutionary processes in the deep-sea has already been emphasized earlier (Poulsen, 1971; Uiblein, 1996a, b; Uiblein, 2000).
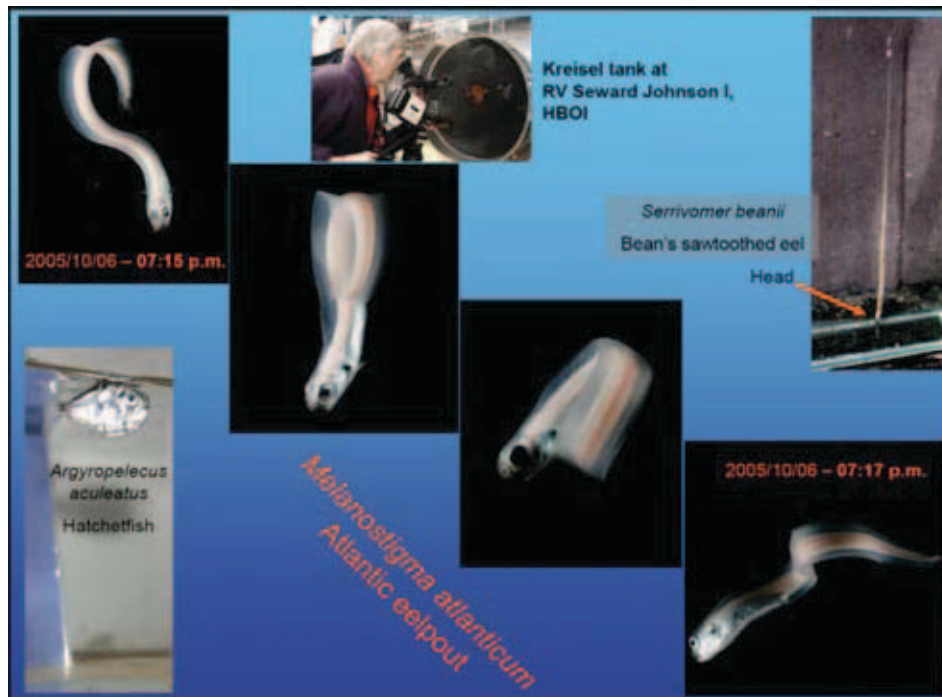
Fig. 7: *Ex-situ* glimpses of deep-sea fish behavior were gathered during recent cruises with the RV Seward Johnson I and II (http://at-sea.org/missions/maineevent6/synopsis.html), after collection of several species with the Johnson Sealink manned submersible and transfer to on-board keeping systems. The Atlantic eelpout, *Melanostigma atlanticum,* was maintained in a Kreisel tank where it displayed elements of curling-up-and-drifting behavior that have been also observed in nature, serving most probably to reduce predation risk (photographs of eelpout by David Shale). This figure also shows images of two other species that were kept in small glass tanks, the hatchetfish *Argyropelecus aculeatus* and the Bean's sawtoothed eel *Serrivomer beanii.* The latter remained in a head-down position over several hours, a vertical body orientation that can be also encountered *in situ*.

Conclusions and outlook

Various methods are currently available for the study of deep-sea fish behavior. Some of these methods have been used already in combination, e.g., acoustics and sampling (Fig. 4), acoustics and *in-situ* observation (Benoit-Bird et al., 2003), or *in-situ* and *ex-situ* observation (Figs. 5,7). In the future it will be important to reach a higher integration of these various methods to gain a more complete picture of behavioral diversity and adaptation to environmental conditions at large depth, an important prerequisite for further progress in deep-sea fish behavioral ecology.

Some fish species may prove especially useful for behavioral studies within an integrative approach such as, for instance, eelpouts of the genus *Melanostigma* which occur widely distributed from near the ocean surface to deep-sea bottoms (e.g., Markle and Wenner, 1979; Silverberg et al., 1987; Silverberg and Bossé, 1994; Robison, 2004; Uiblein et al., 2006; Fig. 5), can be successfully collected in these different habitats, and studied both *in-situ* and *ex-situ*.

As part of an integrative approach, basic taxonomic and systematic work needs to be more actively pursued. Many collections of deep-sea fishes are still awaiting detailed morphological studies that promise exciting and often completely new insights into life in the deep sea.

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