PERSPECTIVE / PERSPECTIVE

Evaluating the role of fish behavior in surveys conducted with underwater vehicles

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Abstract: It is often assumed that visual survey data provide more accurate fish counts than conventional extractive gear. As a result, use of underwater vehicles to assess the abundance and distribution of fishes has increased rapidly over recent years. However, a review of observations reported for 48 demersal marine fish taxa showed that almost all respond in some way to underwater vehicles. Whether or not movements or changes in behavior affect survey bias is more difficult to assess. A simple conceptual model is presented to evaluate relationships between stimulus intensity, distances from the vehicle where reactions occur, and survey bias. Largest bias is caused by attraction or avoidance that occurs outside the field of cameras or observers. While light level and vehicle speed have been explored experimentally in a few cases, much remains to be learned about how bias varies among species, age groups, different vehicles, and operating conditions. Given poor understanding of survey bias, we recommend that surveys be conducted with minimum possible variation in operations and that vehicle time is devoted to experimental evaluation of methods. There is no good substitute for direct observations on fish behavior, distribution, and abundance; and survey design can be improved through experimentation.

Résumé : On assume souvent que les données d'inventaires visuels produisent des dénombrements plus exacts des poissons que les méthodes extractives courantes. En conséquence, l'utilisation de véhicules sous-marins pour évaluer l'abondance et la répartition des poissons s'est accrue rapidement au cours des dernières années. Cependant, une révision des observations faites sur 48 taxons de poissons marins démersaux montre que ces derniers réagissent presque tous d'une manière ou une autre aux véhicules sous-marins. Il est plus difficile d'évaluer si ces déplacements et ces changements de comportement faussent les inventaires. Nous présentons un modèle conceptuel simple pour évaluer les relations entre l'intensité du stimulus, la distance du véhicule lorsque les réactions ce produisent et les erreurs dans l'inventaire. L'erreur la plus importante est due aux attraits ou aux évitements qui se produisent hors du champ des caméras ou des observateurs. Alors qu'on a étudié expérimentalement dans quelques cas les effets de l'intensité lumineuse et de la vitesse du véhicule, il reste beaucoup à découvrir sur la variation de l'erreur en fonction de l'espèce et du groupe d'âge, des types de véhicules et des conditions d'utilisation. Étant donné la connaissance limitée des erreurs d'inventaire, nous recommandons de faire les inventaires avec la variation la plus faible possible dans les opérations et d'utiliser une partie du temps du véhicule pour des évaluations expérimentales des méthodologies. Il n'y a pas de bonne méthode pour remplacer l'observation directe pour étudier le comportement, la répartition et l'abondance des poissons; les plans d'inventaire peuvent cependant être améliorés par l'expérimentation.

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Introduction

Fish populations and communities are surveyed for a variety of management-related objectives, including assessments of abundance, population dynamics, habitat associations, community structure, and patterns of biological diversity. Traditionally, surveys of demersal marine species are conducted with an array of mobile and fixed fishing gear (e.g.,

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bottom trawls, longlines, and pots). However, visual direct-count surveys have long been the method of choice for shallow-water, structure-oriented tropical fishes (see Brock 1954; Sale and Douglas 1981; Edgar et al. 2004). A visual approach is especially critical where fishes cannot be efficiently or effectively sampled with extractive gear types, where destructive sampling is unacceptable (e.g., in marine reserves), and where the goal is identification and conservation of essential fish habitats (Richards 1986; O'Connell and Carlile 1993; Auster 2005). Now, with the expanded use of human-occupied vehicles (HOVs), remotely operated vehicles (ROVs), and autonomous underwater vehicles, visual surveys are increasingly important at higher latitudes and in deep water. All of these underwater vehicle types have been used to assess densities of demersal fish populations in trawlable and untrawlable areas and to make direct observations of animal behavior related to both habitat associations and fishing gear performance.

There are biases associated with all methods of assessing fish populations (Fernö and Olsen 1994). For example, many fish behave differently in the vicinity of trawls, depending upon ambient illumination (Olla et al. 2000; Ryer and Barnett 2006). Similarly, baited gears have differing capture efficiencies depending upon bait type, temperature, light, and current (Auster 1985; Stoner 2004), which are only beginning to be fully understood. Direct visual surveys made possible with underwater vehicles have many advantages over traditional fish-sampling gear; however, the associated biases have not been rigorously quantified and remain mostly undocumented or anecdotal. Underwater vehicles typically utilize powerful illumination to allow for color photographs or video and produce a variety of sounds that may influence fish behavior and survey results. In the worst cases, reactions by fishes can occur well outside the field of view provided to vehicle occupants or cameras. Yet, visual surveys often assume low bias due to gear stimuli and are sometimes used to provide estimates of absolute abundance for target species. Following their early comparison of survey gears for fishes including an HOV, camera sled, and trawl, Uzmann et al. (1977) noted that phototaxis (both negative and positive) could result in under- or overestimates of their abundance and that biases varied with gear type. Since then, others have mentioned potential for attraction and avoidance reactions by fishes to survey vehicles (e.g., Ralston et al. 1986; Richards 1986; Jagielo et al. 2003).

Some fishes may be relatively unaffected by underwater vehicles. For example, rockfishes (*Sebastes* spp.) are commonly surveyed with research HOVs and ROVs, and there is a general impression that responses by rockfishes are minor (Carlson and Straty 1981). Two papers that resulted from dives with the HOV *Delta* on Heceta Bank (Oregon) are cited repeatedly to assuage concerns about fish avoidance or attraction (Hixon et al. 1991; Stein et al. 1992). Their survey transect protocol included a period during which the HOV was allowed to rest on the bottom with lights and motors turned off for periods of 10–15 min. Stein et al. (1992) state that "Turning on the lights at the end of these periods invariably showed that the local distribution and abundance of fishes had not changed appreciably, suggesting that the presence of the submersible *per se* caused little sampling bias due to attraction or avoidance by fishes." However, no data or quantitative tests were provided in the two reports, and in general, studies making use of underwater vehicles rarely test for bias.

This review was conducted to evaluate the apparent and potential biases in visual surveys attributable to fish behavioral reactions to underwater vehicles. Toward this goal, we considered three kinds of information: (*i*) a small but important group of investigations conducted to test the effects of operational variables such as vehicle speed and lighting on survey results (e.g., Trenkel et al. 2004; Lorance and Trenkel 2006), (*ii*) field studies designed to quantitatively test the reactions of fishes relative to underwater vehicles (e.g., Cailliet et al. 1999; Lauth et al. 2004*b*), and (*iii*) qualitative observations on fish reactions to vehicles mentioned throughout the literature and from the authors' collective professional experience. In fact, the vast majority of investigations with underwater vehicles were designed for purposes other than testing fish reactions and survey bias. However, the synthesis of these experimental, quantitative, and qualitative observations allowed us to develop a conceptual framework for prioritizing and addressing bias in future direct-count surveys.

Stimuli associated with underwater vehicles

Artificial light, ordinarily used in visual surveys except in very shallow water, is one of the most obvious elements of operation that can affect fish behavior. Study of visual pigments, as well as whole animal behavioral studies, reveals that most fish have some sensitivity in the range of 400 to 700 nm (Bowmaker 1990; Douglas and Hawryshyn 1990). Peak absorbance can vary greatly among species according to visual pigments, which in turn appear adapted to the spectral environment where these fish occur (Bowmaker 1990). However, different spectral sensitivities notwithstanding, the broad spectral range and shear output of lighting commonly in use aboard HOVs and ROVs assure that these light sources will stand out in stark contrast with the surrounding ambient light field.

Lighting on survey vehicles is usually described in terms of watts; however, the light level experienced by fish in the surrounding waters is better defined by luminosity. Consequently, we used the following relationships for converting wattage to luminosity: 85–100 $lm \cdot W^{-1}$ with hydrargyrum medium-arc iodide (HMI) arc lamps, 50 $lm \cdot W^{-1}$ for high-intensity discharge (HID) arc lamps, and 15–25 $lm \cdot W^{-1}$ for halogen lamps. (M. Olsson, Deep Sea Power and Light, 7033 Ruffin Road, San Diego, CA 92123-1817, USA, personal communication). For large ROVs and HOVs, a combination of arc and halogen lamps can create light levels of 50 000 – 200 000 lm at the source in habitats where fishes are often adapted to very low light or darkness. Smaller ROVs and some HOVs employing lower wattage systems create light source levels on the order of 10 000 lm. To test effects of light level on fish surveys with the *Victor 6000* ROV in the Bay of Biscay (1000–1500 m), Trenkel et al. (2004) compared standard lighting (2700 W of combined arc and halogen lamps = ∼100 000 lm) with reduced lighting (1200 W, halogen only = ∼24 000 lm) in a well-replicated experiment. Density estimates for one common taxon (Moridae) were lower in bright light, while density of northern cutthroat eel (*Synaphobranchus kaupii*) was higher at a fixed distance. The northern cutthroat eel was also attracted when the ROV was held stationary. These experiments provide strong evidence that both artificial light and vehicle motion can affect fish counts through either direct or indirect mechanisms.

A laboratory investigation on response to light is currently underway in the Alaska Fisheries Science Center's fish behavior laboratory in Newport, Oregon, with a variety of species including sablefish (*Anoplopoma fimbria*), lingcod (*Ophiodon elongatus*), Pacific halibut (*Hippoglossus stenolepis*), and six rockfish species (*Sebastes* spp.). To simulate an approaching survey vehicle, groups of fish are exposed to a halogen light at the far end of a 10 m long tank (1.5 m wide, 1.2 m deep), where fish behavior is monitored using videography and infrared illumination. Light level is steadily increased from zero to high intensity and then reduced to zero. Sablefish demonstrated a fivefold increase in swimming speed and strong avoidance in response to small increases in illumination above the low light conditions to which they were accustomed (C.H. Ryer and A.W. Stoner, unpublished data). Corroborating this strong avoidance response, sablefish catch in the field is dramatically reduced in pots illuminated with either red (Widder et al. 2005) or white light (K. Matteson, Oregon Department of Fish and Wildlife, 2030 SE Marine Drive, Newport, OR 97365, USA, personal communication, 2006). These results help to explain the strong avoidance of a camera sled by sablefish (R. Lauth, Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115, USA, personal communication, 2006). However, experiments with artificial lighting do not always yield consistent results. While Trenkel et al. (2004) observed a substantial negative response by roundnose grenadier (*Coryphaenoides rupestris*) to a lighted ROV, Gordon et al. (2002) had higher catches in a trawl fitted with lights than with an unlighted trawl, and we have seen no obvious attraction or avoidance to either the HOV *Alvin* or the ROV *Hercules* (P.J. Auster, personal observation). Also, laboratory studies with numerous species show that fish often prefer areas of dim light occurring at the periphery around an illuminated area (Marchesan et al. 2005). This could have a strong impact on fish counts made with survey vehicles, causing fish to mill about at a specific distance or light intensity. That light level may occur either inside or outside the view of cameras and observers.

Light associated with underwater vehicles is often considered to be the most likely source of survey bias with fishes; however, sounds produced by underwater vehicles can be substantial, resulting in positive or negative responses. Most fish detect sound in the range of 300–1000 Hz (Popper 2003), although some members of the Allosinae can detect ultrasonic sound to over 200 kHz (Mann et al. 2001). It has been widely recognized that many fish respond to the sound radiated by vessels. This is of particular interest with regard to acoustic and trawl survey vessels, where behavioral reactions of fish have potential for introducing bias to abundance estimates. Both Atlantic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus*) move deeper and accelerate away from approaching vessels (Vabø et al. 2002; Handegard et al. 2003), although more recent work indicates the movements of fish relative to an approaching vessel may be more complex; involving movements both away from and towards the vessels as the properties of the sound field around the vessel change (Handegard and Tjøstheim 2005). This has led to adoption of noise radiation standards for survey vessels to minimize these behavioural reactions by fish (Mitson 1995; Mitson and Knudsen 2003), although the efficacy of these standards is not universally accepted (Ona et al. 2007).

Noise radiation can be expected from motors, propulsion systems, hydraulic power units, capacitors in electronic flash units, or bottom contact associated with underwater vehicles, and the noises will vary with vehicle size, motor type, and operating speed and action. While it is likely that fish detect and respond to sounds from underwater vehicles in ways similar to surface vessels, sound signatures are little known for underwater vehicles. However, preliminary observations conducted with two large ROVs operated by the Monterey Bay Aquarium Research Institute (MBARI, Moss Landing, California) show that sound can affect survey bias for at least some fish species. In paired operations with the ROV *Tiburon* (with relatively quiet all electric propulsion) and the ROV *Ventana* (with traditional hydraulic thrusters), it was clear that sablefish and other species responded more strongly to *Ventana*, reducing the numbers observed (B. Robison, Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA, personal communication, 2006). Laboratory experiments conducted by Spanier et al. (1994) have shown that the combination of light and sound produced by an ROV reduced feeding activity in American lobsters (*Homarus americanus*) more than light or sound presented individually. A similar compounding of stimulus effects is likely for fishes.

Vehicle motion and water displacement are generally thought to affect behaviors through either visual or tactile stimuli acting in the near field. However, some species may be sensitive to low-frequency pressure waves and respond to motions at considerable distances. For example, Koslow et al. (1995) acoustically monitored the movements of orange roughy (*Hoplostethus atlanticus*) around a drop camera system equipped with acoustics and a still camera. The fish dispersed strongly from the camera frame at a distance of 130 m. No visual cues were possible since the observations were conducted in deep slope waters without lighting. Orange roughy also responded at a distance of 60 m from a falling steel bar. Similarly, fish can react at large distances from a towed net (Ona and Godø 1990). While it is difficult to evaluate the relative roles of different cues produced by survey vehicles, it is clear that some fishes respond to light, sound, and motion at large distances, well beyond the visual range of cameras.

As with mobile fishing gear, vehicle speed can have an effect on survey results. Trenkel et al. (2004) operated the *Victor 6000* ROV at two different speeds over replicated transects in two deepwater locations in the Bay of Biscay. When the ROV was operated at $0.5\ m\cdot s^{-1}$ versus the standard survey speed of $0.25\ m\cdot s^{-1}$, density estimates for cods of the family Moridae declined by 21%–55%, and densities of northern cutthroat eels declined 21%–51%, despite the fact that the two taxa had opposite responses to lighting experiments (see above). Differences in pressure waves could be responsible for variable responses to vehicle speed and size. It is also plausible that some responses may depend upon indirect effects of a survey vehicle. For example, rock sole (*Lepidopsetta* spp.) and hake (*Urophycis* spp.) are attracted to sediment disturbance created by towed sleds and ROVs, and pollock (*Pollachius virens*) are attracted to euphasiids that accumulate in the artificial lights of stationary survey vehicles (A.W. Stoner, P.J. Auster, and W.W. Wakefield, personal observation). Vehicle speed, of course, is associated with variation in several variables, including sound level, the rate of change in light level, and pressure waves.

Chemical stimuli may also influence attraction or avoidance responses to underwater vehicles. Many different compounds, including lubricants and cleaners, are associated with the vehicles, and olfactory sensitivity of fishes (see Hara 1993; Løkkeborg et al. 1995) could make chemical cues detectable from large distances, depending upon relative current direction. Nothing is known about how the presence of vehicle-related compounds might affect fish reactions, although many of these potential effects may be avoided by vehicles moving into the prevailing currents.

Other stimuli may only be detectable at close range, such as electrical or magnetic fields. This effect is well described for elasmobranches in the laboratory and in field experiments (Kalmijn 1982; Kramer 1990). In one instance, a longnose skate (*Raja rhina*) was observed rising 2 m off the bottom to touch the *ROPOS* ROV power tether (S.J. Parker, personal observation).

Detecting and evaluating fish reactions to underwater vehicles

Fishes may be attracted, repulsed, or unaffected by the stimuli produced by underwater vehicles, and the responses appear to vary in both form and intensity with environmental conditions and vehicle operating modes. Various methods have been used to detect and quantify reactions. These include simple anecdotal observations, systematic measurements of movements over perspective grids (Wakefield and Genin 1987), and field and laboratory experiments designed to test specific stimuli. Approaches to field observation are discussed briefly below to provide the framework for subsequent analysis of observations reported.

Basic movements

Most observers draw conclusions about avoidance or attraction to a survey vehicle based upon movements by fish within the field of view. Many have reported movements in simple descriptive terms, while others report the proportions of fishes exhibiting different behaviors. For example, Adams et al. (1995) used a semiquantitative approach, recording the response of each fish to the ROV in one of five categories: strongly attracted, weakly attracted, no response, weakly avoided, and strongly avoided. Trenkel et al. (2004) summarized the proportions of fish that had no reaction, a reaction initiated within the field of view, or a reaction that began before the fish came into view.

Views from multiple cameras may also be used to detect fish motion related to vehicle approach or passage. O'Connell et al. (1998, 2003) and Yoklavich et al. (2007) used dual, time-synchronized video cameras on the HOV *Delta*, one positioned forward and the other perpendicular along the track line, to test the assumption of no movement (i.e., either avoidance or attraction) in yelloweye rockfish (*Sebastes ruberrimus*) and cowcod (*Sebastes levis*), respectively. No changes in fish behavior or position were observed as the HOV approached; thus, they concluded that there were no significant biases introduced by the survey method for these species. In another study, a stern-oriented camera on the ROV *ROPOS* detected persistent following behavior by yellowtail rockfish (*Sebastes flavidus*) (S.J. Parker, unpublished data).

Distance sampling and detection functions

Surveys for fish density using a line transect or distance estimator can provide information useful in inferring movements in response to vehicles (Buckland et al. 2001). Use of the estimator requires the following assumptions: (*i*) the target species in the center lanes of view have 100% detectability; (*ii*) the fish are uniformly distributed and detected in their initial locations; and (*iii*) distances are measured accurately and in the proper distance category. These assumptions can be evaluated by examining detection functions where counts for a species can be plotted versus perpendicular distance from the vehicle and across the field of view. If the target species is immobile, detections should increase with nearness to the vehicle and the transect center line. Avoidance is indicated by detections that increase with distance from the vehicle or away from the center line. As examples, recent data collected from the HOV *Delta* traveling at 25 cm·s^{-1} in Alaska (Fig. 1) suggest that yelloweye rockfish (*Sebastes ruberrimus*) do not avoid the vehicle, while rosethorn rockfish (*Sebastes helvomaculatus*) show signs of reduced detection in the near field, resulting either from movement away from the transect line or a behavioral response that would reduce detection (e.g., cover seeking). Similarly, detection functions were developed for macrourid and zoarcid fishes in deep-sea habitats off central California using strobe-illuminated still images taken from a towed camera sled (Cailliet et al. 1999). This approach yielded indications of avoidance behavior in the zoarchids. Lauth et al. (2004*b*) conducted one of the most thorough tests of critical assumptions for obtaining unbiased density estimates, targeting thornyheads (*Sebastolobus* spp.) in deep water off Oregon with a large towed camera system. Plots of detection probabilities revealed no evidence for avoidance in three different depth zones. They also reported that only 12.4% of the fish moved from their initial location in the field of view, and the density estimates were considered to be unbiased by sled-related stimuli. It is important to remember, however, that flight or retreat to shelters can occur completely outside the field of view. As an extreme case, the camera sled studies conducted by Lauth et al. (2004*a*, 2004*b*) were originally designed for sablefish, and it quickly became apparent, without the need for statistical evaluation, that sablefish avoided the survey system at the periphery or beyond camera view.

Synthesis of observations

Approach to synthesis

To explore potential reactions by fishes to underwater ve-

Fig. 1. Counts for two rockfish species shown as a function of distances from the starboard viewing port of the HOV *Delta*. Rosethorn rockfish (*Sebastes helvomaculatus*) (*a*) showed avoidance behavior while yelloweye rockfish (*Sebastes ruberrimus*) (*b*) demonstrated no apparent response (modified figure courtesy of D.W. Carlile, V.M. O'Connell, W.W. Wakefield and C. Brylinsky. Deep distance: submarine line transects and rockfish management in Alaska, USA. American Fisheries Society Alaska Chapter meeting, November 2001).

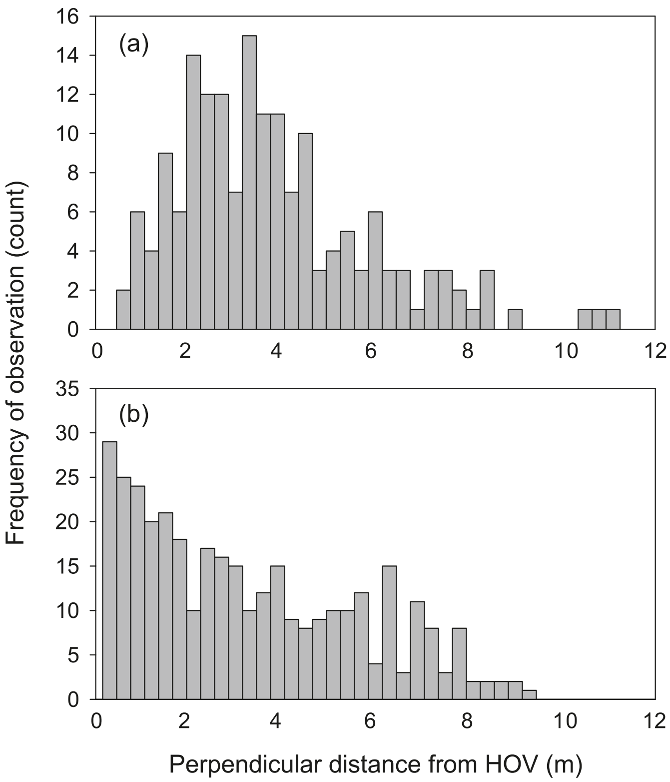
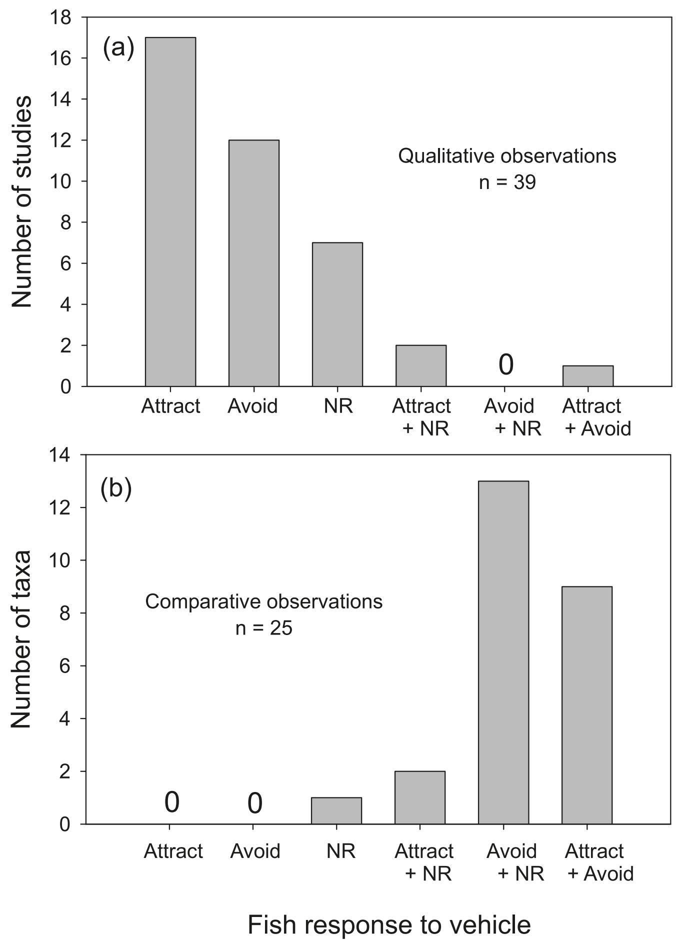


Fig. 2. Summary of behavioral responses by demersal fish species to underwater survey vehicles. (*a*) Number of investigations reporting responses to underwater vehicles in simple qualitative terms, without comment on variation (27 taxa represented by methods Q and CC in Appendix A, Table A1). (*b*) Number of taxa for which observations were made under different conditions (different observers and (or) different vehicles), where the proportions of fish responding in different ways were reported and where variation was observed through experimental approaches (species in bold type in Appendix A, Table A1). The lists of species included in the two figures are not mutually exclusive.



hicles, we summarized the broad range of observations reported in the literature and from our own experience. Observations were gathered from 22 sources representing 48 different fish taxa (Appendix A, Table A1), with reactions classified as attraction, avoidance (including shelter seeking), and no response. Combinations of these three responses were also possible, either under different operational circumstances or among individuals observed at one time.

Observations were compiled for two pools of data that were not mutually exclusive. The first data set included qualitative observations for 39 different study–taxa combinations. These were often simple reports of motions or sheltering observed to occur in the presence of a survey vehicle, with no data on the proportion of fish responding or how reactions varied under different environmental or operational conditions (method Q, Appendix A, Table A1). Positive and negative responses evaluated through probability detection functions and those derived from comparisons of different camera views (method CC) were also included in our meta-analysis of qualitative observations. The latter methods employ a systematic assessment of movement, but the results were usually reported as an overall population response without quantification of variation.

The second data set (taxa in bold type, Appendix A, Table A1) was derived from information in two different forms that combined to provide the most rigorous tests of response variation in 25 different fish taxa. The first sources were individual investigations where variation in reactive behavior was reported for a species (e.g., percentages of fish responding in various ways, intraspecific variation with different vehicles or operating modes). These sources are coded with methods M, MD, and QC in Appendix A (Table A1), yielding data for 19 separate taxa. Six other taxa were added to the data set where multiple studies for an individual taxon provided comparative data on reactions to vehicles.

Qualitative results

Based on singular qualitative observations, 17 of 39 studies reported attractions to underwater vehicles (Fig. 2*a*). For example, Pearcy et al. (1989) observed that hundreds of yellowtail rockfish (*Sebastes flavidus*) were attracted to and followed the HOV *Mermaid II*, and yellowtail, canary (*Sebastes pinniger*), and black (*Sebastes melanops*) rockfish were attracted to and followed the HOV *Delta* (V. O'Connell, Alaska Department of Fish and Game, 304 Lake Street, Sitka, AK 99835-7563, USA, personal communication, 2006). Similarly, Krieger (1993) found that Pacific ocean perch (*Sebastes alutus*) were attracted to the HOV *Delta*, particularly when they were in large numbers. An aft-viewing video camera on the ROV *ROPOS* confirmed following behavior in the rockfishes *Sebastes flavidus*, *Sebastes ruberrimus*, and *Sebastes wilsoni* (S.J. Parker, personal observation). Attraction to underwater vehicles has also been observed in a variety of shallow-water flatfishes (Norcross and Mueter 1999; A.W. Stoner and C.H. Ryer, personal observation) and certain hakes (*Urophycis* spp.) (P.J. Auster, personal observation). Northern cutthroat eels were strongly attracted to the *Victor 6000* ROV in slope waters (Trenkel et al. 2004). The overall bias due to attraction would be to overestimate abundance and create habitat associations where they may not exist.

Avoidance of vehicle-related stimuli is a large concern because flight or sheltering can result in underestimates of fish density, undetected taxa, or inaccurate assessments of habitat associations. Avoidance behavior was noted in 12 of 39 qualitative reports (Fig. 2*a*). However, avoidance can take a wide range of forms, from slow dispersal away from the paths of the survey vehicle as observed in Atlantic cod (*Gadus morhua*) (P.J. Auster, personal observation) to strenuous retreat beyond the field of view, as determined by Koslow et al. (1995) for orange roughy. Juvenile rockfishes on the continental slope have been observed diving for cover when the HOV *Delta* hit hard substratum (V. O'Connell, Alaska Department of Fish and Game, 304 Lake Street, Sitka, AK 99835-7563, USA, personal communication, 2006).

Quantitative and comparative assessments of reactions

When our analysis of reactions to underwater vehicles was limited to taxa represented by quantitative and comparative observations, it became clear that responses by most species were variable (Fig. 2*b*). Thirteen of the 25 fish taxa demonstrated avoidance or neutral responses to vehicles, with the response depending upon vehicle type and operational mode. Two taxa were either attracted or neutral, and nine different taxa were attracted to or avoided underwater vehicles under different circumstances. Only one taxon was consistently neutral to vehicles — the Atlantic thornyhead (*Trachyscorpia cristulata echinata*) responded only in low numbers (10%) and at very close range (Lorance and Trenkel 2006). This was similar to the low responsiveness observed in two scorpaenid congeners (*Sebastolobus* spp.) in North Pacific slope waters (Lauth et al. 2004*b*). None of the 25 taxa for which good comparative data exist responded with only attraction or avoidance.

The more in-depth assessment of reactions provided by quantitative studies and comparisons shows that generalizations about an individual species should not be made on the basis of a single set of observations, because response variation will be context specific for most species. For example, direct observations have been made for the commercially important yelloweye rockfish (*Sebastes ruberrimus*) with several different HOVs and ROVs, and a wide range of vehicle-associated behaviors have been reported, including no response, retreating to crevices, strong attraction, and following behavior. Yelloweye rockfish were attracted to a stationary vehicle and showed territorial display when the vehicle was in motion (S.J. Parker, personal observation); however, juveniles often swim downward and enter crevices when a vehicle approaches (D. Fox, Oregon Department of Fish and Wildlife 2030 SE Marine Science Drive, Newport, OR 97365, USA, personal communication, 2007). O'Connell and Carlile (1994) reported that large rockfishes and Pacific halibut were attracted to the *MiniRover MKI* ROV, increasing the risk of double counting, and this was exacerbated by slow ROV speed. Silver hake (*Merluccius bilinearis*) avoided vehicles skidding on the sea floor but not when the vehicles were off bottom (P.J. Auster, personal observation). Also, reactions can always be influenced by variation in environmental variables such as temperature, light level or turbidity, and substratum type. For example, lingcod on low relief and cobble habitats were observed to move away from the HOV *Delta*, while those on rocky bottom were more likely to have no response (V. O'Connell, Alaska Department of Fish and Game, 304 Lake Street, Sitka, AK 99835-7563, USA, personal communication 2006).

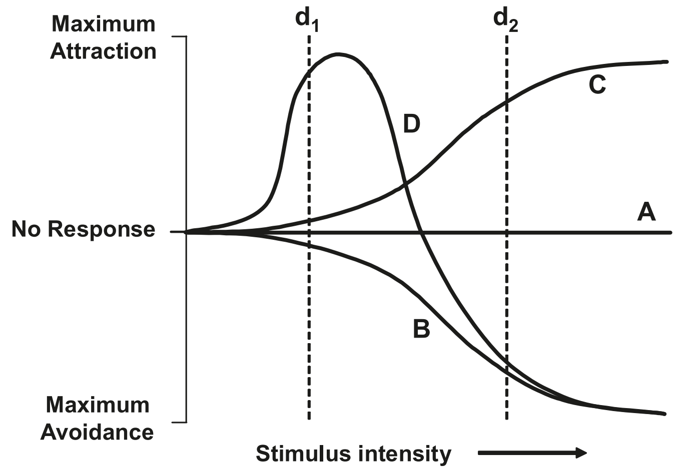
Do reactions cause survey bias?

The use of underwater vehicles in fish research began with basic analysis of community structure and qualitative observations on fish behavior and habitat associations. As with SCUBA, these tools continue to provide important insights into fish ecology, and the research has become increasingly quantitative. In fact, numerous comparative studies demonstrate the superiority of visual surveys over towed fishing gear for fish density estimates and for quantifying community structure in various shallow and deepwater environments (e.g., Uzmann et al. 1977; Adams et al. 1995; Krieger and Sigler 1996). However, any survey technique has biases, and it is critical to evaluate, understand, and adjust for those biases. Brock (1982) pointed out long ago that visual survey methods for shallow-water reef fishes do not provide 100% accuracy in density estimates or species composition, and diver surveys have been continuously evaluated and improved (e.g., Sale and Douglas 1981; Willis 2001; Edgar et al. 2004). Assessment of biases associated with underwater vehicles lags far behind, no doubt because of the expense and logistical complexity of operations. However, the same criteria should compel vehicle users to gain a greater understanding of potential biases.

It is clear from our review that most fishes react to underwater vehicles under at least some circumstances, and many species can respond both positively and negatively. However, avoidance and attraction responses may or may not have an impact on survey bias and density estimates. Actual impact will depend upon reaction intensity, the proportion of fish responding to vehicle stimuli, and the distance from the vehicle at which the response occurs. For example, Acadian redfish (*Sebastes fasciatus*) in the Northwest Atlantic retreat to the seafloor and shelter upon close approach by survey vehicles, but this behavior appears consistent and is assumed to have a minimal and systematic effect on counts if the vehicle is moving forward (P.J. Auster, personal observation). Overall reaction intensities exhibited by most *Sebastes* species appear to be relatively low and bias is probably minimal. This is fortunate, since many of the more than 70 *Sebastes* species off North America live in deep, rugged topography where in situ observation is one of few feasible approaches for multispecies surveys. Exceptions are some schooling rockfishes that are strongly attracted to underwater vehicles. In such cases, survey bias could be large because the fish may be responding from distances well outside the radius of detection. It is also possible that flight, retreat to crevices or burrows, or shifts in habitat association can occur completely outside the field of view. For example, Pearcy et al. (1989) noted that small individuals of *Sebastes* spp. were particularly prone to flee or seek shelter in the presence of an HOV, suggesting potential for size bias in visual surveys.

The response of fish to underwater vehicles can be modeled by response curves that take into account the type of response, its strength, and the distance from the vehicle (which also effectively influences stimulus intensity). The magnitude of survey bias created by reactions to survey vehicles will depend upon the shape of the response function (Fig. 3). Clearly, fishes that do not respond to stimuli produced by a vehicle will be surveyed with a high degree of accuracy if they occur naturally in open habitat within the field of view. With simple avoidance or attraction responses (Fig. 3, lines B and C) magnitude of bias will depend upon the distance from the vehicle where the response occurs. For example, if attraction is strong and occurs at large distance from the vehicle, the positive bias would be large. Also, it is likely that some species are attracted at low stimulus levels (either sound or light) and repelled at higher levels (Fig. 3, line D). This could result in fish hovering or even following the vehicle at some preferred distance. This is most likely with the light stimulus, and bias would depend upon whether or not the preferred light level occurred within the field of view. Fish being frequently observed milling around a vehicle could result from fish choice for an optimal level in the gradient of a single variable such as light or a more complex balance between attraction and avoidance of different stimuli (e.g., attraction to a food source versus avoidance of vehicle sound). Highest risk of survey bias will occur when fishes respond to vehicle-related stimuli at a distance greater than can be detected by observers or video cameras.

Fig. 3. Basic responses of fishes to stimuli (i.e., light and sound) created by underwater survey vehicles shown as a function of stimulus intensity. Four response types are shown: no response (A), increasing avoidance (B), increasing attraction (C), and attraction at low stimulus intensity followed by avoidance (D). The table shows the likelihood of survey bias caused by responses occurring at two different distances (*d*) from the survey vehicle. It is assumed that the observers or cameras on the vehicle have a range of view substantially shorter than the distances at which lights and sound can be detected by the fish.



Response type	Distance from vehicle d_1	d_2
A	No bias	No bias
B	Small bias	Large negative bias
C	Small bias	Large positive bias
D	Large positive bias	Large negative bias

Conclusions and recommendations

One of the primary goals of this analysis was to raise awareness of potential biases in surveys caused by fish reactions to survey vehicles. Assuming success in that first goal, we have several recommendations for future research with underwater vehicles.

Provide details on gear and operations

Early in the history of quantitative submersible operations, Uzmann et al. (1977) published details on the propulsion systems, survey speed, lighting, cameras, field of view, and photos and drawings of their equipment. Since that time there has been a general decline in the amount of information provided. While some of the same vehicles are used repeatedly for survey research, lighting systems, cameras, and fields of view are routinely changed and survey speeds are highly variable. Detailed descriptions of equipment and operating modes will allow for better comparative analysis of observations. Further, given the relatively small number of HOVs and ROVs currently in use, we recommend that effort be made to acquire the broad-spectrum sound signatures for those vehicles over a range of operating speeds and distances. Similarly, it would also be useful to have information on the radial distribution of light around the vehicles, not just the power of lamps carried.

Identify study goals and evaluate potential biases

It will be critical to determine whether or not the behavior of a subject species or group of species is altered sufficiently by vehicle operations to have an impact on the required observational data. Simple qualitative assessments of community composition based on relative abundance or patterns of habitat association will be less susceptible to bias than studies where absolute densities or abundance are required. The simplest assessments of bias involve examining the percentage of fish moving within a field of view (e.g., Trenkel et al. 2004) or comparing positions of fish over two different views (e.g., Adams et al. 1995). A more rigorous approach is analysis of video records using a perspective grid to plot probability of detection functions (e.g., Wakefield and Genin 1987; Cailliet et al. 1999). Better still is to evaluate movement patterns within the perspective grid (e.g., Lauth et al. 2004*b*). Analogous statistical approaches that consider activity and angular distribution of fish tracks (Albert et al. 2003) have been used to evaluate the effects of external stimuli (e.g., light) on fish movements and capture efficiencies related to towed fishing gear (McKinstry et al. 2005). These kinds of analyses, simple or complex, provide for systematic evaluation of survey efficiency for specific taxa and show whether potential bias threatens the goals of the project.

Expand comparative and experimental assessments of survey bias

While a basic understanding of species differences in the behavioral reactions to survey vehicles has been or can be acquired through observer experience, our simple synthesis of observed fish behavior reveals almost universal variation in responsiveness. We need to understand the potential effects of light intensity and wavelength (e.g., halogen vs. various arc lamps), effects of sound intensity and frequencies (in the context of fish hearing abilities), and effects of vehicle speed and size on survey bias in a variety of conditions with different communities of fishes. We also need to understand survey bias with respect to fish size classes. Many of these questions can be pursued through relatively simple field experiments such as manipulations of vehicle lighting and speed. However, new tools will be important for evaluating behavior in the far field. One such tool is high-frequency imaging sonar. For example, Rose et al. (2005) used a DIDSON imaging sonar (soundmetrics.com/) to observe the behavior of fishes in the distant field around fixed gear (fish pots and hooks) in 220–370 m depth off Oregon. The sonar was superior to traditional videography with infrared lighting and useful in analyzing the movements of several large species. Imaging sonars are currently in use to record the behavior of fishes moving in front of trawl gear (C.H. Ryer and W.W. Wakefield, unpublished data), and they should also be useful for observing fishes at distances well beyond the range of low-light cameras carried on survey vehicles. Of course, even the best currently available imaging sonar systems do not provide video-like observations or allow for identification of closely related or small species, and alternative forms of lighting for photographs or video continue to be valuable. Strobes currently used on new autonomous underwater vehicles (Singh et al. 2004) may prove useful for surveying fishes; however, the effects of strobed versus constant lighting on fish behavior have not been tested. Laser line scan is another useful tool for direct imaging of the seafloor and associated fauna that can be used to supplement vehicle-acquired observations (Yoklavich et al. 2003).

In summary, while no survey method or gear offers perfect information on fish distribution and abundance, underwater vehicles provide invaluable direct observations on the animals in their environment, and there is no good substitute for these tools in structurally complex habitats. Given the increasing importance of survey vehicles in assessing fish populations and communities, we recommend that vehicle time and future projects be devoted specifically to optimizing survey operations. In the meantime, surveys should be conducted with minimum possible variation in operations. Once biases are evaluated and experiments related to response variation have been conducted, it will be possible to adjust methods and design a new generation of underwater tools to minimize fish reactions, reduce survey bias, and meet survey goals.

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Appendix A

Appendix A appears on the following pages.

Table A1. Observations on responses (attract, avoid, or no response (NR)) by fish species observed from a variety of vehicles.

Taxon	Common name	Method[a]	Response type: Attract	Avoid	NR	Vehicle[b]	Location	Citation[c]
Chondrichthyes								
Chimaeridae	**Ratfishes**	M		X	X	*Victor 6000* (R)	Bay of Biscay	11, 19
Hydrolagus colliei	Spotted ratfish	Q	X			*Pisces IV* (S)	British Columbia	12
Hexanchidae								
Hexanchus griseus	Bluntnose sixgill shark	Q	X			*Pisces IV* (S)	British Columbia	12
Squalidae	**Dogfish sharks**	M		X	X	*Victor 6000* (R)	Bay of Biscay	11, 19
Squalus acanthias	Spiny dogfish	Q	X			*ROPOS* (R)	Oregon shelf	15
Scyliorhinidae	**Cat sharks**	M		X	X	*Victor 6000* (R)	Bay of Biscay	11, 19
Rajidae	**Skates**	MD		X	X	*Ventana* (R)	Central California	1
Actinopterygii								
Synaphobranchidae								
Synaphobranchus kaupii	Northern cutthroat eel	Q	X			*Victor 6000* (R)	Bay of Biscay	19
Alepocephalidae	**Slickheads**	M		X	X	*Victor 6000* (R)	Bay of Biscay	11, 19
Macouridae								
Coryphaenoides rupestris	**Roundnose grenadier**	M		X	X	*Victor 6000* (R)	Bay of Biscay	11
Moridae	Codlings	Q		X		*Victor 6000* (R)	Bay of Biscay	19
Ophidiidae								
Genypterus capensis	Kingklip	Q	X			*Jago* (S)	Namibia	7
Phycidae								
Urophycis chuss	Red hake	Q	X			*Johnson-Sea-Link* (S) *Delta* (S)	Georges Bank Gulf of Maine Mid-Atlantic Bight	2
Urophycis tenuis	White hake	Q	X			*Johnson-Sea-Link* (S) *Delta* (S)	Georges Bank Gulf of Maine Mid-Atlantic Bight	2
Merlucciidae								
Merluccius bilinearis	**Silver hake**	QC		X	X	*Delta* (S) *Johnson-Sea-Link* (S) *MiniRover MkII* (R) *Kraken* (R) *Hela* (R)	Georges Bank Mid-Atlantic Bight	2
Merluccius productus	**Pacific hake**	MD	X	X	X	*Ventana* (R)	Central California	1
Gadidae								
Brosme brosme	**Cusk**	QC	X	X	X	*Delta* (S) *Kraken* (R) *Hela* (R)	Gulf of Maine Georges Bank canyons	2
Gadus morhua	**Atlantic cod**	Q			X	*Pisces IV* (S)	Newfoundland	8
		Q		X		*Kraken* (R) *Hela* (R) *Delta* (R)	Gulf of Maine	2

Table A1 (*continued*).

Taxon	Common name	Method[a]	Response type: Attract	Avoid	NR	Vehicle[b]	Location	Citation[c]
Pollachius virens	Pollock	Q	X			*Johnson-Sea-Link* (S)	Gulf of Maine	2
							Georges Bank	
						Delta (S)		
						Kraken (R)		
						Hela (R)		
Theragra chalcogramma	Walleye pollock	Q	X		X	*Delta* (S)	Gulf of Alaska	9
Trachichthyidae								
Hoplostethus atlanticus	**Orange roughy**	M		X	X	*Victor 6000* (R)	Bay of Biscay	11
Scorpaenidae								
Sebastes alutus	**Pacific ocean perch**	QC	X		X	*Delta* (S)	Gulf of Alaska	9
Sebastes entomelas	Widow rockfish	Q		X		*Delta* (S)	Oregon shelf	21
Sebastes fasciatus	**Acadian redfish**	QC	X	X		*Delta* (S)	Gulf of Maine	2
						Kraken (R)	Georges Bank canyons	
						Hela (R)		
Sebastes flavidus	Yellowtail rockfish	Q	X			*Mermaid II* (S)	Heceta Bank	16
		CC	X			*ROPOS* (R)	Heceta Bank	15
Sebastes gilli	Bronzespotted rockfish	Q			X	*Phantom HD2+2* (R)	Southern California	4
Sebastes helvomaculatus	Rosethorn rockfish	DP		X		*Delta* (S)	Gulf of Alaska	14
Sebastes maliger	Quillback rockfish	Q	X			*Phantom HD2+2* (R)	Oregon shelf	6
Sebastes mystinus	Blue rockfish	Q		X		*Phantom HD2+2* (R)	Oregon shelf	6
Sebastes nigrocinctus	Tiger rockfish	Q		X		*Pisces IV* (S)	British Columbia	12
Sebastes levis	**Cowcod**	CC			X	*Delta* (S)	Southern California	22
		Q	X			*Phantom HD2+2* (R)	Southern California	4
Sebastes paucispinus	Bocaccio	Q	X			*Phantom HD2+2* (R)	Southern California	4
Sebastes ruberrimus	**Yelloweye rockfish**	Q	X			*Nekton Gamma* (S)	Gulf of Alaska	5
		Q			X	*Pisces IV* (S)	British Columbia	17
		QC	X		X	*MiniRover MK1* (R)	Gulf of Alaska	13
		Q		X		*Pisces IV* (S)	British Columbia	12
		DP			X	*Delta* (S)	Gulf of Alaska	14
		CC	X			*ROPOS* (R)	Oregon shelf	15
		Q		X		*Phantom HD2+2* (R)	Oregon shelf	6
Sebastes wilsoni	Pygmy rockfish	CC	X			*ROPOS* (R)	Oregon shelf	15
Sebastolobus spp.	Thornyheads	DP			X	Towed sled	Oregon shelf	10
Trachyscorpia cristulata echinata	**Atlantic thornyhead**	M			X	*Victor 6000* (R)	Bay of Biscay	11, 19
Anoplopomatidae								
Anoplopoma fimbria	**Sablefish**	Q		X		Towed sled	Oregon slope	20
		Q	X		X	*Delta* (S)	Gulf of Alaska	9
		MD	X	X		*Ventana* (R)	Central California	1
Hexagrammidae								
Ophiodon elongatus	**Lingcod**	Q	X	X		*Nekton Gamma* (S)	Gulf of Alaska	5
		Q			X	*Phantom HD2+2* (R)	Oregon shelf	6

Table A1 (*concluded*).

Taxon	Common name	Method[a]	Response type: Attract	Avoid	NR	Vehicle[b]	Location	Citation[c]
Carangidae								
Trachurus capensis	Horse mackerel	Q	X			*Jago* (S)	Namibia	7
Bathymasteridae								
Bathymaster signatus	Searcher	Q		X		*Phantom II* (R)	Bering Sea, Alaska	3
Zoarcidae								
Lycodes cortezianus	**Bigfin eelpout**	MD		X	X	*Ventana* (R)	Central California	1
Zoarces americanus	**Ocean pout**	QC	X	X		*Delta* (S) *Kraken* (R) *Hela* (R)	Gulf of Maine Georges Bank canyons	2
Anarchichadidae								
Anarrhichthys ocellatus	Wolf-eel	Q		X		*Nekton Gamma* (S)	Gulf of Alaska	5
Trichiuridae								
Aphanopus carbo	**Black scabbardfish**	M		X	X	*Victor 6000* (R)	Bay of Biscay	11
Pleuronectidae								
Glyptocephalus zachirus	**Rex sole**	MD		X	X	*Ventana* (R)	Central California	1
Hippoglossus stenolepis	**Pacific halibut**	QC	X		X	*MiniRover MK1* (R)	Gulf of Alaska	13
		Q		X		Towed sled	Kodiak, Alaska	18
Lepidopsetta polyxystra	**Northern rock sole**	QC	X	X	X	Towed sled	Kodiak, Alaska	18
Microstomus pacificus	**Dover sole**	MD		X	X	*Ventana* (R)	Central California	1

Note: Not all of these responses result in survey bias (see text). Bold type shows the taxa where observations were considered sufficiently quantitative or comparative for analysis (Fig. 2).

[a]Methods for determining the response include simple qualitative observations on movement (Q), qualitative observations with descriptions of variation with operational context (QC), percentage of fish moving (M), movements and direction quantified (MD), comparison of different camera views (CC), and detection plots (DP).

[b]S, submersibles; R, remotely operated vehicles.

[c]1, Adams et al. 1995; 2, P.J. Auster, personal observations; 3, Busby et al. 2005; 4, J. Butler, Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038, USA, personal communication; 5, Carlson and Straty 1981; 6, D. Fox, Oregon Department of Fish and Wildlife, 2030 SE Marine Science Drive, Newport, OR 97365, USA, personal communication.; 7, Gibbons et al. 2000; 8, Gregory and Anderson 1997; 9, Krieger 1993; 10, Lauth et al. 2004*b*; 11, Lorance and Trenkel 2006; 12, Murie et al. 1994; 13, O'Connell and Carlile 1994; 14, V.M. O'Connell and W.W. Wakefield, unpublished data; 15, S.J. Parker, personal observations; 16, Pearcy et al. 1989; 17, Richards 1986; 18, A.W. Stoner and C.H. Ryer, personal observations; 19, Trenkel et al. 2004*a*, 2004*b*; 20, Wakefield 1990; 21, W.W. Wakefield and M.M. Yoklavich, personal observations; 22, Yoklavich et al. 2007.

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