Information transfer, heterogeneity, and local environmental effects on emergent group patterns defining fish schools: perspectives from different scales of observation

Sarah C. Stienessen

A dissertation

Submitted in partial fulfillment of the

requirements for the degree of

Doctor of Philosophy

University of Washington

2015

Reading Committee:

Julia Parrish, Chair

Tim Essington

James Ha

Program Authorized to Offer Degree:

Aquatic & Fishery Sciences

©Copyright 2015

Sarah C. Stienessen

University of Washington

Abstract

Information transfer, heterogeneity, and local environmental effects on emergent group patterns defining fish schools: perspectives from different scales of observation

Sarah C. Stienessen

Chair of Supervisory Committee:

Dr. Julia Parrish

Aquatic & Fishery Sciences

It is widely understood why animals group, but much less is known about how animals group. Not all group structure provides functional benefit to the individuals therein; however, those group structures that do provide functional benefits help to explain how animals group. To determine whether group structure is functional, it is necessary to keep track of every individual and the corresponding group patterns over long periods of time. Because this typically requires two different scales of observation, I examined grouping behavior of fish from two different perspectives: the individual-up and the group-down. In the individual-up approach, I used giant danios, *Devario aequipinnatus*, in tank experiments, and manipulated the level of heterogeneity within various groups, expressed in the form of knowledge, to determine whether the level of heterogeneity within a fish group affects information transfer between individuals and the cohesiveness of the group. In the group-down approach, I examined *in situ* groups of juvenile walleye pollock, *Gadus chalcogrammus*, in the Gulf of Alaska and the Bering Sea to determine how groups of fish respond to their biological (i.e., predator and prey densities) and physical (i.e., water temperature, bottom depth) environment, and whether the response is influenced by the age/size of the fish. The results of the tank experiments indicate that heterogeneous groups of fish acted cohesively, and members within the group exhibited behaviorally integrated responses. That is, they adopted some behaviors from both knowledge sets –those behaviors that are the most costly to give up. However, there was a threshold when the group minority became hindered by conformity (i.e., when the group minority was ~ 20%). These heterogeneous groups exhibited behaviors only from the knowledge set of the majority. The *in situ* studies indicate that grouping behavior of fish in the wild is consistent with expectations based on predation and foraging theory, possibly influencing the distribution patterns of age classes and the grouping patterns of mixed-age groups. Additionally, these results indicate that there appears to be no structural cost to forming mixed-age groups; rather, mixed-age groups can provide advantages for smaller, more preyed upon fish. Together, the individual-up and group down-approach show that fish that form heterogeneous groups (with respect to knowledge or age of the fish) are cohesive and offer advantages to their members.

Table of Contents

A synthesis of individual-level and group-level perspectives on animal grouping behavior

Many species of animals aggregate to form temporary or permanent groups (Allee 1927). It is well understood why animals do this. Typically the benefits to group-living, such as protection from predators (e.g., Hamilton 1971, Pitcher and Parrish 1993, Watt et al. 1997, Nøttestad and Axelsen 1999), increased reproductive fitness (e.g., Svensson and Petersson 1992, Wikelski et al. 1996, Canestrari et al. 2007, Molloy et al. 2011), and foraging success (e.g., Krebs et al. 1972, Pulliam and Millikan 1982, Pitcher 1982, Waite 1982, Baird et al. 1991), offset potential costs such as increased competition and disease transmission (e.g., Alexander 1974, Rubenstein 1978, Tella 2002, Bilde et al. 2007, Majolo et al. 2008). For these species of animals, individual fitness should be higher for a group member than it would be for a solitaire.

How animals group is less clear. In most groups, structural order exists because of coordination exhibited by the members. Group structure can be maintained by multifaceted social hierarchies, ranging from cooperative to dominance based. In cooperative hierarchies, such as those formed by honeybees (Winston 1987; Caron 1999), vervet monkeys (Seyfarth and Cheney 1984) and vampire bats (Wilkinson 1984), animals voluntarily share resources. There is also, typically, some degree of relatedness between any two group members (Bourke and Franks 1995, Crozier and Pamilo 1996), and the degree of relatedness often correlates to the strength of the associated bond (Biggs et al. 1990). Relatedness allows some animals in cooperative groups to forgo reproduction and help with group needs such as defense or foraging (Hart and Ratnieks 2005) to increase their personal fitness though kin-selection (Hamilton 1971). Killer whales in coastal waters of British Columbia and Washington State have a high degree of relatedness between group members. There is no immigration into or emigration from their matrilineal groups, and these whales form one of the most stable, non-human societies, providing the individuals in the natal group with reliable associates with which to hunt, defend, and/or breed (Biggs et al. 1990).

In dominance based hierarchies, such as those formed by some species of wolves (Zimen 1975, 1982, Mech 1970, 1999), primates (Swedell 2011), and chickens (Guhl 1956), animals act selfishly to increase personal fitness. Dominance based hierarchies are the result of often aggressive interactions between group members in which a ranking system is formed. In this system, individuals are dominant over those that rank below it and submissive to those that rank above it (Drews 1993). The knowledge of the ranking order keeps both the dominant and submissive individuals from suffering the costs from prolonged or frequent fights (Pusey and Packer 1997), with the higher ranking individuals often having more access to more resources (Huntingford and Turner 1987). However, dominance based systems do not always involve absolute ranking. Some animals, including species of seals (Le Boeuf 1974), birds (Searcy 1979) and equids (Berger 1977, Schilder and Boar 1987), form polygynous harems which typically consists of a group of females, their offspring, and only one to two dominant males. Harems provide resource benefits for the male(s) and protection for the females (McCann 1981, Ridley and Hill 1987). In reality, groups with social hierarchies often exhibit both cooperative and dominance based traits. For example, ponerine ants have multiple unrelated queens, and the dominant queen remains in the nest and guards the brood, whereas the subordinate queens leave to find food (Kolmer and Heinze 2000); and individuals in a lion pride, i.e., a harem, work together to cooperatively hunt, defend resources, and rear young (Nowell and Jackson 1996).

Group structure can also be maintained by coordinated movements between non-related members with no clear hierarchy (e.g. Aoki 1980, Partridge 1980, 1981, Huth and Wissel 1992, Parrish et al. 2002). This type of group is particularly interesting, because without a leader, groups of animals are able to produce such coordinated movement that the group itself appears to move as a single entity. For example, at dusk migrating swifts gather by the thousands into large tornado-like flocks and then abruptly descend as a narrow vortex into their roosting chimney (Steeves et al. 2014). This extremely coordinated motion allows groups to perform tasks not always possible at the individual level. This is evident in some species of fish that use directed motion to form group shapes including a ball, fountain, hourglass, and flash expansion when under attack by predators (Pitcher and Parrish 1993, Nøttestad and Axelsen 1999, Axelsen et al. 2001). Similarly, flocks of starlings under attack will expand, contract, and split (Ballerini et al. 2008a). Although these groups are constantly changing density and structure, no individual becomes isolated. These shapes and movements confuse predators (Milinski and Heller 1978, Jeschke and Tollrian 2007), thereby increasing the survival rate for any given group member (Turner and Pitcher 1986), assuming detection rate is unaltered (Krause et al. 1998). Animals with decentralized strategies typically have limitations on their cognitive and physical capabilities that are not as apparent at the group-level: as a group they react more efficiently, quickly, and accurately.

The key to understanding how group structure is maintained is to determine which individual behaviors produce group-level patterns that are functionally advantageous to its members (Parrish and Edelstein-Keshet 1999, Parrish et al. 2002). Natural selection acts on individual traits and behaviors (e.g., Fisher 1930, Williams 1966), but can also act on groups that have functional organization (Wilson 1997). That is, if one group outperforms or outcompetes another group, the fitness of the individuals in the more competitive group is increased, because those individuals survive and reproduce more than individuals in underperforming groups (Sober and Wilson 1998). For this to happen, competition between groups must dwarf competition between individuals (O'Gorman et al. 2008). As an example, in domesticated chickens, aggressiveness is a favorable individual trait but docility is a favorable group trait. The overall advantages of group docility outweigh the advantages of individual aggressiveness, so docility evolved even though it is disserving at the individual level (Muir 2009, Wade et al. 2010). However, not all group behaviors are beneficial; some may be detrimental in specific situations. For example, members in a group typically benefit from greater group density when a predator is nearby (Pitcher and Parrish 1993), but some predators (e.g., killer whales) cooperatively herd prey into tight balls to increase feeding efficiency (Similä and Ugarte 1993, Nøttestad and Axelsen 1999). Other group behaviors are merely the by-product of individual interactions and serve no real benefit to the members (Parrish and Edelstein-Keshet 1999). Ballerini et al. (2008b) discovered that starlings maintain a constant group shape, regardless of group size, group direction, or position of individuals within the group (Ballerini et al. 2008b); yet, it is difficult to verify whether the shape is functional. There is no evidence to suggest the shape serves a benefit to the group members, and without knowledge of longer term moment-to-moment movement patterns of individual starlings, it is impossible to know if the individuals are active in achieving the shape. Isolating individual behaviors that do produce functional group advantages help to explain how animals group, because those behaviors have been selected for at the group level. To reveal functional group behaviors, individual behaviour and associated group structure must be monitored simultaneously (Parrish et al. 2002).

Individual and group behavior patterns alone are often insufficient to understand how animals group because of the importance of the physical and ecological context. The environment dictates both short-term (e.g., predator avoidance; Pitcher and Parrish 1993) and longer-term movement patterns of individuals (e.g., restriction by a thermocline or congregation around a food or source; Swartzman et al. 1994, Croze et al. 2000, Pitman et al. 2011). Shifts toward a more favorable group structure are thus the result, in part, of individuals responding to the behavior of their neighbors (e.g., Viscido et al. 2004, Grünbaum et al. 2005) and their particular interpretation of the local environment (Bertrand et al. 2006, Gerlotto et al. 2006).

It is difficult to study the role individual behavior plays in group structure, because it is almost impossible to keep track of many individuals over long periods of time at a scale where individual recognition is possible yet group patterns are obvious (Parrish et al. 2002). Most of the research on this has consequently taken one of two approaches: the individual-up or the group-down. At the core of the individual-up approach is examining how information is transferred between group members, and how the interactions between members produce group movement patterns. Much of this research has focused on movement patterns in fish schools, bird flocks, insect colonies, and ungulate herds (e.g., Huth and Wissel 1992, Gueron et al. 1996, Couzin et al. 2002, Viscido et al. 2004, Buhl et al. 2006, Ballerini et al. 2008b, Bazazi et al. 2008, Stienessen and Parrish 2012), but associated sampling technologies often limit these studies to highly artificial, or even theoretical, environments. The group-down approach quantifies group structure and behavior relative to the environment to infer corresponding behaviors of individuals therein. A lot of this research has focused on describing *in situ* fish group structure (e.g., Rose 1993, Barange 1994, DeBlois and Rose 1995, Axelsen et al. 2000, Soria et al. 2003, Wilson et al. 2003, Gerlotto et al. 2004, Stienessen and Wilson 2008), but limitations in associated sampling technologies essentially prevent direct observations of individual group members. Although neither the individual-up nor group-down approach currently is able to provide a strong mechanistic link between individual and group behaviors, both approaches, especially in tandem, have provided insight into how group structure is maintained.

Individual-Up Approach

Information transfer

Information transfer and self-organization are central to the individual-up approach. Individuals in groups acquire information both from personal experience and from observing or interacting with others (Coolen et al. 2003, van Bergan et al. 2004, Kendal et al. 2004, 2009). Transmission of social information occurs though basic imitative responses including being drawn to an area because of the presence of another individual (Waite 1982; Reader et al. 2003), following others (Helfman and Schultz 1984; Laland and Williams 1997), and increasing the intensity or frequency of a behavior in the presence of an individual already engaged in that behavior (Ryer and Olla 1992). When individuals learn, or acquire new behaviors, as a result of social information, social learning is taking place (Brown and Laland 2003). The combination of using social learning and personal experience (Miller et al. 2013) allows individuals within a group to reach consensus decisions (Conradt and Roper 2003, 2005, Ward et al. 2008), resulting in behavioral conformity (Stienessen and Parrish 2013). There is no single individual coordinating the group’s decision; instead, the group uses a quorum sensing mechanism to determine when a decision has been achieved (Seeley and Visscher 2004). In large groups, it is impossible for individuals to interact with all group members; yet consensus decisions typically prevail. This is because interactions with only a few neighbors are sufficient to allow information to transfer rapidly throughout the group. For example, the flight response in fish can cascade throughout a group more quickly than a predator is able to approach, and in this way members that have not independently perceived the predator are made aware of the predator’s presence (Magurran et al. 1985, Brown and Warburton 1999). This suggests social learning and quorum sensing, along with other mechanisms which enhance information transfer, are evolutionary beneficial (Parrish et al. 2002) and are at the foundation of how group structure is maintained.

Self-organization theory

Self-organization theory explains how simple imitative responses of individuals to short-term behaviors of neighbors can produce seemingly complex group behaviors and patterns (Couzin and Krause 2003). Simulation studies have been frequently employed to demonstrate this. These studies represent individual movement behavior by using forces to accelerate individuals (e.g., Aoki 1982, Gueron et al. 1996, Romey 1996). The strength and direction of these forces vary based on the number of influential neighbors and social interactions (e.g., repulsion, alignment, and attraction) for each individual within a group (Fig. 1). Studies are not consistent in which parameters they explore or in which relationship they assign to social interactions (e.g., see Parrish et al. 2002 for examples used in fish school simulations); however, the basic idea behind the models is that individuals are either repulsed, aligned, or attracted to their neighbors, depending on the neighbors' proximities. The focal individual will simultaneously move away from neighbors that are too close (i.e., move away from neighbors within its repulsion zone), toward neighbors that are further away (i.e., move toward neighbors that are within its attraction zone), and align with neighbors that are at a preferred distance (i.e., align with neighbors that are within its alignment zone; Fig 1a). Often, either a limit is set on how many neighbors a given individual pays attention to, or a maximum detection distance is applied, and overall movements of all individuals are continuously updated at consecutive time steps.

Self-organization theory is attractive as a mechanism for grouping, because simple "rules" assigned to simulated individuals produce complex group behaviors observed in the wild. By using relatively simple individual-based rules of existing trail reinforcement, Deneubourg et al. (1989) were able to show that army ants are capable of producing complex behaviors seen in swarm raids. Hemelrijk (2000) used simple dominance reinforcement rules to show that high-ranking individuals ended up in the central positions within a group, which is where the dominant individuals in many species (e.g., chub, spine finches, primates) are found (Krause and Rexton 2002). Self-organization models have demonstrated that individuals can sort phenotypically without knowledge of their relative phenotype (Couzin et al. 2002). Phenotypic sorting is common in fish groups; heterogeneous groups of fish often assort by size (e.g., Hoare et al. 2000, Krause et al. 1996, 2000, Svensson et al. 2000). If larger individuals contain a different set of rules (i.e., a larger zone of repulsion) from smaller individuals, they could find themselves segregated within the group (i.e., on the periphery of the group; Hemelrijk and Kunz 2004) without individual knowledge of their position or role within the group (Couzin and

Krause 2003). In the context of decision making, self-organization explains how a group given two or more choices can immediately and cohesively choose only one action (Sumpter and Pratt 2009), and how only a few members with specific knowledge can entice an entire group toward a destination (Gueron and Levin 1993, Conradt et al 2009). If some of the group experiences a unique behavior (e.g., attraction toward a specific location), the number of "naïve" individuals that copy this behavior depends on the strength of the unique behavior and the proportion of individuals displaying it (Couzin et al. 2005, Mirabet et al. 2008). However, when the cost of acquiring information is high (e.g., investing in measuring environmental cues while migrating), most of the group will remain naïve and instead will rely on cheaper social cues. This results in a stable evolutionary outcome (e.g., collective migration) in which the individuals adapt to their environment using fission-fusion processes (Couzin and Laidre 2009, Guttal and Couzin 2010, Pais and Leonard 2013).

Self-organization theory also accounts for how individuals are able to maximize their fitness though simple local interactions. By changing the way individuals respond to one another, individual movement patterns can change the structure of the group. Simulation studies show group size depends on the number of influential neighbors; the larger the number, the larger the group (Hoare et al. 2004, Viscido et al. 2005). Smaller groups are advantageous because there is less competition for food (Morgan 1988, Janson and Goldsmith 1995), and larger groups are advantageous because there is safety in numbers (Turner and Pitcher 1986, Pitcher and Parrish 1993). If animals have the ability to change "rule sets", group structure could change in response to changes in individual internal (e.g., hunger) and external (e.g., a predator) stimuli (Hoare et al. 2004). An individual that uses an inappropriate rule set would not maximize its fitness. If in the presence of a predator, an individual pays attention to fewer neighbors and consequently does not stay in a large group, it most likely would not survive an attack (Pitcher and Parrish 1993). However, when the collective rule set changes, the type of group structure that emerges may not always be a given. That is, identical rule sets can produce at least one of two different group states, depending on the previous group structure, suggesting that the evolution of behavioral responses –or selection for the appropriate rule set –may be quite complex (Couzin et al. 2002).

The limitation to self-organization theory is the difficulty in determining which behaviors, or rules, are biologically relevant. As previously mentioned, studies are not consistent in which parameters they explore or the strength they assign to social forces (Parrish et al. 2002, Schellinck and White 2011). Different parameters can produce similar results, begging the question whether the results are robust or just easily contrived. There is also some evidence that simulation results cannot realistically depict group sizes that are seen in nature (Viscido et al. 2005). Certainly in some species of animals (e.g., wolves, primates, and killer whales) complex group patterns are the result of conscious communication between individuals (Theberge and Bruce Falls 1967, Hare et al. 2000, Pitman and Dorman 2011), but even species with higher cognitive capabilities show evidence of self-organization, especially when members have limited information. For example, ungulates use trail reinforcement to create natural pathways, and one-way “bands” of pedestrians from to navigate crowded sidewalks (Couzin and Krause 2003). In large aggregations with many thousands of animals, it is highly unlikely an individual will be capable of determining its true position within the group (Gueron et al. 1996), regardless of its cognitive capability. However, for other species, it is unlikely that the individuals are capable of coordinating their movements at a group level because they lack conscious communicational capabilities (Seeley 2004, Edwards and Pratt 2009). Thus, there is an appeal to self-organization theory because it allows for intricate group structure to be created by straightforward individual interactions under many scenarios and situations, irrespective of individual cognitive capabilities, computational restrictions, or group size.

Empirical observations

Self-organization models alone have not been able to isolate mechanisms of aggregation utilized by specific species (Schellinck and White 2011); therefore, empirical observations are needed to verify whether results generated by the models are valid. These types of observations are limited, because of the large effort needed to extract the smallest amounts of quantitative data. Early empirical observations on fish schools and bird flocks used optics, such as static photogrammetry and stereo-photography, to extract inter-individual distances and basic group properties such as volume or density (e.g., Miller and Stephen 1966, Major and Dill 1982, Pitcher and Partridge 1979, Partridge et al. 1980, Caraco and Bayham 1982, Aoki et al. 1986), and more recent studies have used stereo-videography to observe two- or three-dimensional positional changes of individuals in groups over time (e.g., Bumann et al. 1997, Hiramatsu et al. 2000, Budgey 1998). These latter types of studies have found empirical evidence that individuals may switch between rule sets (Hoare et al. 2004, Tien et al. 2004, Grünbaum et al. 2005), rely on a given number of nearest neighbors (Tegeder and Krause 1995), use attraction and repulsion zones (Tien et al. 2004), and vary the strength of the alignment force (Viscido et al. 2004). Because it is almost impossible for software to reliably track every individual without user input (e.g., Handegard and Williams 2008, Stienessen and Parrish 2013), and it becomes exponentially more difficult to track individuals over time as group membership increases, these studies describe only a small number of individuals in loosely organized groups, and in the case of fish schools, often in highly artificial and homogeneous environments (i.e., in tanks). However, recent advancements in technology have allowed for a more complete look at aggregation behavior of much larger groups in the wild, including tracking individual fish *in situ*. For example, Ballerini et al. (2008a,b) used stereophotography and trifocal techniques (Hartley and Zisserman 2003) to obtain three-dimensional positional data on individuals in large flocks of starlings, with membership numbering in the thousands. Handegard and Williams (2008) developed an identification procedure using duel acoustic-frequencies to make observations of walleye pollock in midwater travels, and Capello et al. (2011) tagged several bigeye scad with acoustic pingers and used an acoustic detection system to track the fishes' three-dimensional *in situ* movements around a fish aggregation device. These results show that individual interaction decays with distance (Ballerini et al. 2008a), fish density and observation range may influence the perceived behavior of individuals in trawls (Handegard and Williams 2008), and attraction between individuals is crucial to grouping, even when the group is congregating around an object (Capello et al. 2011). Unfortunately, these advancements in technology are not without their own set of limitations. Individual starling movement patterns could only be tracked continuously over a short period of time (i.e., 8 seconds); although the group structure of walleye pollock had not been assessed, had it been, it would have been confounded by the presence of the net; and it is unclear whether the acoustic pingers altered the behavior of the bigeye scad. Additionally, movement patterns of individuals could only be monitored if the birds and fish stayed within a small area of detection.

What's next?

In the individual-up approach, making the direct link between a known mechanism that enhances information transfer (e.g., social learning) and specific emergent group patterns has proved elusive. Empirical observations have found evidence of self-organization, but they cannot verify whether it exists as a mechanism of information transfer. Given that mechanisms that enhance information transfer are at the foundation of how group structure is maintained, and continuous individual tracking is important in verifying group functionality, an important "next-step" for the individual-up approach would be to track short-term behaviors of individuals while they acquire information from their neighbors (e.g., while they specifically demonstrate social learning). Isolating such mechanisms in the form of physically-expressed interactions should prove invaluable in elucidating the relationship between individual behavior and group-level structure.

In addition to isolating short-term behaviors, extracting the physically-expressed movement patterns of individuals while they participate in broader-scale ecological interactions is also essential. Currently, grouping rules can be extracted from moment-to-moment behaviors of individuals (e.g., Tien et al. 2004, Grünbarum et al. 2004), and rule sets can be created with self-organizational models (e.g., Fig. 1) that mimic positional changes of individuals in actual groups (e.g., Viscido et al., 2004). An important "next-step" would be to apply multiple rule sets (i.e., social zones and forces) extracted from data on extant individuals to simulated groups to see whether the existing rule sets are inflexible, evolve, or spontaneously change, and what this ultimately does to group structure. Stienessen and Parrish (2013) were able to track all members in a group of giant danios to disarticulate the physically expressed process of decision-making among individuals with one of two different knowledge sets. The resulting group was cohesive, and individuals exhibited integrated responses by adopting some behaviors from both knowledge sets, which suggests that all individuals advocate for behaviors they perceive to be most beneficial. That is, none of the individuals, even when in the minority, were completely passive in the decision making process; all individuals were actively responsible for accessing both public and private information to create a cohesive group structure. This study did not examine specific interactions between individuals; therefore, grouping rules were not determined. However, social zones and forces could be extracted from this type of positional data. For example, the rules used by individuals in groups of danios possessing one of the two knowledge sets could be established. Simulated groups containing various proportions of individuals with either rule set could then be created to help explain *how* individuals access both public and private information to form cohesive groups. Fine tuning the outcomes of such a model, while staying true to empirical results, should provide information as to how individuals adapt specific rule sets in changing situations to maintain group cohesion.

With the advancement of technologies, the individual-up approach is getting closer to making the link between individual behavior and the resulting group structure. First, it is likely that tracking all individuals in an *in situ* group will become feasible in the future. Second, as improvements are made in isolating the empirical physically-expressed processes of information transfer, models can be used to extrapolate such behavior seen in small groups to larger simulated groups. In spite of this, one of the biggest limitations of the individual-up approach is the conflicting need to control the setting in which the animals group versus the need to understand how the animals behave in their natural setting. In nature, shifts toward a more favorable group structure are not dependent on any one given behavior or reaction to any one stimulus: individuals are responding to both their particular interpretation of the environment and the behavior of their neighbors, filtered through their internal physiology and experience (Couzin and Kruase 2003). A controlled setting eliminates confounding variables and makes the relationship between specific individual movement patterns and group-level structure more discernible. However, a controlled setting, even *in situ*, is still artificial. Another limitation of the individual-up approach is the small likelihood that a complete set of interaction rules is applicable for all individuals in all situations. Rules will likely differ between species as well, because grouping has evolved due to very different selective pressures on different species in different habitats (Parrish and Hamner 1997).

Group-Down Approach

It is often difficult to quantify the group structure of animals in the wild. Obtaining accurate and precise measurements from photographs or video typically either requires concurrent, and multiple, measurements with a rangefinder (e.g., Shrader et al. 2006, Webster et al. 2010) or the use of stereoscopic methods (e.g., Longuet-Higgins 1981, Bumann et al. 1997, Grünbaum et al. 2005), both difficult to achieve with large or fast-moving groups. Additionally, calibration and matching points between images are two difficulties that make quantification of groups challenging with stereoscopic methods (Osborn 1997). Ballerini et al (2008a,b) used stereo-photography to capture size, shape, orientation, and movement patterns of starling groups engaged in aerial display. This effort required that the group had sharp borders, that the birds were both within 250 m and within the common field view of all cameras, and that group membership had to be less than 8,000. Less than 10% of the collected data fit these criteria. Due to difficulties such as these, there have been a limited number of studies that capture group movement patterns and structural characteristics, including group size and shape, of terrestrial animals in their natural environment. However, there have been many field studies that examine *in situ* groups of aquatic animals, especially grouping patterns of fish. Since the end of the Second World War, scientific echosounders, often mounted to the bottom of fishery research vessels, have been used to collect high-resolution acoustic data on the distribution of commercially important fish species (Misünd 1997). Acoustic data show a degree of diversity in the structural patterns of fish aggregations (e.g., schools, shoals, layers), but all aggregations have discrete boundaries and can be defined with quantitative metrics such as length, height, density (Reid et al. 2000) –i.e., aggregation typology. Aggregation typology of fish has been described in efforts to study the relationship between fish groups and their environment, and in attempt to delineate between sympatric species without having to ground-truth species identification with nets (Misünd 1997).

Acoustic data: a brief review

Because most bony fishes have swimbladders, many of these species can be easily detected with an echosounder. An echosounder transmits an acoustic signal into the water, and the signal will reflect or scatter off objects that have a different density than that of the water, such as the swimbladders (or hard parts) of the fish (Foote 1980, Clay and Heist 1984), unless the object is very small compared to the acoustic wavelength (Simmonds and MacLennan 2005). However, when fish aggregate, single target detection is usually not possible because the acoustic pulse length is too long to discriminate between individuals in close proximity (Simmonds and MacLennan 2005). Calibrated acoustic data thus provide information on both shape and density estimates of aggregations. However, unless individuals stay relatively far apart from one another, the acoustic data cannot be used to detect positional information on individual members of the aggregation.

An echogram is a visual representation of the returned acoustic signal (i.e., backscatter), and descriptive metrics can be estimated from the backscatter data depicted as aggregations in echograms (Fig. 2b,c). The type of metrics typically extracted from echograms include morphological (e.g., group height, width, perimeter roughness), energetic (e.g., acoustic intensity, acoustic roughness), and positional (e.g., group depth in the water column, group distance above the seafloor) measurements. However, these types of measurements are not absolute. Beamwidth and pulse length effects of the acoustic system will distort the group shape, but this can be corrected (Diner 2001). The processing threshold level will also influence the overall shape of the group. For example, a group will appear bigger when a lower threshold is used (Reid et al. 2000). Therefore, acoustic systems cannot capture absolute group measurements; but, if instrument settings are kept constant, metric estimates can provide comparative information on the relative variability of group structure (Fréon et al. 1996, Reid et al. 2000).

Single-beam echosounders can only insonify a “slice” through an aggregation, forcing the majority of characterization to be in two dimensions (i.e., the vertical and alongship dimensions; Fig. 2a,b). A much more complete view of aggregation structure can be attained using multibeam echosounder. Multibeam sonars can potentially insonify entire groups (i.e., schools or shoals) using a fan or number of beams simultaneously. These instruments can be mounted to a stationary or drifting platform to study the instantaneous group reaction to the environment. They can also be mounted to the bottom of a moving platform to describe the group in three dimensions (i.e., the vertical, alongship, and athwartship dimensions; Fig. 2a,c). Most studies on aggregation typology have used either single beam or multibeam echosounders due to the prevalence of these technologies in fisheries research and the comparatively well-established protocols for extracting data. Other technologies such as side scan sonar (e.g., Rusby et al. 1973, Farmer et al. 1999), long-range sonars (e.g., Weston and Revie 1989, Markis et al. 2006), and lidar, an optical device that uses a pulsed laser mounted from an aircraft (e.g., Churnside et al. 1997, Jaffe et al. 2001), have also been used in a limited capacity.

Reactions to the environment

Data collected with acoustic sampling tools have provided information on overarching behaviors of individuals within aggregations. At the population level, aggregation typology has been used to depict predator-prey interactions (DeBlois and Rose 1995, Swartzman 2001), migration patterns (Rose 1993), and daily movement patterns (Markis et al. 2006), and describe fish reactions to changes in the physical environment (Nero and Magnuson 1989, Barange 1994, Swartzman et al. 1994, Swartzman 1997). At a smaller scale, group typology (i.e., typology describing schools or shoals) has proved a useful way to characterize *in situ* responses of fish to their environment. For example, walleye pollock groups observed during a commercial fishery were less dense with a more complex shape than were groups observed prior to the fishery (Walline et al. 2012), suggesting the fish were more scattered during the fishery. Group typology has been used to demonstrate that some species exhibit avoidance to specific vessels. For these species, the number of groups was higher in deeper water (Misünd and Coetzee 2000), and groups found closer to the vessel were more horizontally elongated (Gerlotto and Paramo 2003, Soria et al. 2003) or deeper (Gerlotto et al. 2004). Together with group speed and movement patterns, group typology can discriminate between general behaviors (i.e., between immigration, emigration, searching, spawning, or feeding) and between specific components of a general behavior (i.e., between pre-spawning, spawning, and post-spawning) of the group (Nøttestad et al. 1996, Axelsen et al. 2000). However, without direct behavioral observations of individuals, it is impossible to characterize the interactions between group members using group typology.

One promising application of using the group-down approach to understand how group structure is maintained is to use group typology to correlate group-level patterns widely across environments and/or species. Some species of fish have been reported to maintain a relatively constant group shape irrespective of fish size (Abrahams and Colgan 1985, Coetzee 2000, Muiño et al., 2003, Stienessen 2015 chapter 4). Is there a species-specific shape for these fish that offers advantages to the individuals (e.g., Fréon and Misund 1999), or is the appearance of a general characteristic across all ages or sizes indicative of an epiphenomena –something the fish cannot avoid doing? Isolating prevalent relationships between group typology and the environment can help to direct studies on group functionality. For example, fish often respond to predation threats by displaying highly synchronized movement patterns that result in a few complex elusive group structures (Pitcher and Parrish 1993, Nøttestad and Axelsen 1999), and in hypoxic environments, some fish create more vertically flattened groups (Israeli and Kimmel 1996, Domanici et al. 2007). These group behaviors are predictable, but without associated empirical or modelling studies, it would be difficult to know from aforementioned studies whether individuals that do not adhere to highly synchronized movement patterns are more likely to draw attention and be eaten (sensu Pitcher and Parrish 1993), and whether a flattened shape maximizes individual energetic demands (sensu Israeli and Kimmel 1996, Domanici et al. 2007).

Intermediate scale

Another promising application of using the group-down approach to understand how group structure is maintained is to use group typology to look at large-scale interactions of fish within groups. Multibeam echosounders and long-range sonars exploiting waveguide remote-sensing technology have produced *in situ* evidence of self-organization. Gerlotto and Paramo (2003) were able to look at large schools of sardines in the field and observe the internal patterns of structure. They found both high-density nuclei and vacuoles to be omnipresent in sardine schools, and they concluded that the nuclei and vacuoles were emergent structures arising from reactions of individuals to one another. Gerlotto et al. (2006) were able to detect a 'wave of agitation' that spread though the school when a predator approached and noted the internal school structure was more homogeneous after the disturbance. This type of internal wave has been observed to occur repeatedly in much larger groups of fish (i.e., groups that extend for kilometers and contain millions of members), and likely allows such a large aggregation to rapidly communicate and maintain internal structural integrity (Markis et al. 2006). Neither of these acoustic techniques allow observation of the moment-to-moment reactions of individuals to their neighbors, but if these technologies allow observation of the constructs of these reactions (i.e., constructs of information transfer and self-organization), they can potentially be used to study the "intermediate" scale of grouping behavior. That is, they can be used to collect simultaneous information on broad individual interactions and emergent patterns of *in situ* groups.

Generally, there are two ways these intermediate data can be described. The first is to average internal structure over many groups to make comprehensive comparisons, such as comparisons of internal structure within species (e.g., Gerlotto et al. 2004), between species or geographic areas (e.g., Paramo et al. 2007), or between age classes (Stienessen 2015 chapter 4). The second is to explore how internal structure changes over time. These type of data can be collected by repeated passes over a focal group (e.g., Weber et al. 2014), or observation of a group from a stationary platform (e.g., Gerlotto et al. 2006, Markis et al. 2006). Although not continuous, repeated passes provide sequential snapshots of the group in three-dimensions with relatively short time gaps (i.e., minutes) in between each viewing. Stationary observation provides continuous recordings, but it can only capture a two-dimensional slice though the group. Nonetheless, both these techniques capture group typology and internal movement patterns of fish in real time, putting this area of research at the forefront in group-down efforts to understand how fish group.

Making the connection

Of these two approaches, the individual-up specifically focuses on how animals group: from how individuals transfer information and make consensus decisions, to how individual behaviors and interactions produce group-level patterns. Most group-down studies are an outgrowth of fisheries science; therefore, their principal motivation is often not to determine how animals group but to describe grouping patterns of fish to understand how distributions of fish change in response to the environment. Yet the characterization of both *in situ* group typology and internal movement patterns of individuals therein (i.e., the intermediate scale) provides an important perspective to the individual-up approach. That is, the field studies provide insight into realistic behavior of large groups in natural settings. Additionally, in the group-down approach, distribution patterns of fish are often described at the population level. This provides insight into how animals aggregate at a much larger scale, including how groups cluster (e.g., Swartzman 1997, Mackinson et al. 1999) and split-and-fuse (e.g., Rose 1993, Mackinson et al. 1999). Markis et al. (2006) observed that densely packed fish in extremely large population-sized groups did not exhibit synchronized motion often seen in equally dense, but much smaller, groups. This highlights the importance of understanding how individual behavior transcends to the population-level. Being able to create rules that produce both realistic group and population patterns is central to understand the process for how animals group, but is largely not considered in the individual-up approach (but see e.g., Gueron et al. 1996, Guttal and Couzin 2010). Because the individual-up and group-down approaches address two different scales, both contribute important, but incomplete, pieces to the "how do animals group?" puzzle (Table 1). Thus, it is important to ultimately link these approaches.

Certainly there is not a universal answer to "how do animals group?" Although making the connection between the individual-up and group-down approaches is necessary, the group-down approach has largely focused on the aquatic environment, and it is unlikely the associated results will directly translate to terrestrial animals, especially those confined to two-dimensional movements, or between different species within the aquatic environment. Not all animals in the same environment experience the same selective pressures, and as such, different mechanisms and processes are responsible for the evolution of different group behaviors in different species (Parrish and Hamner 1997). For example, how krill group is different from how bluefin tuna group. The trade-off between predator avoidance and oxygen acquisition is thought to influence the shape of krill aggregations (Brierley and Cox 2010), whereas the trade-off between hydrodynamic and visual advantages are thought to influence internal spacing in bluefin tuna groups (Newlands and Porcelli 2008). Additionally, it is unlikely that fitness levels of individuals can be fully known in groups with evolving behaviors (Parrish et al. 2002). However, making the connection between the two approaches will help provide information on how specific species group in specific situations. It should also identify general mechanisms that are applicable across various taxa and environments.

Modeling studies will be required to make the connection between the individual-up and group-down approaches in at least one of two ways. First, they can be used to help determine whether correlations between group structure and the environment might serve a functional purpose for individuals at the group-level. As eluded to earlier, characterization of associations between environmental changes and group typology can reveal relationships that warrant future experimental efforts. Brierley and Cox (2010) found the surface area-to-volume (SA:V) measurements of Antarctic krill shoals to be relatively constant and similar to SA:V measurements of various clupeid fish groups found in tropical regions of the Atlantic and Pacific. They postulated that because this shape was common, it likely incurred advantages to individuals within the group. They then used models to show this shape potentially maximized a tradeoff between predator avoidance and oxygen acquisition. Second, as technological innovations are applied to the work in the field, tracking the moment-to-moment movement patterns of all individuals for longer (i.e., minutes) periods of time within *in situ* groups will not be far behind. However, this is likely to occur in small groups in relatively controlled environments. Models can extrapolate the behaviors and patterns extracted from these experiments to create explicit patterns of movement seen within larger groups of fish observed in a more natural setting. This in turn will help to identify what basic rules, or rule sets, produce functional group behavior and show how animal behavior contributes to group-level patterns of large groups in natural settings.

Table 1. Summary of principal areas of research, with a few examples of the types of studies in each area, and the associated limitations that focus on *how* animals, particularly fish, group.

			Sampling Methods			
	Focus	Research Examples	Sampling Tool	Group Members	Major Findings	Challenges
			INDIVIDUAL-UP APPROACH			
Information Transfer		Ryer and Olla (1991, 1992)	Video and observer blind	9, 1-8	Individuals acquire information about their environment or adopt new behaviors as a result of interacting with neighbors	Highly contrived situations: focus on how an individual, or a few individuals, respond to a very small group, often in a well-lit tank Not designed to address how information transfer influences group structure
Social Learning	Short term behavior	Laland and Williams (1997), Brown and Laland (2002)	[a]None	5, 8		
		Reebs (2000)	Video	12		
Consensus Decisions	Short term behavior	Ward et al. (2005), Sumpter et al., (2008), Miller et al. (2013)	Video	1-8, 1-8, 16	Individuals are likely to conform to the behavior of the majority through nonlinear consensus decisions, taking into account both personal and public information	Highly contrived situations: focus on how a small group responds to stimuli in experimental arenas Not designed to address how information transfer influences group structure
Self-Organization	Structural interactions	Huth and Wissel (1994), Couzin et al. (2002), Viscido et al. (2005)	Zone model with a range of zone sizes and acceleration forces	8, 10-100, 2-128	Decisions made by individuals though imitative short-term responses to their neighbors produces emergent group patterns often seen	Difficult to determine if behaviors are biologically relevant. They typically reflect the presumptions of researches rather than actual data
Simulation	Ecological	Romey (1996),	Zone model with	8, 100, 10-100,		

Studies	interactions	Hemelrijk (2005),Couzin et al. (2002, 2005), Mirabet et al. (2008)	[b]different zone sizes or [c]biased motion in only a select number of members	10-200, 100-8100	in the wild Choosing the correct set of "rules" in various situations should increase personal fitness	Models are not consistent in which parameters they explore and what relationship they assign to individual interactions
	Population patterns	Gueron et al. (1996), Guttal and Couzin (2010)	[d]Zone model with [e]unevenly applied social forces	10-100, 320 or 16384		Some evidence that models are less realistic as group sizes approximate those seen in nature
Tracking (controlled environment)	Structural interactions	Viscido et al. (2004), Grünbaum et al. (2005)	Stereo-videography	4-8, 4-8	Individual movements result in changes in group patterns, which are often ecologically advantageous to the members	Based on behaviors in artificial environments (i.e., well-lit tanks)
	Ecological interactions	Bumann et al. (1997), Hoare et al. (2004), Tien et al. (2004), Stienessen and Parrish (2013)	Video	10, 10, [f]40, 15		Relatively small sample sizes (exponentially more difficult to track individuals as group-membership increases) Difficult to verify if extrapolated group behaviors occur *in situ*
*Tracking (*in situ*)*	Structural interactions	Ballerini et al. (2008a,b), Capello et al. (2011)	Stereo-photography and trifocal techniques, acoustic pingers	1000s, [g]40	Individual interactions are essential to animals that group in nature	Movement patterns can only be monitored if animals stay within a small area of detection
			GROUP-DOWN APPROACH			
Group Typology	Group-level	Misund and Coetzee (2000), Gerlotto and Paramo (2003), Soria et al. (2003),	Vertical echosounders and [h]multibeam sonars	100s-1000s	Emergent patterns of *in situ* groups provides overarching information on the	Often only captures 2 dimensions of grouping patterns Group patterns may be

		Stienessen and Wilson (2008), Walline et al. (2012)			behavior of the individuals within the group	influenced by the sampling platform (i.e., ship avoidance)
Environmental Influences	Population-level	Nero and Magnuson (1989), Rose (1993), Barange (1994), DeBlois and Rose (1995), Swartzman et al. (1994)	Vertical echosounders	1000s		Does not allow for observation of individual behavior within a group
Intermediate Scale	Group-level	Gerlotto and Paramo (2003), Gerlotto et al. (2004), Gerlotto et al. (2006), Paramo et al. (2007)	Multibeam sonars	100s	Broad-scale interactions between individuals (i.e., areas of low- and high-density within the group) are likely constructs of self-organization and give rise to emergent group structure	Does not allow for observation of the moment-to-moment reactions of individuals to their neighbors [i]The dependence of measured backscatter on incidence angle and fish orientation can confound results
	Population-level	Markis et al. (2006)	Long-range sonar with waveguide remote-sensing technology	10000s		

[a] Observation by the experimenter: no technology was used to record the behavior.

[b] The size of the zone regions were inconsistent between group members in Romey (1996), Hemelrijk and Kunz (2005), Couzin et al. (2002).

[c] Biased motion was only applied to a subset of group members in Romey (1996), Couzin et al. (2005), Mirabet et al. (2008).

[d] The general model used in self-organization studies (Fig. 1).

[e] The social forces in the zone model were applied unevenly to various group members in Guttal and Couzin (2010).

[f] Only 8 individuals within the group were tracked.

[g] Only 12 individuals within the group were tagged and tracked.

[h] Multibeam sonars were exclusively used in Gerlotto and Paramo (2003) and not used in Stienessen and Wilson (2008) or Walline et al. (2009).

[I] Holmin et al. (2012).

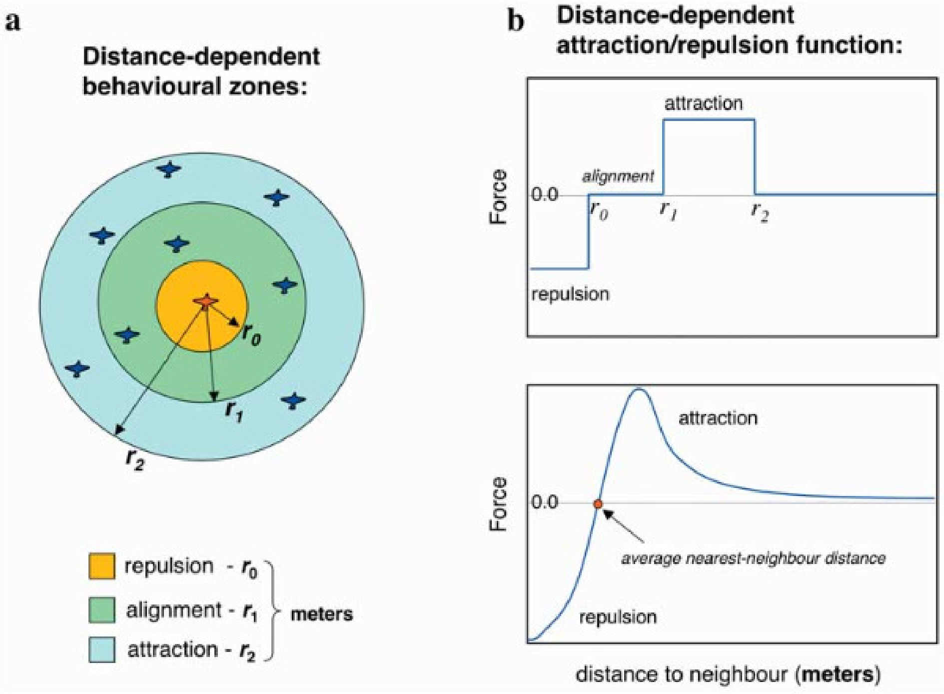

Figure 1. The general model used in self-organization studies. A schematic showing a) the zones of repulsion, alignment, and attraction, and b) examples of two common methods used to assign the strength of the forces used to accelerate individuals relative to the distance of their nearest neighbors. From Giardina (2008).

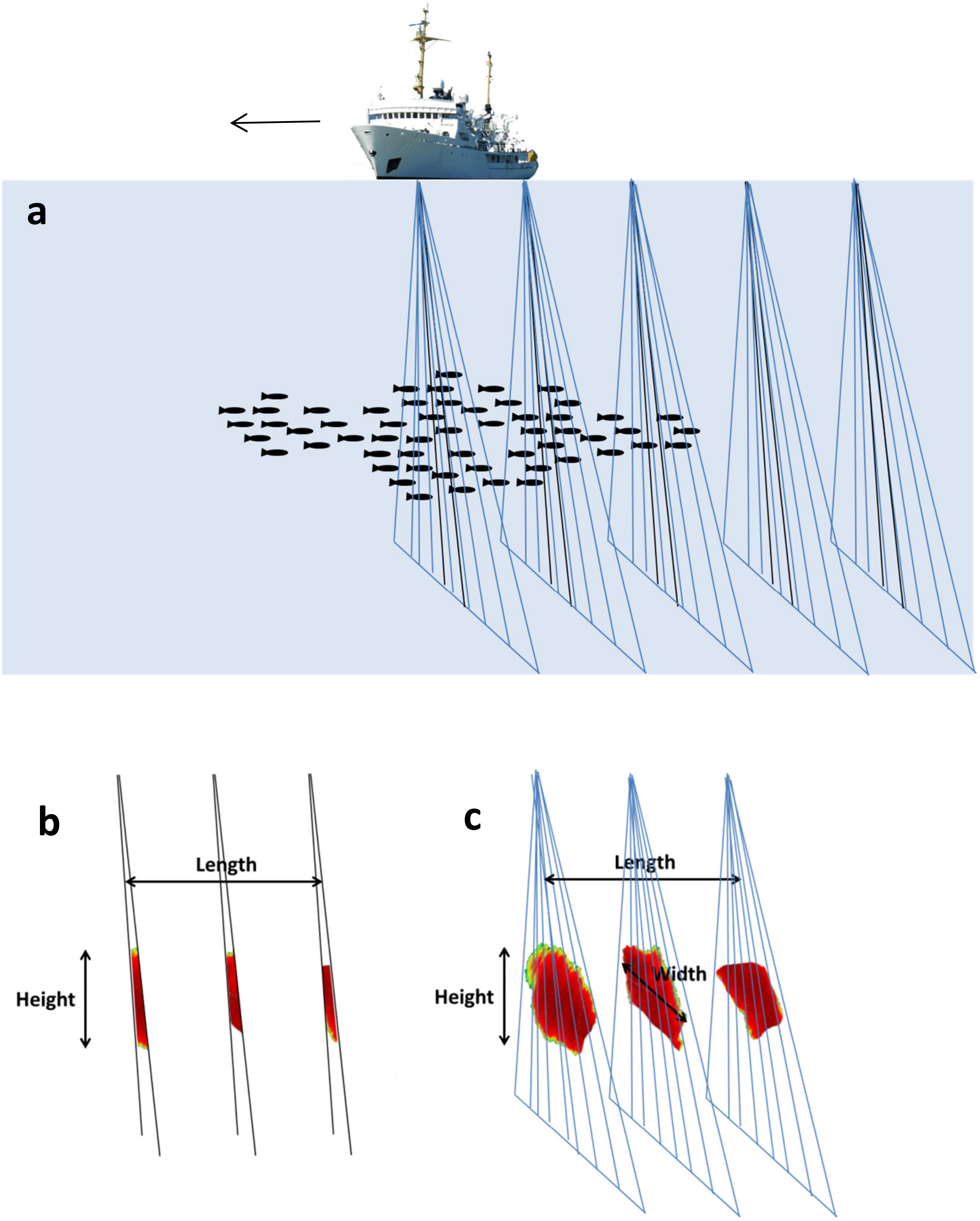

Figure 2. Insonification of fish as a ship passes above the group. A schematic showing a) a fish school insonified in each acoustic signal produced by a single beam echosounder (black triangle) and multibeam sonar (blue triangle) as the ship passes above. The backscatter from b) a single beam echosounder depicts a two-dimensional characterization of the fish group, and c) from a multibeam sonar depicts a three-dimensional characterization of the fish group. The backscatter color represents density, from low (light green) to high (dark red).

The effect of disparate information on individual fish movements and emergent group behavior

Abstract

Within a group, the level of knowledge held by any individual often differs from that held by other members. Such heterogeneity can be advantageous, potentially allowing groups to cope with situations novel to the majority. It can also affect group integrity, inciting sorting or group fission. To better understand how heterogeneity affects school structure and the physical expression of decision-making, we manipulated the ratio of knowledgeable-to-naïve fish within groups of giant danios, *Devario aequipinnatus*, and examined the relationship between collective knowledge, individual behavior, and emergent group properties. Specifically, we varied the proportion of naïve fish within groups of 15 individuals, quantified horizontal trajectories of individual fish, and calculated various individual and group swim metrics. When presented with a learned signal (red light) associated with the presence of prey, groups of all knowledgeable fish exhibited searching behavior (fast, broad turns resulting in diffusely polarized groups) whereas groups of all naïve fish remained unaffected and continued to mill (slow, tight turns resulting in greater packing and lower polarity). In heterogeneous groups, influences of knowledgeable and naïve fish were unequally weighted across each measured swim metric, favoring knowledgeable behaviors (fast, broad turns), but incorporating elements of naïve behaviors (greater packing). However, at a minority threshold of 20%, knowledgeable individuals conformed to the behavior of the majority and group response echoed all naïve. A null model, composed of independent behaviors of knowledgeable and naïve fish, predicted significantly different swim metrics from those observed, suggesting actual heterogeneous groups were performing integrated rather than separate behaviors.

Introduction

Fish schools display remarkable organization, structure, and coordination and are able to perform many coordinated tasks not possible at an individual level (Pitcher and Parrish 1993). These highly synchronized collective movements are the result of many moment-to-moment decisions of school members, where each fish is responding to their particular interpretation of the local environment and the behaviors of their neighbors, filtered through their internal state, including physiology (e.g., hunger level, reproduction stage) and experience (e.g., familiarity with a predator; Couzin and Krause 2003). Because the majority of individuals in large groups are effectively blocked from visual access to direct information gathering, they acquire information about their environment as a result of interactions with their neighbors, i.e., ‘social learning’ (Laland and Williams 1998; Brown and Laland 2003; Laland et al. 2011).

Social learning is a mechanism for information transfer among gregarious animals, allowing individuals to rapidly and correctly respond to changes in their environment by adopting such behaviors as local enhancement (i.e., when an individual is drawn to an area because of the presence of another individual; Waite 1982; Reader et al. 2003), guided social learning (i.e., when an individual learns by following the example of others; Helfman and Schultz 1984; Laland and Williams 1997), and social facilitation (i.e., when an individual engages in increased intensity or frequency of a behavior in the presence of an individual already engaged in that behavior; Ryer and Olla 1992).

Within a fish school, the rate of information transfer is dependent on many variables including group size (Lachlan et al 1998; Brown and Warburton 1999), number of knowledgeable fish (Lachlan et al. 1998; Brown and Laland 2003), and degree of familiarity between group members (Swaney et al. 2001). In general, a small number of knowledgeable individuals can elicit a response, such as following, from both small and large groups (Gueron et al. 1996; Reebs 2000; Huse et al. 2002; Mirabet et al. 2008), especially if naïve group members are not exhibiting an alternative response (e.g., moving in the opposite direction; Couzin et al. 2005). However, in smaller groups a greater proportion of knowledgeable individuals is needed to elicit a response (Huse et al. 2002; Couzin et al. 2005; Guttal and Couzin 2010), and it is more likely that inaccurate decisions will be made (Ward et al. 2008).

Individuals make decisions by using their own personal information, the information of other members of the group (i.e., public information), or a combination of personal and public information that exploits the most reliable information source (Coolen et al. 2003; van Bergen et al. 2004; Kendal et al. 2004, 2009). For the most part, individuals are likely to conform to, or adopt, the behavior of the majority (Day et al. 2001) often through highly nonlinear consensus, or quorum, decisions (Conradt and Roper 2003; Conradt and Roper 2005; Ward et al. 2008; Sumpter and Pratt 2009). Social conformity may limit the spread of novel behavior, which likely explains why most innovative behaviors in wild populations diffuse slowly or often do not ‘take’ (Kummer and Goodall 1985). Finally, not all information transferred between group members is beneficial. Suboptimal behavior patterns can also be socially learned (Laland and Williams 1997). However, the probability of a group choosing a suboptimal action (i.e., ‘voting’ incorrectly) is much less than the probability of an individual error (Conradt and Roper 2003, 2005).

Self-organization theory explains how decisions made by individuals, through simple imitative responses to short-term behaviors of their neighbors, generates emergent group patterns. In the context of decision-making, self-organization accounts for how a group given two or more choices can immediately and cohesively choose only one action (Sumpter and Pratt 2009). Simulation models have shown that by regulating the number of influential neighbors and social forces (e.g., repulsion, alignment, and attraction) between individuals, it is possible for only a few fish with directed motion to lead an entire school to a given location (Gueron et al. 1996; Romey 1996; Huse et al. 2002; Couzin et al. 2005, Mirabet et al. 2008). When decisions involve conflict, as between destinations, local self-organization rules can entrain undecided individuals and at least slow down individuals with a conflicting destination (Couzin et al. 2005; Conradt et al 2009). In cohesive groups of organisms, modeling and empirical work have shown that individuals pay attention to relatively few neighbors (Viscido et al. 2005, 2007), especially in the absence of predators (Hoare et al. 2004), which would seem to restrict the ability of a minority opinion to permeate the group.

In the wild, schools are not static structures but groups of individuals that constantly re-assort through fission and fusion behaviors (Helfman 1984; Hoare and Krause 2003; Hoare et al. 2004). As a consequence, it is highly likely that any one school contains an assortment of knowledge held collectively across individual members. Such heterogeneity is an important feature potentially allowing fish to adaptively manage short-term situations that may be novel to the majority. The ratio of knowledgeable-to-naïve individuals may influence how quickly and effectively learned information spreads throughout a group. On the other hand, heterogeneity may also limit the transmission of information and/or group integrity. The addition of multiple individuals to a pre-existing school, each with their own set of movement rules, can provoke sorting and, ultimately, group fission (Gueron et al. 1996; Romey 1996; Couzin and Krause 2003; Hemelrijk and Kunz 2005). Thus it is unclear where the balance between heterogeneity, information transfer, and school integrity lies.

In this study, we created heterogeneity by manipulating the amount of information individuals possessed, specifically by conditioning a subset of ‘knowledgeable’ fish to respond to a stimulus by searching for food. We were interested in the physical expression of the decision making process resulting in, or destroying, schooling; and in particular the relationship between the ratio of knowledgeable-to-naïve fish and the tendency of the group as a whole to manifest majority behavior. Our results contribute to the growing body of work defining the conditions under which a decentralized intelligence, exemplified by schooling fish, can effectively use its collective knowledge.

Methods

Experimental design

To manipulate the level of knowledge within a group, we used giant danios, *Devario aequipinnatus* (ca. 5.3 cm; purchased from African NW, Inc. in Seattle, WA), a freshwater tropical fish known to form loose aggregations or schools (Kerr 1963; Spence et al. 2008), in a sequence of experimental trials. Fish were housed in 115-liter closed system holding tanks, but all experiments were conducted in a 1.8m x 1.8m x 1.0m plexiglas tank, equipped with recirculating filtration. All tanks were maintained at 20 °C. To generate a learned response, two red 100 Watt PAR weather-resistant floodlights were positioned at opposite upper corners of the experimental tank (Figure 3). A funnel, which housed live zooplankton prey (*Daphnia* sp.) and had a solenoid switch at its base, was positioned above and adjacent to the tank. A feeding tube connected the base of the funnel to the tank at one of two interchangeable locations (Figure 3). A timer simultaneously activated the red lights and the solenoid switch, allowing remote release of food coincident with signal (red light) generation. Four Panasonic 300x digital palmcorder video cameras (model no. PV-DV4D1D) and eight 100 W floodlights equipped with fresnel diffusers were located above the experimental tank to record fish movement.

Our "knowledgeable” population consisted of a subset of 17 fish, and our “naïve” population consisted of a subset of 75 fish, all arbitrarily selected from the general population of approximately 380 fish. The knowledgeable fish were used for stimulus-response training in the large experimental tank, and the naïve fish were housed in five holding tanks (15 naïve fish per tank) on the other side of an opaque dividing screen from the experimental tank.

All knowledgeable danios were subcutaneously marked with an ~1mm injection of orange visible implant fluorescent elastomer (VIFE), on the left side just below the dorsal fin, according to previously established protocols (Dewey and Zigler 1996; Frederick 1997). We used these marks to differentiate knowledgeable from naïve danios following experimental trials (see below). Tags were not detectable in the videos.

After one day of acclimation in the experimental tank, all 17 fish in the knowledgeable population were subjected to daily conditioning bouts for 2 weeks. During each conditioning bout, red lights came on for one minute between 09:00 and 18:30 while *Daphnia* prey were simultaneously introduced into the tank at one of the two feeding locations (time and location selected from a random numbers table). To disassociate the presence of people with the red light stimulus or food, *Daphnia* were placed in the funnel 1-3 hours before the start of each conditioning bout. Because food could be released in more than one location, danios responded with searching behavior, wherein individuals engaged in quick movements collectively covering most of the tank volume. To ensure that these danios were successfully conditioned, at the conclusion of conditioning we exposed the knowledgeable fish group to one minute of red light without food reinforcement and observed searching behavior. Danios were not tested individually, as isolation caused fish to exhibit extreme stress behaviors (freezing, elevated ventilation). Additional red 100 Watt PAR weather-resistant floodlights were positioned next to the holding tanks containing the naïve population and were connected to the experimental tank timer. Naïve fish were thus exposed to the red light stimulus during the daily conditioning bouts of the knowledgeable fish, without receiving food.

All trials occurred in the experimental tank and consisted of exposing groups of 15 fish composed of individuals from both knowledgeable and naïve populations to one minute of red light without food (*Daphnia*) reinforcement. Although relatively large, the size of the experimental tank still permitted individuals to be within eyesight of one another. For each experimental trail, fish were allowed to habituate to the experimental tank, and each other, for ~14 hours before the cameras and filming floodlights were turned on, and ~20 hours before the red light stimulus, during which time the fish were not fed. This timeline corresponds to an acceptable acclimation period for tank experiments involving giant danios (Viscido et al. 2004), as well as other species of fish (e.g., Laland and Williams 1998; Laland and Reader 1999; Reebs 2000; Day et al. 2001; Coolen et al. 2003; Kendal et al. 2009). All experiments were conducted in the afternoon. Six filmed experimental trials were conducted sequentially with the following ratios of knowledgeable-to-naïve fish: 15:0, 12:3, 9:6, 6:9, 3:12, and 0:15. We began with the 15:0 knowledgeable-to-naïve ratio, and systematically proceeded to replace 3 knowledgeable danios (recognizable because of the VIFE tags) as well as *all* naïve fish with new naïve fish from the larger control population such that there were always 15 fish in the experimental tank. In between each experimental trial, but before fish removal, all fish in the experimental tank received two conditioning bouts (i.e., red light plus *Daphnia*) over the course of 2 days to maintain the stimulus-response association (Warburton 2003). We did not randomize our trails intentionally, in order to minimize the handling stress of knowledgeable fish (i.e., removal to a holding tank and later reintroduction to the experimental tank, etc.). This design is a modified version of the transmission chain in which members of a knowledgeable founder population are gradually replaced with naive individuals (e.g., Curio et al. 1978, Laland and Williams 1997 & 1998). However, because we were interested in quantifying if/how naïve individuals respond to knowledgeable behavior, and not how long it takes naïve individuals to learn knowledgeable behavior, we replaced the naive fish between trials such that no naïve fish was used more than once. In total, 15 knowledgeable fish and 45 naïve fish were used in each replicate (of the initial 17 and 75, respectively, where additional fish were maintained in test populations in case of illness or death).

At the conclusion of all six trials, video cameras were calibrated by recording a two-dimensional calibration grid (196 vertices spaced 12.07 cm apart in a 156.9 cm x 156.9 cm arrangement) placed sequentially at the top and bottom of the experimental tank. The entire process (i.e., conditioning 17 fish for two weeks, running a series of six experimental trials and associated conditioning reinforcement, and video camera calibration) took ~1 month, and was repeated twice for a total of three replicates. None of the knowledgeable or naïve fish were used in more than one replicate.

Video processing and tracking

The resulting digital videos (DV) were synchronized to the frame *a posteriori* by matching a series of random beeps recorded onto the DV audio track. For each trial, 41 minutes of video were recorded: 20 minutes prior to the red light stimulus, 1 minute when the red lights were turned on, and 20 minutes after the red light stimulus. For this analysis, we extracted the minute of video footage when the red lights were turned on (or 1800 frames of data per camera) from 2 opposite camera views. To quantify our visual observation that knowledgeable fish responded to the red light stimulus by searching, we also extracted 1 minute of video footage prior to the stimulus during replicate 1, specifically the footage between the 4th and 5th minute before the red light turned on. In total, 43,200 video frames were examined.

Video, audio, and calibration grid stills were transferred to a Linux workspace using Kino freeware (Dennedy, D., Kino, California, USA). Video was captured as DV AVI type 2 files, and the corresponding audio inputs were captured as WAV files. The still images of the calibration grid were captured as JPEG files. The fish in the AVI video footage were isolated as point sources using Avidemux2 freeware (Mean, fixounet at free dot fr), with the filters ‘SubtrackBg’ (to filter out stationary objects such as tank edges and shadows) and ‘Threshold’ (to filter out pixel intensity: minimum value of 255, maximum value between 90-120, and a debugging value of 0). The resulting output file listed each fish as an x,y pixel location for each frame of video based on the calculated centroid position of each fish. Position (i.e., x,y) coordinate lists of the calibration grids were created using ImageJ freeware (Rasband, W.S., ImageJ, U.S. National Institutes of Health, Bethesda, Maryland, USA). We created two-dimensional trajectories for each identified fish using Tracker3D (Grünbaum et al. 2005), an in-house movement analysis software generated with Matlab software (MathWorks, Massachusetts, USA), and finally merged the trajectories from both camera views into a single composite trajectory for each fish. Tracking therefore involved four steps: calibration, synchronization (using WAV files), single camera single fish tracking (using Tracker3D), and cross camera single fish path merging. The final output consisted of an x,y location for each fish for each frame without time breaks.

The results in this study are based on 2D (x,y) movement patterns, describing the horizontal range of motion of individuals and the group: they do not take simultaneous vertical motion into account. Because three-dimensional data does not always capture additional phenomena from 2D data (Hemelrijk and Kunz 2005), fish schools are often more spread out in the horizontal plane than the vertical plane (Bumann et al. 1997), and the majority of forward motion is typically in the horizontal plane (Bumann et al. 1997), we made the assumption that valuable comparative information could be obtained.

Swim metrics

Swim metrics were calculated at the individual and group levels. We chose three swim metrics to describe movement behavior of individual fish: speed (s_i), a measure of horizontal distance travelled (d_i) between time steps *t* and *t+1*

$$s_i = \frac{d_i}{t}, \tag{1}$$

path curvature (γ_i), a measure of 2D path tortuosity that is expressed as the turning angle (τ_i) over the horizontal distance travelled between time steps *t* and *t+1*, where the turning angle is the angle between the velocity vectors at time steps *t* and *t+1*

$$\gamma_i = \frac{\tau_i}{d_i} \tag{2}$$

and range (δ_i), a measure of the horizontal distance between the position of an individual fish (X_i) and the position of the group centre (C_g)

$$\delta_i = \sqrt{(X_i - C_g)^2} \tag{3}$$

$$C_g = \frac{\sum X_i}{15}. \tag{4}$$

Speed and path curvature data were smoothed using a 10 frame center moving average. For each individual fish, speed, path curvature, and range metrics could be calculated at each time step (i.e., 1800-1 frames). We calculated speed, path curvature, and range means for each individual fish, resulting in a sample size of n = 15 for all individual swim metrics. Separate variance measures (standard deviation) were not informative in differentiating among replicates or knowledgeable-to-naïve ratios, so they were dropped from further analyses.

Four swim metrics were calculated to describe movement behavior of the group:
speed (s_g), a measure of horizontal distance travelled by the group centre (d_g) between time steps *t* and *t+1* (see Eqn (1)); path curvature (γ_g), a measure of 2D path tortuosity that is expressed as the turning angle of the group centre (τ_g) over the horizontal distance travelled by the group centre between time steps *t* and *t+1* (see Eqn (2)); area (α_g), a measure of the 2D area within the convex hull of the positions of all 15 fish at time step *t*. The convex hull (η_i) of a set of points (Y) is the smallest convex polygon that contains every one of those points. For n points in Y (p_1….p_n), the convex hull is

$$\eta_i = \left\{ \sum_{j=1}^{n} \lambda_j p_j \mid \lambda_j \geq 0 \text{ for all } j \text{ and } \sum_{j=1}^{n} \lambda_j = 1 \right\}, \text{ where } \lambda \text{ are real numbers, and} \qquad (5)$$

and polarity (ϕ_g), a measure of the angle deviation (ϕ_i) between the headings of the group centre and each individual,

$$\phi_g = \frac{1}{15} \sum \phi_i \ . \qquad (6)$$

If $\phi_g = 0º$, the fishing headings are parallel, and if $\phi_g = 180º$, the fish headings are perpendicular. The polarity was further transformed into non-dimensional polarity (ϕ^*_g)

$$\emptyset *_g = \frac{(180 - \emptyset_g)}{180}. \qquad (7)$$

If $\phi^*_g = 1$, fish in the group are completely aligned, and if $\phi^*_g = 0$, individual fish orientation is random with respect to one another. Group swim metrics were calculated at each time step (i.e., 1800-1 frames), and then smoothed using a 10 frame center moving average. To account for autocorrelation in group metrics, the data were bin averaged based on lag values (i.e., into 2 second bins for speed and polarity and into 6.67 second bins for path curvature and area) as determined by time series autocorrelation results obtained using S-PLUS (TIBCO Software Inc., California, USA). This resulted in a sample size of n = 30 for speed and polarity metrics and n = 10 for path curvature and area metrics.

Analyses

To quantify the response of knowledgeable and naïve groups to the red light stimulus, we examined the behavior of all-knowledgeable (i.e, 15:0) and all-naïve (i.e., 0:15) fish in the minute of film processed from the pre-experimental sequence relative to the minute of film processed from the experimental trail (replicate 1 only), using a single-factor ANOVA and *a posteriori* multiple comparisons using Tukey's honestly significant difference test for each swim metric.

To elucidate the impact of changing the knowledgeable-to-naïve ratio on individual and group behavior, we conducted a multiple factor analysis (MFA) using formulas provided by Abdi and Valentin (2007). MFA analyzes observations described by several 'blocks' of variables (Escofier and Pagès 1994; Abdi and Valentin 2007). First, MFA performed a separate principal component analysis (PCA) on each of the 3 replicates. The data for each replicate was then divided by the square root of the respective first eigenvalue (i.e., first singular value) to normalize the results. Normalized results were concatenated to form a global data set, and a global PCA was performed to simultaneously describe the ratios in multivariate space. To examine how each replicate influenced the position of the group ratios in multivariate space, the normalized results of each replicate were projected onto the global analysis.

To clarify the impact of the knowledgeable-to-naïve ratio on discrete swim metrics, we conducted a two-way model III ANOVA, using ratio as the fixed effect and replicate as the random effect, and *a posteriori* multiple comparisons using Tukey's honestly significant difference test for each swim metric. Linear and sigmoid curves were fitted to the observed data for each metric, as a function of knowledgeable-to-naïve ratio.

To assess whether the responses observed during heterogeneous trails were simply a concatenation of both knowledgeable and naïve response types, we constructed a null model of expected responses from iterative sampling of all-knowledgeable and all-naïve fish data, specific to replicate and ratio as follows: Within each replicate, we randomly selected p actual individual fish trajectories from the all-knowledgeable (i.e., 15:0) group and q actual individual fish trajectories from the all-naïve (i.e., 0:15) group, where $p + q = 15$ and were set to the relevant ratio combinations. For each ratio we created ten simulated groups by sampling with replacement, and calculated average individual and group metrics for each ratio-replicate combination. We then used single sample mean tests to compare the observed heterogeneous responses to the expected (i.e., null model) responses.

Results

Knowledgeable vs. naive groups

We used the comparison of pre-stimulus to during-stimulus behaviors to establish whether differences observed in our experiments were due to the difference in learned behavior, or were the result of a pre-existing condition. Prior to the red light stimulus, knowledgeable and naïve fish both milled about the tank. Individuals moved slowly (Figure 4a) and both groups exhibited slow speed, tight turns and low polarity (Table 2, Figure 4d, e, g). Naïve fish were closer together (Figure 4c) and turned more sharply (Figure 4b), resulting in a greater packing density (Figure 4f).

The red light stimulus caused minimal responses in the naïve fish group: individual fish maintained their speed, turning radius, and inter-individual distance (Figure 4a, b, c), with a modest straightening of group centroid path accompanied by a slight increase in group speed (Table 2, Figure 4d, e). By contrast, knowledgeable fish reacted to the red light by swimming much faster (Table 2, Figure 4a) along straighter and more polarized paths (Figure 4b, g). The only unchanged metrics for the all-knowledgeable group were range and area, suggesting that the knowledgeable fish were already occupying the majority of the tank prior to the imposition of the red light. These results show, irrespective of pre-existing (i.e., pre-light) behavior, a demonstrable difference between the reaction of knowledgeable and naïve fish to the light.

Although our conditioning bouts delivered food to two specific locations, the light stimulus did not cause the all-knowledgeable group to react by assembling, or shuttling between, those locations. Had the group coalesced into a single school shuttling between food dispersal locations, individual range and group area would have been significantly smaller than in the pre-light condition. If the group had bifurcated into two groups, one at each food source, the known nearest neighbor distances across all possible pairs would have had a bimodality; however, it was continuous, approximating a linear distribution (R^2 = 0.985, 0.985, and 0.983 for replicates 1, 2, and 3, respectively). Had all individuals shuttled between food source locations, the resulting group area would have been elliptical; however, measured area of the group (based on convex hull calculations) was actually larger than the calculated area of the circle (using range for the radius), indicating the presence of an amoeboid-type of convex hull. Thus, knowledgeable fish reacted with a behavioral change (searching) rather than a location change (assemble at food sources).

When all three replicates were considered, the differences in the responses of knowledgeable and naïve fish were reinforced (Figure 5, 4). Knowledgeable individuals darted about the tank, swimming significantly faster (Figure 5a) along significantly straighter paths (Figure 5b). Although knowledgeable fish occupied a greater total area (Figure 6c), they were more polarized (Figure 6d) than their naïve fish counterparts, suggesting that the knowledgeable individuals were not exploding outwards (i.e., flash expansion; Pitcher and Parrish 1993) but instead were moving with a degree of coordination. As a result of these behaviors, the centroid of knowledgeable fish groups also moved significantly faster, albeit slightly slower than the individual fish themselves moved (best-fit linear relationship: group speed = 0.7 * individual speed -0.2; r = 0.92).

Taken together, these results describe our observation that knowledgeable fish initiated searching behavior when the red lights turned on, but the naïve fish did not. If anything, the experimental tank had a ‘small universe effect’, limiting the extent of forward motion by knowledgeable fish groups. Consistency in the relationship between individual speed and group speed suggests that knowledgeable and naïve fish were exhibiting similar behaviors during the red light stimulus, but at different scales. Naïve fish milled forming clumped centrally stationary groups, whereas knowledgeable fish moved quickly covering the entire tank such that these expanded groups were confined within the tank walls.

Heterogeneous groups

In trials of heterogeneous groups, group response, and to a lesser extent individual response, was an amalgam of both extremes, but tended to conform to the all-knowledgeable trials (Figs. 3, 6, 7). In general, individual fish in heterogeneous groups favored knowledgeable behavior and moved faster (Figure 5a) and straighter (Figure 5b) than predicted by the null model, forming faster (Figure 5a) and straighter (Figure 6b) groups that were more cohesive (Figure 6d). Individual fish in heterogeneous groups also favored naïve behavior and moved closer together (Figure 5c) than predicted by the null model, forming more cohesive groups (Figure 6c). Thus, it appears that individuals in heterogeneous groups did not react to the stimulus independently – i.e., separately as knowledgeable fish and naïve fish as described by our null model – but instead reacted to one another as well as to the stimulus. As no particular replicate was consistently farthest away from the MFA’s global analysis centroid (Figure 7), and replicate loadings were comparable particularly for the first axis (Table 3), differences across the ratios influenced overall results more than did differences among replicates.

As the proportion of naïve fish changed, the metrics that favored knowledgeable behavior relative to the null model (i.e., speed, path curvature, and polarity) appeared to follow a more obvious stepped response; and the metrics that favored naïve behavior relative to the null model (i.e., range and area) followed a more gradual response (Figs. 5 and 6, Table 4). However, both knowledgeable and naïve metrics exhibited a quorum response, but in directions opposite to one another. Speed, path curvature, and polarity favored knowledgeable behavior relative to the null model until only ~20% of the individuals were knowledgeable (i.e., ratio 3:12 in Figs. 5a, b and 6a, b, d). Likewise, range and area favored naïve behavior relative to the null model until only ~20%

of the individuals were naïve (i.e., ratio 12:3 in Figs. 5c and 6c). At the extreme ratios, these metrics switched, or began to switch, to favor the behavior associated with the group majority.

The abrupt transition in individual and group metrics (Figs. 5 and 6) could have been produced by a sudden shift in the composition of knowledgeable individuals, if all individuals in this cohort were not trained, and/or did not retain information, equally (i.e., if there was a loss of overall knowledge by knowledgeable fish). We were unable to individually test knowledgeable danios due to extreme stress responses these fish exhibit when isolated. However, the probability that a loss of overall knowledge occurred at the same trail in all three replicates is vanishingly small. For instance, the chance 3 such individuals remained through the 3:12 trail (when metrics abruptly shifted) across all three replicates is <0.001%. Additionally, the variance between ratios was much higher than the variance within ratios (Figure 7).

Discussion

Our study examined the physical expression (i.e., swim metrics) of the decision-making process in groups of giant danios. Our results indicate that heterogeneous groups of danios exhibit behaviorally integrated responses by adopting some behaviors from knowledgeable members and other behaviors from naïve members –i.e., various swim metrics favor either the knowledgeable or naïve response. From a cost-benefit perspective, the behaviors that favor the knowledgeable response (i.e., speed and path curvature) are the most beneficial of the analyzed metrics for searching. Fish anticipating zooplankton prey would profit by moving faster and straighter to cover more of the environment (Dill 1983; Hart 1993). Likewise, the behaviors that favor the naïve response (i.e., range and area) are the most beneficial of the analyzed metrics during times of uncertainty. Group cohesion provides individuals with increased protection (the safest position possible is close to other individuals; Hamilton 1971; Ioannou et al. 2007) and allows for immediate group decision-making and consensus decisions (Sumpter and Pratt 2009). Increased polarity favors searching behavior but is also beneficial during times of uncertainty. Individuals already aligned towards one another are able to respond more quickly to movement changes made by their neighbors (Couzin et al. 2002), and therefore respond more rapidly to the location of prey or unknown changes in their environment (Laland et al. 2011). However, in our study, the increase in polarity during searching behavior is likely intrinsically related to increased movement. As individual fish move faster, they can either become aligned, collide with one another, or take off in many different directions which would result in group dispersal and little net group movement (Viscido et al. 2004). At faster speeds, the danios essentially needed to become more aligned to maintain group integrity.

A challenge in the study of synchronized collective movement is discriminating between a common individual response and behaviors that result from interactions with neighbors –i.e., social interaction (Pillot et al. 2011). Our null model predicts the outcome of individual responses. Because knowledgeable and naïve fish in heterogeneous groups did not behave as predicted by this model, some form of social interaction occurred. This suggests that the danios may have utilized consensus decision-making strategies (e.g., Conradt and Roper 2003, 2007, 2009, Sumpter et al. 2008, Conradt et al. 2009). Consensus decision-making describes a continuum, from a single individual in charge ("unshared" or "despotic" decisions) to all members performing "equally shared" decisions (Conradt and Roper 2003, 2005, 2007). It is not likely that the danios in our study made unshared decisions. If so, heterogeneous schools would have been expected to completely mimic either the all-knowledgeable schools (if a knowledgeable fish was the despot) or all-naïve schools (if a naïve fish was the despot), which clearly was not the case. Heterogeneous groups also did not exhibit a proportionally blended knowledgeable-naïve response, or equally shared decisions, because even in the minority, danios were able to exert disproportionate influence: speed, path curvature, and polarity favored the knowledgeable response in 6:9 (ratio knowledgeable-to- naïve) groups, and range and area favored the naïve response in 9:6 (ratio knowledgeable-to- naïve) groups. Therefore, the danios were most likely making partially shared decisions (Sumpter and Pratt 2009). The presumed degree of asymmetry in costs/benefits to the trained versus naïve danios for various swim metrics could have modified the consensus decision-making mechanism to allow for partially shared decisions (Conradt and Roper 2003; Conradt et al. 2009). That is, both knowledgeable and naïve fish could have exerted undue influences over the group with respect to the individual and/or emergent group behaviors perceived to be most costly to loose: knowledgeable fish pushed for increased movement and naïve fish pushed for greater cohesion.

In our study, there was an apparent threshold under which no searching occurred in heterogeneous groups. This suggests that two things are likely happening in heterogeneous groups: First, naïve fish are not automatic followers and instead actively make a choice to not search. Second, knowledgeable fish are not insulated from social conformity. Simulation studies have often rested on the assumption that uninformed, or naïve, individuals are socially sympathetic followers that use a given set of rules to make local adjustments to knowledgeable individuals with biased leadership, or to neighbors already adjusted to knowledgeable leaders (e.g., Gueron et al. 1996; Romey 1996; Huse et al. 2002; Couzin et al. 2005; Mirabet et al. 2008). Such passivity in decision-making can produce a long line of simulated followers and/or end in group bifurcation. However, studies on fish (Ward et al. 2008) and sheep (Pillot et al. 2011) have suggested that uncommitted individuals make a specific decision whether to pursue leaders or stay put. Our study supports the concept that individuals are not blind followers, because the naïve danios appear to be making a choice whether to search or continue to mill. When the naïve danios presumably choose to not search, the knowledgeable danios in the group are suddenly presented with an alternative choice to searching, and when this occurs, the knowledgeable fish stay with and behave similarly to the naïve majority. That is, knowledgeable danios appear to become hindered by conformity. Evidence of social conformity has been demonstrated in other species of fish (Lachlan et al. 1998; Day et al. 2001; Pike and Laland 2010) and is critical for consensus decisions and group cohesion. Petit et al. (2009) demonstrated that white-faced capuchin monkeys, *Cebus capucinus*, were highly prone to cancel their initial movement when too few group members followed this movement with an acceptable latency. The knowledgeable fish in our study may have experienced a similar "school trap" (sensu Bakun and Cury 1999), or a strong propensity to remain a member of the group even if that action incurred disadvantages such as a missed foraging opportunity.

In the context of group synchronization, studies have typically presented individuals with the choice of two or more location options (e.g., Helfman and Schultz 1984; Gueron et al. 1996; Romey 1996; Laland and Williams 1997; Huse et al. 2002; Couzin et al. 2005; Mirabet et al. 2008; Ward et al. 2008; Pillot et al. 2011). In addition, many studies have addressed the effects of changing the level of knowledge, or general heterogeneity, in the group by measuring the rate of information transfer or quantifying the final decision of the members (e.g., Lachlan et al. 1998; Swaney et al. 2001; Brown and Laland 2002, 2003; Couzin et al. 2005; Mirabet et al. 2008). To our knowledge, ours is one of the few studies that disarticulates the physically-expressed process of that decision-making into multiple metrics of group structure by setting up a choice among behaviors (e.g., searching vs. milling) rather than locations. Our results suggest that while the type of information individuals possess may unduly influence group structure (e.g., knowledgeable individuals had a greater overall influence), all information categories had some influence (e.g., naive individuals had a relatively greater influence on the range and area metrics), and the result of that dynamic conflict was a single, integrated group response (i.e., naive and knowledgeable fish did not assort into physically separate groups). One realization of the tension implied by unequally weighted consensus decision-making is that at some minority threshold individuals with certain information may ignore the benefits associated with that information in order to remain a member of the group. As group size has been shown to influence the propensity towards "correct" decision-making (e.g., Grünbaum 1998; Sumpter and Pratt 2009), examining if/how the physically-expressed process of decision-making changes as a function of group size would be an informative next step.

Funding

This work was supported by the National Science Foundation (BE-0313250 to K.A.M., J.K.P., and D.G.).

Acknowledgements

I am grateful to the many people who supported us through the course of this study. I would like to thank Rob Ames for his remarkable transformation of the danio lab and the digital tracking lab; Kristian Haapa for the many hours he spent tracking fish and advancing the efficiency of the tracking lab; Danny Grünbaum for writing the Tracker 3D code and Kudah Mushambi for updating the Tracker 3D code to make it applicable to our experimental tank/ design; Kristy Morgansen and Dan Klein for providing the much-needed Linux support; Amy Groesbeck, Rob Ames, and Kristian Haapa for the many hours they spent taking care of the danios and preparing the lab for the experiments; and Julia Parrish, Chris Wilson, Cliff Ryer, Stéphan Reebs, and anonymous reviewers for the valuable comments and remarks on earlier drafts of this manuscript.

Table 2. Single factor anova results (p-values) and Tukey's honestly significant difference test results, for the all-trained and all-naïve swim metrics, both before and during the red light stimulus during replicate 1. Only the relationships between means (μ) that are not significantly different from one another (based on α = 0.05) are listed.

	Schooling Metric	F-value	p-value	Tukey's Multiple Comparison [a]
Individual	Speed	305.98	< 0.01	$\mu_{TB}=\mu_{NL}$ & $\mu_{NB}=\mu_{NL}$
	Path Curvature	58.09	< 0.01	$\mu_{NB}=\mu_{NL}$
	Range	69.74	< 0.01	$\mu_{TB}=\mu_{TL}$ & $\mu_{NB}=\mu_{NL}$
	Swim Efficiency	2.48	0.07	$\mu_{TB}=\mu_{NB}=\mu_{TL}=\mu_{NL}$
Group	Speed	162.43	< 0.01	$\mu_{TB}=\mu_{NB}$
	Path Curvature	17.42	< 0.01	$\mu_{TB}=\mu_{NB}$ & $\mu_{TB}=\mu_{NL}$
	Area	170.92	< 0.01	$\mu_{TB}=\mu_{TL}$ & $\mu_{NB}=\mu_{NL}$
	Polarity	24.18	< 0.01	$\mu_{TB}=\mu_{NB}=\mu_{NL}$

[a] μ_{TB} = means for the Trained group Before the stimulus, μ_{TL} = means for the Trained group during the Light stimulus, μ_{NB} = means for the Naïve group Before the stimulus, and μ_{NL} = means for the Naïve group during the Light stimulus.

Table 3. Partial intertias, total inertia, and total variance (%) for the first three components of the global MFA analysis. The contribution of each partial intertia to the total inertia is given in parentheses.

	Axis 1		Axis 2		Axis 3	
Replicate 1	0.866	(31%)	0.160	(30%)	0.094	(26%)
Replicate 2	0.988	(36%)	0.095	(18%)	0.110	(31%)
Replicate 3	0.926	(33%)	0.284	(53%)	0.154	(43%)
Total inertia	2.781		0.539		0.358	
Percent of total variance	68.8%		*13.3%*		*8.8%*	

Table 4. R^2 values for linear and sigmoid functions that best describe the response of the swim metrics as the proportion of knowledgeable fish decreases, and the standardized slope of the sigmoid curve at its steepest point.

	Swim Metric	Linear Fit R^2	Linear Fit slope[b]	Sigmoid[a] Fit R^2	Sigmoid[a] Fit slope[b]
Individual	Speed	0.6587	-0.21	0.9929	-0.35
	Path Curvature	0.5305	0.18	0.9989	0.37
	Range	0.5680	-0.20	0.9774	-0.22
Group	Speed	0.3043	-0.21	0.9567	-0.66
	Path Curvature	0.3478	0.19	0.9903	0.55
	Area	0.6122	-0.23	0.9743	-0.27
	Polarity	0.1142	-0.17	0.8797	-7.96

[a] Swim metric results are based on a four parameter sigmoid function (i.e., sigmoid curve: f = y0+a/(1+exp(-(x-x0)/b))), except range and area results are based on a three parameter sigmoid function (i.e., y0 = 0).

[b] For each metric, the slope has been standardized for an equal response range.

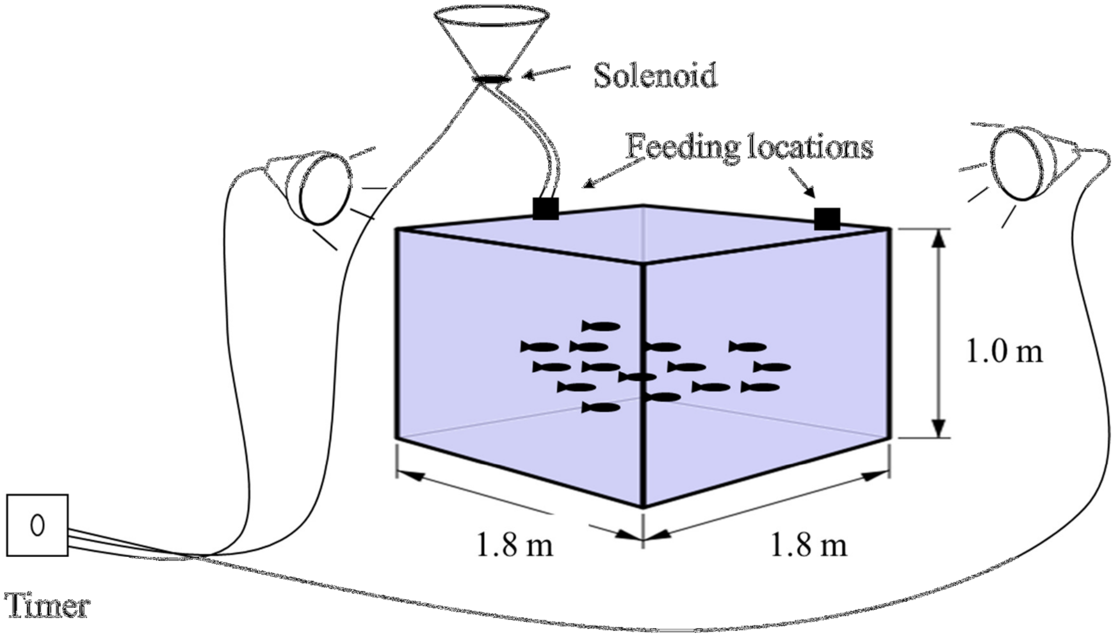

Figure 3. Experimental set-up showing the position of the two red lights, the funnel and solenoid apparatus, and the feeding locations (the feeding tube can connect to either location) in relation to the experimental tank.

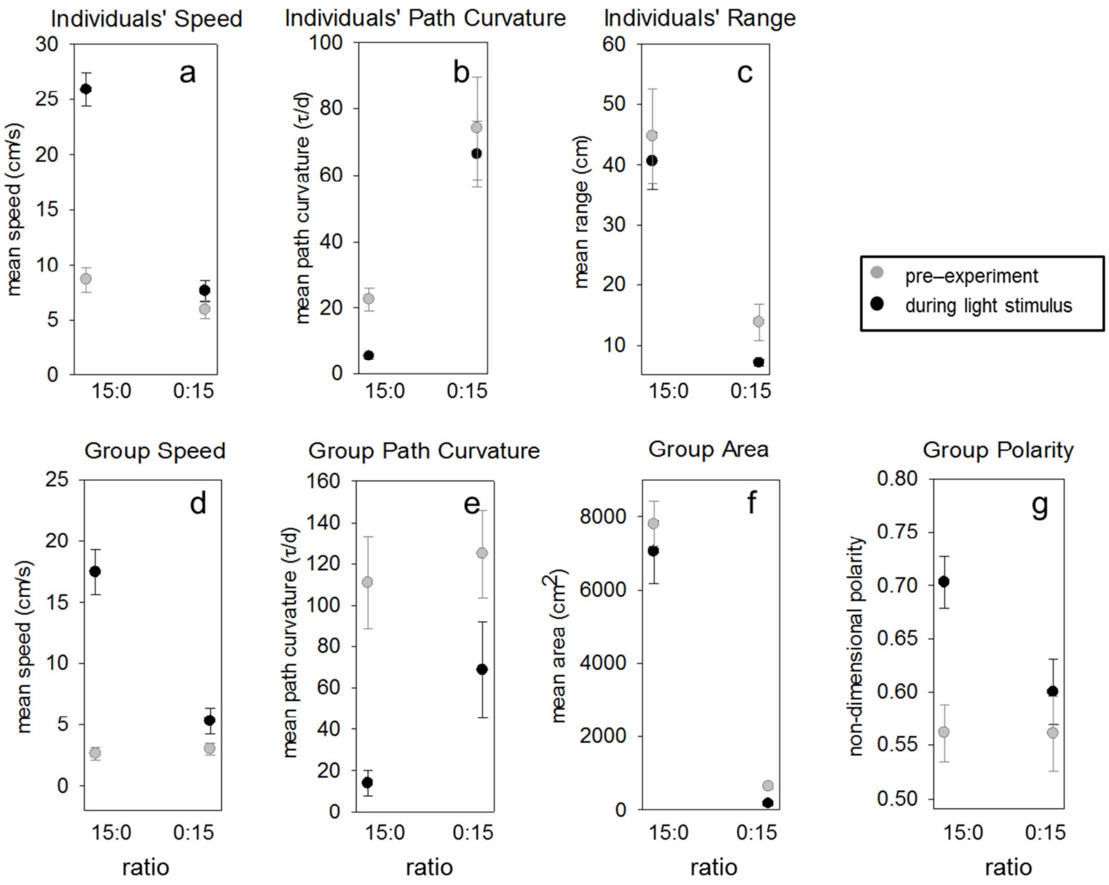

Figure 4. Results of the red light stimulus on swim metrics for the trained and naïve groups. Gray circles represent the mean metric for each ratio of replicate 1 prior to the red light stimulus. The error bars represent 95% confidence intervals about the mean.

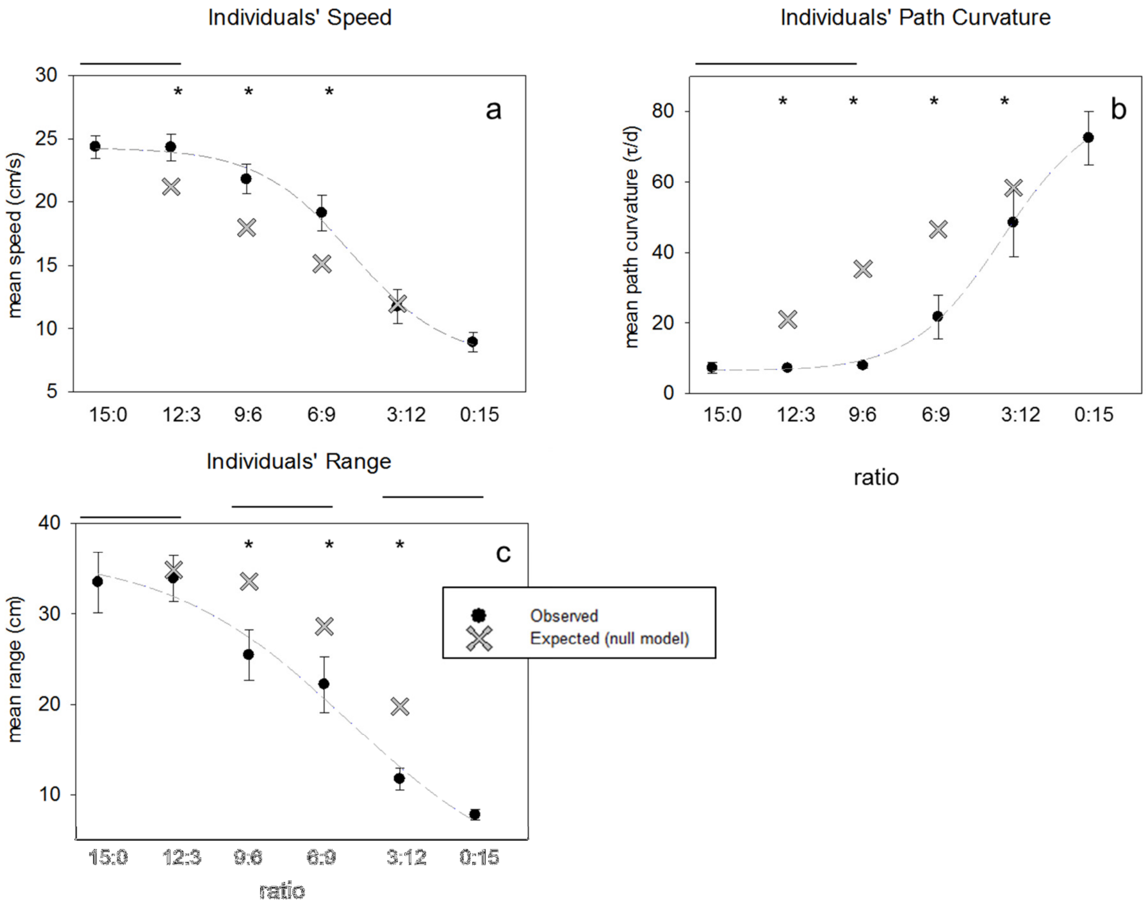

Figure 5. Results of Individual Swim Metrics. Black circles represent the mean metric for each ratio (pooling all replicates) and the error bars represent 95% confidence intervals about the mean. The gray X represent the expected swim metric values for heterogeneous schools. The lines above the plots indicate that means for the corresponding ratios are not significantly different from one another, based on Tukey's multiple comparison tests. An asterisk at the top of the plots indicate the observed value is significantly different from the expected value for a given ratio, based on the single sample mean test. Gray dashed lines represent the best fit sigmoid function to the observed data.

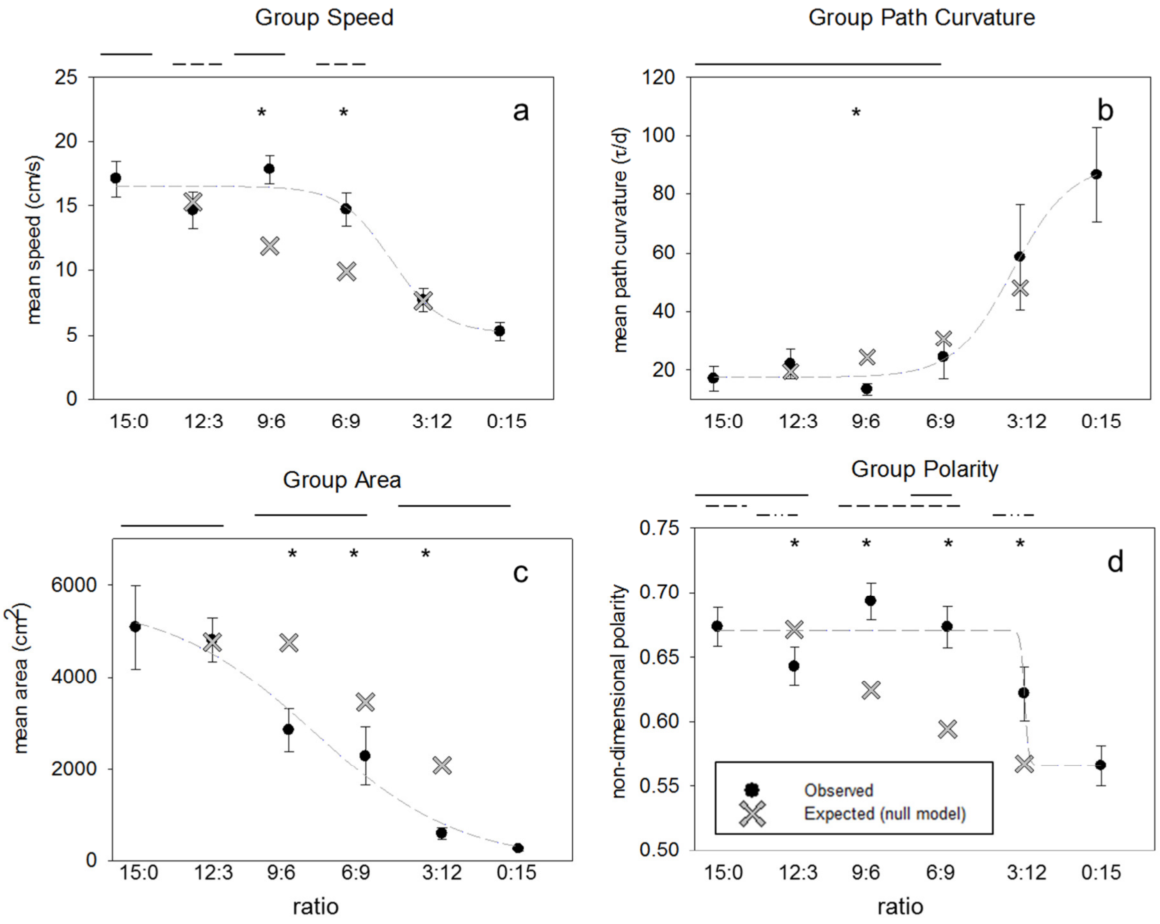

Figure 6. Results of Group Swim Metrics. Black circles represent the mean metric for each ratio (pooling all replicates) and the error bars represent 95% confidence intervals about the mean. The gray X represent the expected swim metric values for heterogeneous schools. The lines above the plots indicate that means for the corresponding ratios are not significantly different from one another, based on Tukey's multiple comparison tests. An asterisk at the top of the plots indicate the observed value is significantly different from the expected value for a given ratio, based on the single sample mean test. Gray dashed lines represent the best fit sigmoid function to the observed data.

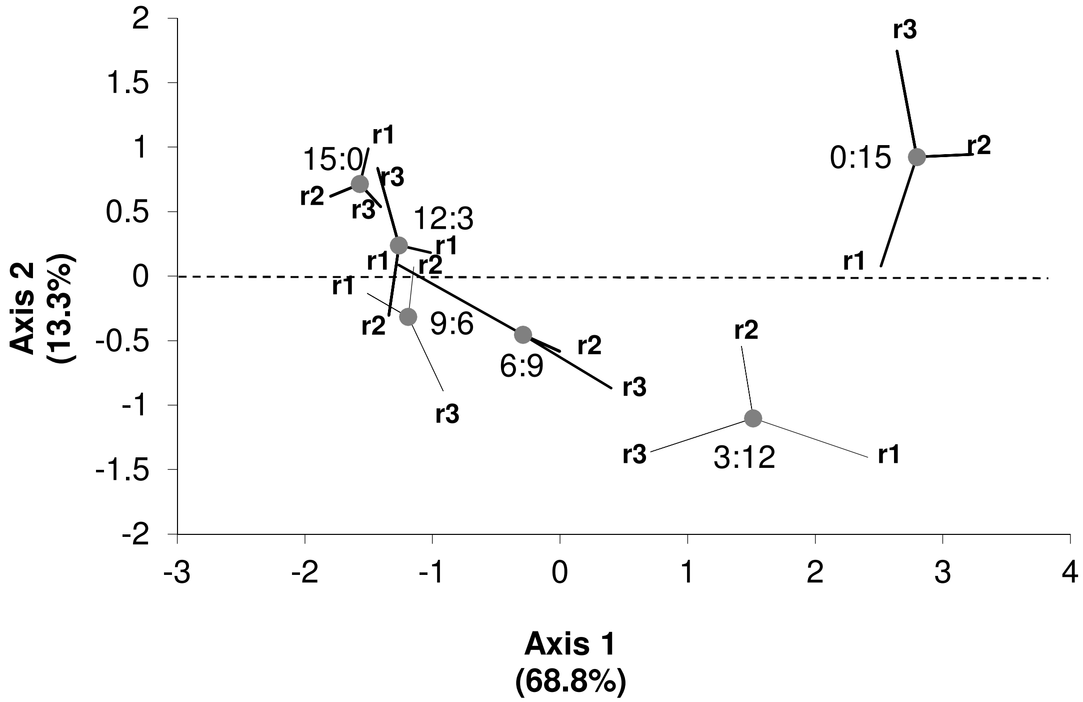

Figure 7. Projection of group ratios and replicates onto the global MFA analysis. Gray circles represent the centroid location of each group ratio during the 3 replicates. Replicate 1 is designated by ‘r1’, replicate 2 by ‘r2’, and replicate 3 by ‘r3.’ These designations indicate the position of each group ratio in the corresponding replicate.

Juvenile walleye pollock aggregation structure in the Gulf of Alaska

Abstract

Size and shape patterns of juvenile walleye pollock (*Theragra chalcogramma*) aggregations in the Gulf of Alaska are described in relation to bio-physical factors such as depth of the aggregation in the water column, water temperature, and age and body condition of the aggregation members. Aggregation characteristics were measured with acoustic data collected with a vertically-oriented echosounder, and bio-physical data were collected with a large midwater trawl and temperature-depth sensors from two areas near Kodiak Island, Alaska, during 1995-1997 and 2000-2002. Juvenile walleye pollock spatial patterns were expressed using fish aggregation length, height, fractal dimension, and density. Redundancy analysis (RDA) was used to examine the associations of the bio-physical factors with the size and shape descriptors of juvenile walleye pollock aggregations. Fish aggregation height increased as a function of fish age, and there was a negative association between depth of the aggregation in the water column and density of fish in the aggregation. There was also a negative association between body condition of the fish and the fractal dimension of the aggregation. These results demonstrate that relatively easily measurable environmental and biological factors can be useful in describing and potentially predicting spatial patterns of fish aggregations. Associations in the fish aggregation structure and bio-physical measurements were consistent with expectations based on predation and foraging theory.

Introduction

There are many functions of fish shoaling behavior that are associated with predator-prey interactions (Pitcher and Parrish 1993). For example, the attack success of a predator declines with increasing prey group size (Neill and Cullen 1974), and fish find patchy-distributed food faster when in a school (Pitcher et al. 1982). In addition, an increase in group cohesiveness and a decrease in nearest neighbor distance often results from increased predation risk, whereas the reverse occurs as fish hunger levels increase (Morgan 1988).

Other factors contribute to the formation, maintenance, and structural characteristics of fish aggregations. Many fish species congregate at regular intervals to form spawning aggregations (Misund et al. 1998). Group structure may also change as a function of ontogeny. Adult sardines form larger and less dense schools than juveniles (Muiño et al. 2003), and some species of fish lead relatively solitary lives as adults although as juveniles they form well organized schools (Keenleyside 1979). Physical factors can influence the small-scale spatial patterns of fishes. The effect of temperature on the distribution of fish aggregations has been well documented (e.g., Krause et al. 1998, Swartzman 1997). Some species of schooling fish will avoid cold water at the expense of missed foraging opportunities (Misund et al. 1998), yet others will enter cold water only to feed (Olla et al. 1985). The effect of ambient light has also been found to influence fish shoaling structure with declining light intensities generally producing less cohesive groups of fish (O'Conner and Krause 2003).

Walleye pollock are one of the most abundant and commercially important fish in the Gulf of Alaska and Bering Sea (Megrey 1989, Kim 1990). Adults are semi-demersal and in some cases can form 'carpet' aggregations near the seafloor that can extend for miles, whereas juvenile pollock are typically found higher in the water column in more discrete groupings (Wilson et al. 2003). Temperature and ambient light levels are two physical factors that influence the distribution of walleye pollock aggregations. Pollock have been observed to exhibit diel migrations to shallower nighttime depths where they form more dispersed layers (Bailey 1989, Brodeur and Wilson 1996b). Adult aggregations appear to avoid cold water regardless of prey density, yet can otherwise be associated with areas where food abundance is high (Swartzman et al. 1994, 1995, Kotwicki et al. 2005).

Although the juvenile stage of walleye pollock has been the focus of numerous behavioral and ecological studies (Brodeur and Wilson 1996a), very few field studies have described juvenile aggregation characteristics and the bio-physical factors that may influence their formation and maintenance. Kang et al. (2006) described juvenile walleye pollock school characteristics but only in relation to the age of the school members. Wilson et al. (2003) described juvenile walleye pollock aggregation characteristics and related these to commercial fishing activities. Several laboratory studies have investigated the impact of trade-offs between hunger and predation risk on school patterns of juvenile walleye pollock. For instance, juvenile walleye pollock formed less cohesive groups as food levels decreased (Sogard and Olla 1997). However, in the presence of a predator, juveniles foraging for clumped food formed more cohesive groups, but larger juveniles and those foraging for dispersed food maintained less cohesive groups (Sogard and Olla 1997, Ryer and Olla 1998b). Although additional laboratory studies have examined the effects of other factors, such as temperature and light, on the behavior of individual juvenile walleye pollock (Olla and Davis 1990, Ryer and Olla 1998a), it is unknown how these and other factors might affect juvenile walleye pollock group structure. Field studies, in particular, are needed to better understand what specific environmental cues are associated with the range of juvenile walleye pollock aggregation patterns in nature. Thus, the objective of our study is to describe juvenile walleye pollock aggregation patterns from two areas of the Gulf of Alaska, and to explore whether associations of these patterns exist with easily measured bio-physical data such as depth of the aggregation in the water column, water temperature, and age and body condition of the aggregation members. We also discuss whether the detected associations between aggregation patterns and bio-physical data are consistent with expectations based on predation and foraging theory.

Methods

Study area

Spatial patterns of juvenile walleye pollock were described for two areas during two seasons within the Gulf of Alaska near Kodiak Island: 1) during the summers of 2000-2002 in Chiniak and Barnabas Troughs on the east side of Kodiak Island (hereafter referred to as "East Kodiak"), and 2) during the winters of 1995-1997 in Shelikof Strait on the northwest side of Kodiak Island (Fig. 1). During these years, strong year classes of juvenile pollock were detected. The abundance of juvenile aggregations during this time facilitated this work to describe aggregation patterns of juvenile pollock. Additionally, the presence of a strong year class over consecutive years provides an opportunity to study aggregation patterns of fish as a function of age.

Field methods

Acoustic-trawl surveys consisted of a series of uniformly spaced parallel transects, from 5.6 km apart SE of the Kodiak Island to 13.9 km apart W of Kodiak Island (Fig. 8). In some instances, more than one survey pass was conducted over a study area during the same field season (Table 5). A survey pass consisted of a complete acoustic sampling of all transects within an area, and multiple passes were separated in time by 3-4 days. Echo-integration data were collected with a calibrated Simrad[1] EK500 quantitative echo-sounding system operating at 38 kHz (Bodholt et al. 1989) and were initially logged with a horizontal resolution of about 5–6 m (dependent on vessel speed) and vertical resolution of 0.1–0.5 m using standard methods described in Wilson et al (2003).

Samples were collected with a large pelagic trawl (Guttormsen et al. 2002) to confirm the identity of the species attributed to specific acoustic backscatter and to provide length, weight, and age composition of walleye pollock. Trawl hauls were conducted in areas of high backscatter, so areas with high densities of fish were sampled most heavily. Catches of walleye pollock were sampled to determine fork length (FL) to the nearest 1.0 cm, total body weight to the nearest 2.0 g, and age of the fish.

---

[1] Reference to trade names or commercial firms does not constitute U.S. government endorsement.

Temperature profiles were obtained with a temperature-depth probe attached to the trawl headrope in East Kodiak and with a micro bathythermograph attached to the trawl headrope in Shelikof Strait. Conductivity-temperature-depth casts and expendable bathythermograph probes were used to collect water temperature profile data in East Kodiak and Shelikof Strait at selected locations throughout the study areas (e.g., NMFS 1996, Wilson et al. 2003).

Fish aggregation descriptors

Because walleye pollock in East Kodiak and Shelikof Strait disperse at night (Guttormsen et al. 2002, Wilson et al. 2003), only aggregations observed between one hour after sunrise and one hour before sunset were used in this analysis. Areas where backscatter attributed to adult pollock or unidentified organisms (e.g., euphausiids) overlapped with that from juvenile walleye pollock were also excluded from the present analysis.

Juvenile walleye pollock backscatter was classified into aggregations using Echoview software (SonarData, Tasmania, Australia). The classification designated all aggregations as schools, whether the aggregations were discrete small groupings or long low-density layers (Reid 2000). Echoview software applies school recognition algorithms that correct for pulse-length effects and beam width effects following the methods of Reid and Simmonds (1993), Barange (1994), and Diner (1998) generating corrected estimates of various school descriptors. School size and shape descriptors used in this analysis include fish aggregation length, height, fractal dimension, and density. Fractal dimension (D) relates the perimeter (P) of a fish aggregation to its area (A, where $D = 2 \ln(P/4) / \ln(A)$) and is an informative measure of shape complexity (Barange 1994, Freon et al. 1996, Coetzee 2000). A fractal dimension of one characterizes the most basic outline shape (i.e., a square), and a fractal dimension of two characterizes the most complex outline shape (Coetzee 2000). To determine fish aggregation density (i.e., number of fish within each aggregation; fish/10^3m^3), the mean volume back-scattering strength, S_V (dB re 1 m^{-1}), for each aggregation was converted to a mean volume back-scattering coefficient, s_V (m^{-1}; MacLennan et al. 2002). The s_V was then divided by the mean backscatter cross-section, $\overline{\sigma}_{bs}$, of juvenile walleye pollock ($\overline{\sigma}_{bs}$ in m^2/fish). The $\overline{\sigma}_{bs}$ was calculated using a target strength (TS) to fish length (L_{cm}) model for walleye pollock ($TS = 20 \log(L_{cm}) - 66$; Foote and Traynor, 1988) and was based on the population length composition for a given area.

The classification of acoustic backscatter into schools by Echoview software required a series of user-controlled parameters. These parameters were examined over a range of values and evaluated, and the final criteria were chosen based on their ability to provide the best definition of a juvenile walleye pollock aggregation when compared by eye to the original echograms. The final values selected were: S_V threshold (-70 dB), minimum school length (40 m), minimum height (5 m), minimum connected length (5 m), minimum connected height (2 m), maximum vertical linking distance (5 m), and maximum horizontal linking distance (20 m). These values were used for all analyses. The criteria chosen to define an aggregation likely contain substantial and unknown biases, and it has been shown that changing the criteria can affect the results (Burgos and Horne 2007). However, if the criteria are kept constant, as in the present study, they should provide useful comparative information about the variability of the fish aggregation structure (Freon et al. 1996, Reid et al. 2000).

Biophysical factors

Water temperature at the location of each fish aggregation (hereafter referred to as "temperature") was determined by matching the mean depth of the aggregation in the water column (hereafter referred to as "aggregation depth") to the corresponding temperature of the nearest vertical temperature profile. The age and body condition of fish within each aggregation were determined from the nearest haul information. The mean body condition of juvenile pollock within each aggregation was calculated using a morphometric body condition factor index determined by body weight deviations from a least-squares fitted length (L)-weight (W) relationship (Jakob et al. 1996; $L = aW^b$, where a and b are constants). The index eliminates the effect of body size on the data. Two condition factor indices were generated: one for fish off East Kodiak and another for fish in Shelikof Strait.

Statistics

Redundancy analyses (RDA) were used to test the associations of bio-physical factors with the juvenile walleye pollock aggregation descriptors using 'vegan,' a community ecology package for R software (R Foundation for Statistical Computing, Vienna, Austria). Each survey area was considered a separate data set. The data for East Kodiak and Shelikof Strait are separated both in space and season, so it was not possible to discern whether patterns in the resulting ordination were due to differences in the location or the season between the two areas. RDA is a form of constrained ordination analysis that seeks to partition dominant patterns of variation into a reduced number of gradients that are maximally correlated with explanatory variables (Makarenkov and Legendre 2002). For the present study, a matrix of fish aggregation descriptors was analyzed with respect to a corresponding matrix of bio-physical factors. RDA assumed the matrix of bio-physical factors to be dependent on the explanatory matrix of fish aggregation descriptors. RDA was appropriate for these data because it preserved the Euclidean distance among the fish aggregation descriptors. Aggregation length, height, and density estimates were natural log transformed to stabilize the variance prior to conducting the RDA, and fish aggregation descriptor data were scaled to unit variance. Differences were considered significant at $p < 0.05$.

Both bio-physical factor gradients and fish aggregation descriptor gradients were represented in RDA triplot figures as vectors, where vector length is proportional to the strength of the gradient (see Results, Figs. 9-10). The vectors indicate how the gradients load along the first two RDA axes. For example, if a vector gradient bisects the first quadrant of a triplot, the fish aggregations within the first quadrant would have relatively high values for that gradient. The third quadrant is opposite the first quadrant; therefore fish aggregations within the third quadrant would have relatively low values for that gradient. Fish aggregations close to a vector gradient have higher values for the gradient, and fish aggregations with greater perpendicular distance to a vector gradient have weaker associations with the gradient.

Results

Fish aggregations in both study areas and each year were composed of juvenile walleye pollock from a single year class. In Shelikof Strait, the strong 1994 year class of fish was observed in 1995 (age-1, 11.5 mean FL), 1996 (age-2, 20.7 mean FL), and 1997 (age-3, 27.2 mean FL). In East Kodiak, a strong age group of 2 year old fish was present in both 2000 (19.5 mean FL) and 2001 (20.6 mean FL) and a strong age group of 3 year old juveniles was present in 2002 (32.6 mean FL).

The redundancy analysis produced ordinations significantly different from a random distribution for both study areas. A total of 4974 fish aggregations were analyzed, 2639 in East Kodiak and 2335 in Shelikof Strait (Table 5). A range of pre-log-transformed fish aggregation descriptor values and a range of bio-physical values are listed in Table 6. For clarity, only the distribution centers of fish aggregation descriptors for each survey pass (e.g., Chiniak Trough 2000, Chiniak Trough 2001) are plotted in ordination space (Figs. 9-10). The first and second axes of the RDA explained 83.9% and 15.7% of the total variation in fish aggregation size and shape descriptors for the East Kodiak data. Both axes were statistically significant ($p < 0.001$). The first and second axes of the RDA explained 93.2% and 6.1% of the total variation in fish aggregation size and shape descriptors for the Shelikof Strait data. The first axis was statistically significant ($p < 0.001$).

Fish age and aggregation depth were associated with juvenile walleye pollock spatial patterns in both study areas. Fish age and aggregation depth had the highest loadings of the bio-physical factors along all significant RDA axes both in East Kodiak and Shelikof Strait (Table 6). In both areas there was a positive relationship between increased age loading and aggregation height, and there was a negative relationship between increased depth loading and aggregation density (Figs. 9-11). This suggests the importance of fish age and aggregation depth in structuring juvenile walleye pollock aggregations, most specifically in structuring aggregation height and density. This also suggests fish age and aggregation depth have a consistent effect on fish aggregation structure across areas and/or between seasons.

Body condition of juvenile walleye pollock was associated with juvenile aggregation patterns only in East Kodiak, but there was no clear association between temperature and juvenile pollock aggregation patterns. Body condition had moderate loadings along the first RDA axis in East Kodiak but not in Shelikof Strait (Table 6), and in East Kodiak there was a negative relationship between increased condition loading and fish aggregation fractal dimension (Figs. 9 and 11). Temperature had moderate loadings along the first RDA axes in both East Kodiak and Shelikof Strait and had high loadings along the second RDA axis in East Kodiak (Table 6). There was a negative relationship between increased temperature loading and aggregation height in East Kodiak (Fig. 9), but there was a positive relationship between these two variables in Shelikof Strait (Fig. 10). These results suggest body condition and temperature were less important in structuring juvenile walleye pollock aggregations than were fish age and aggregation depth. These results also suggest body condition and temperature did not have a consistent effect on aggregation structure across areas and/or between seasons as did fish age and aggregation depth.

Discussion

Many of the trends that were detected among juvenile walleye pollock aggregation descriptors and the measured bio-physical factors, including aggregation depth and body condition of the fish, were consistent with expectations based on predation and foraging theory. In some cases, however, the results were more difficult to explain. The fact that aggregation height increased for older juveniles in both areas was one such finding. In this case, other researchers have reported that a spheroid school structure is advantageous to fish because it minimizes the detection envelope of the fish school to underwater predators (Pitcher and Parrish 1993). Because juvenile walleye pollock aggregations were longer horizontally than vertically, the aggregations must decrease in length and/or increase height to produce a more spherical structure. Thus, the increase in aggregation height reported in our work would serve to produce an aggregation shape less detectable to predators. However, predation intensity is typically greater for smaller individuals of many fish species, including walleye pollock (Milinski 1993, Hollowed et al. 2000). Therefore, it is puzzling that the older, larger juveniles rather than younger, smaller fish would form a more spheroid aggregation structure. Other studies have shown that swimming speed of fishes are generally proportional to body length (Misund and Aglen 1992), and it may be that the reduced swimming speeds for smaller fish, in some way, prevents formation and maintenance of the more spherical aggregation.

Findings based on walleye pollock acoustic data collected off Japan support the association between fish age and aggregation height reported in our study (Kang et al. 2006). They reported that age-1 walleye pollock formed schools of less vertical height than age-2 and adult fish, although this was not the case when compared to age-0 walleye pollock. Their results may have been confounded because they did not use schools of pure age groups in their analyses (a school was designated based on the age group of the majority of the members). Nevertheless, the consistent results between these two studies indicate that the trend in fish aggregation height among age-1 and older age groups may extend over a broad geographical range.

Other results from the present study were consistent with what one might expect based on the advantages that schooling behavior confers to its members in predator-prey interactions. Fish aggregation density estimates decreased for deeper dwelling aggregations in both the East Kodiak and Shelikof Strait study areas. Although the effects of depth on spatial patterns of fishes are poorly known, numerous studies have shown that fish schools become less cohesive as light intensity decreases (Ryer and Olla 1998a, O'Conner and Krause 2003). In the presence of predators, however, fish typically form more compact schools so they can communicate rapidly and perform well-coordinated escape tactics (Pitcher and Parrish 1993). Light is essential to this communication because visual and behavioral cues are important components in information transfer among fish (Ryer and Olla 1991, Lachlan et al. 1998). Laboratory studies showed that juvenile walleye pollock will disperse as light levels decrease, even in the presence of a predator, most likely because it becomes more difficult for the fish to see one another (Ryer and Olla 1998a). In the Gulf of Alaska, potential demersal predators of juvenile walleye pollock such as arrowtooth flounder (*Atheresthes stomia)*, halibut (*Hippoglossus stenolepis)*, and adult walleye pollock increase with proximity to the sea floor (Bailey 1989, Hollowed et al. 2000). The influence of diminishing light levels on the activity and foraging success for these predators is unknown. However, it is conceivable that group compaction might be favored by juvenile walleye pollock when they are deeper and in closer proximity to these demersal predators, but ambient light levels are simply too low for this to occur.

Increased body condition for juvenile walleye pollock off East Kodiak was associated with a decrease in aggregation fractal dimension. An increase in body condition is generally attributed to an increase in feeding or an increase in prey concentration (Pedersen and Jobling 1989, Kloppmann et al. 2002), and body condition can be used to approximate long- and short-term changes in food abundance and quality (Grant and Brown 1999). The high body condition of fish in Barnabas Trough in 2002 suggested that the fish had recently consumed high quality or large quantities of prey. This could have occurred prior to the fish moving into the area or while they were within Barnabas Trough. If the later were true, then prey concentrations in the East Kodiak study area were likely greatest within Barnabas Trough in 2002. The less complex aggregation shape, as indicated by a lower fractal dimension in Barnabas during 2002, implies the fish were not dispersing from the aggregations. Other studies have demonstrated two potential mechanisms behind this observation. Group cohesiveness decreases with hunger (Morgan 1988), because fish disperse from the safety of their school to forage (Godin and Smith 1988). If the fish in Barnabas Trough in 2002 had recently consumed high quality or large quantities of prey, the need to disperse from the aggregation to seek additional prey may have been reduced. Alternatively, being part of a group often intensifies competition for food (Bertram 1978), but competition costs can be reduced if prey densities are high (Eggers 1976). If the East Kodiak prey field was more abundant within Barnabas Trough in 2002, competition costs would be reduced and the fish could have foraged from within the safety of the aggregation.

Fish aggregation size and shape patterns were not associated with body condition of juvenile walleye pollock during the winter in Shelikof Strait. Walleye pollock feed intensely in summer but only feed sporadically during winter months (Sogard and Olla 2000, Yamamura et al. 2002). As a consequence, body condition falls during winter and recovers quickly in summer (Yamamura et al. 2002). Thus, during summer, foraging behavior may be a more important component for mediating fish aggregation behavior, whereas during winter months, when fish feed less frequently, other factors may become more influential in structuring the group.

This study demonstrated that relatively easily measurable environmental and biological factors can be useful in describing and predicting spatial patterns of juvenile walleye pollock aggregations. Because the data for East Kodiak and Shelikof Strait are separated both spatially and temporally, it was not possible to discern whether observed patterns are due to differences in location or season. However, the consistent effect that fish age and aggregation depth had on juvenile aggregation patterns across these locations and/or seasons suggest that these two factors may act as strong, stable forces that continuously influence and structure juvenile walleye pollock aggregations through predator avoidance and evasion. Foraging behaviour may also be important in structuring the fish aggregations but only during times when prey availability is relatively high.

Acknowledgements

I thank the scientists and crew of the NOAA ship *Miller Freeman* for their hard work in helping with the data collection. I thank Julian Olden for his multivariate input and Chris Wilson, Kevin

Bailey, Alex De Robertis, Anne Hollowed, John Horne, Paul Walline, and two anonymous reviewers for valuable comments and remarks on earlier drafts of this paper.

Table 5. Survey areas, survey pass number, number of hauls, and number of analyzed aggregations from Shelikof Strait and East Kodiak (Chiniak and Barnabas Troughs).

Study year	Survey pass	No. hauls	No. schools	No. hauls	No. schools
		Shelikof Strait			
1995	1	19	483	-	-
1996	1	36	867	-	-
1997	1	28	812	-	-
	2	2 [a]	173	-	-
		East Kodiak			
		Chiniak Trough		Barnabas Trough	
2000	1	7	142	12	- [b]
	2	13	81	10	- [b]
2001	1	8	274	12	131
	2	6	267	9	104
	3	10	177	10	120
	4	-	-	2	169
2002	1	8	216	12	104
	2	14	215	10	107
	3	12	205	15	148
	4	-	-	2	179

[a] Pass 2 was a partial pass that only surveyed transects north of 57˚ 20' N.

[b] No juveniles were detected in Barnabas Trough in 2000.

Table 6. Minimum and maximum (pre-log-transformed) values of fish aggregation descriptors and bio-physical factors, and loadings of the first and second RDA axes. Eigenvalues and the percent of variance explained by the RDA are given.

		East Kodiak				Shelikof Strait			
		Min	Max	RDA1	RDA2	Min	Max	RDA1	RDA2
Aggregation Descriptors	Length (m)	16	7115	-0.65	0.32	2	38121	-0.76	0.40
	Height (m)	4	162	0.25	-0.31	4	124	1.101	0.23
	Fractal Dimension	1.06	1.99	-2.13	0.63	1.02	1.99	-1.64	-0.19
	Density (fish/10^3m^3)	0.53	1.30×10^5	1.72	0.95	0.79	5.07×10^4	0.85	-0.29
Bio-physical Factors	Aggregation Depth (m)	16	239	-0.69	-0.67	67	244	-0.68	0.58
	Temperature. (^oC)	5.25	10.26	-0.20	0.61	2.88	5.24	0.27	0.31
	Fish Age (years)	2	3	0.39	-0.85	1	3	0.73	0.63
	Body Condition	-0.09	0.11	0.35	-0.003	-0.29	0.19	0.05	0.73
	Eigenvalue			0.31	0.15			0.21	0.01
	% Variance			83.88	15.72			93.24	6.10

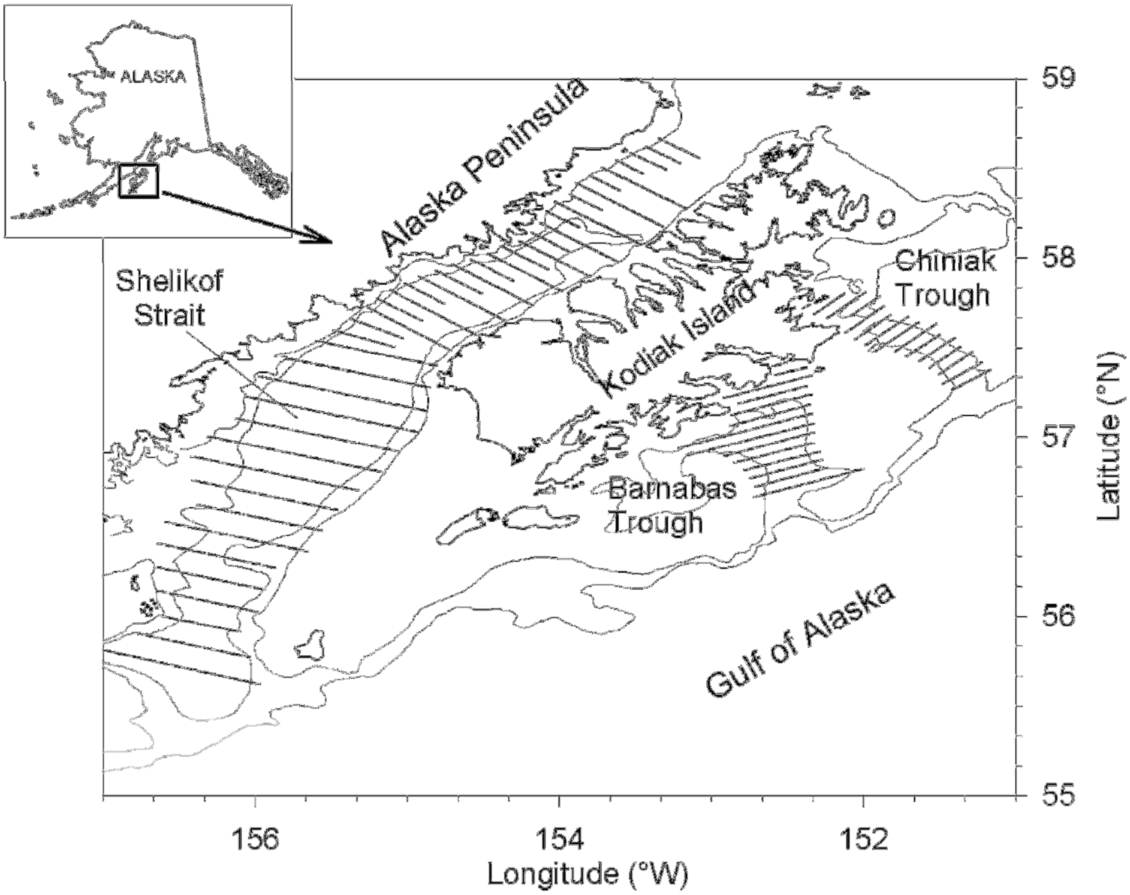

Figure 8. The two survey areas near Kodiak Island, Alaska: East Kodiak (Chiniak Trough and Barnabas Trough) surveyed in 2000-2002 and Shelikof Strait surveyed in 1995-1997. Lines indicate acoustic-trawl survey transects.

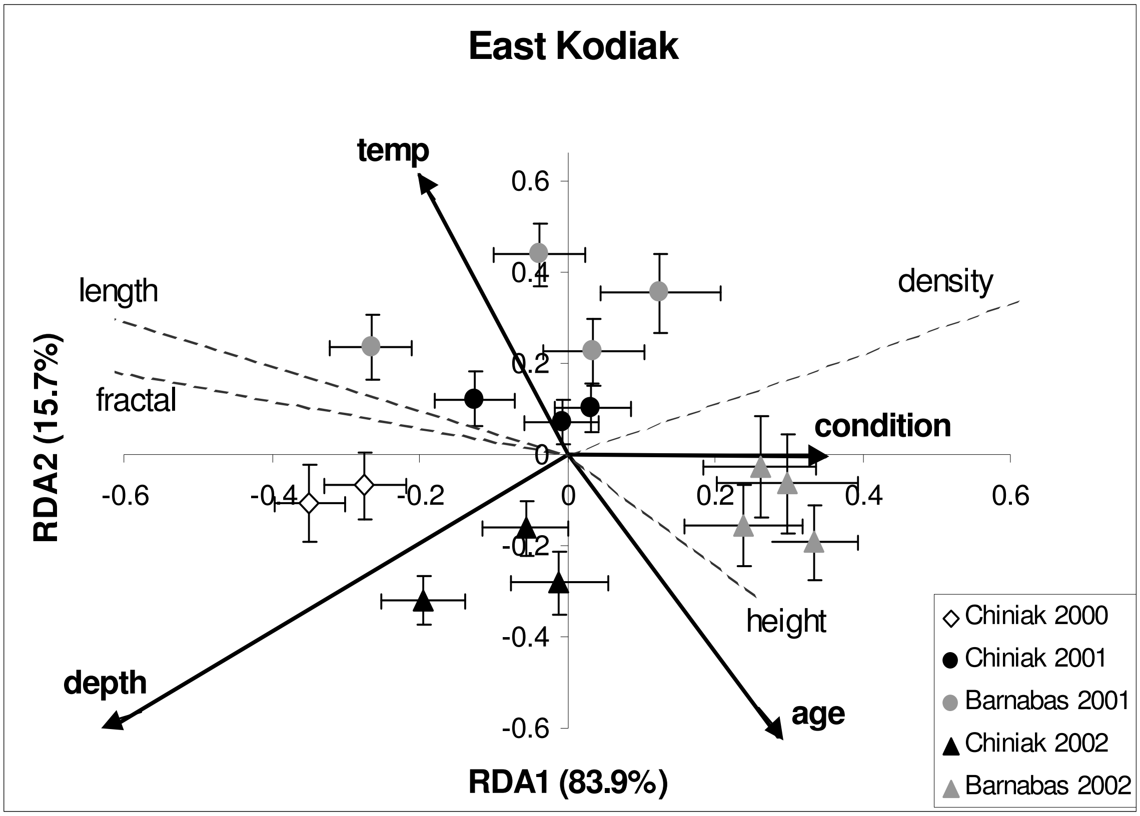

Figure 9. Redundancy analysis diagram showing the estimated distribution center for each East Kodiak trough-pass combination in ordination space. Error bars represent 95% confidence intervals about the mean of each distribution. Identical symbols are indicative of multiple survey passes. The dashed lines represent the aggregation descriptor gradients, and the solid lines represent the bio-physical gradients.

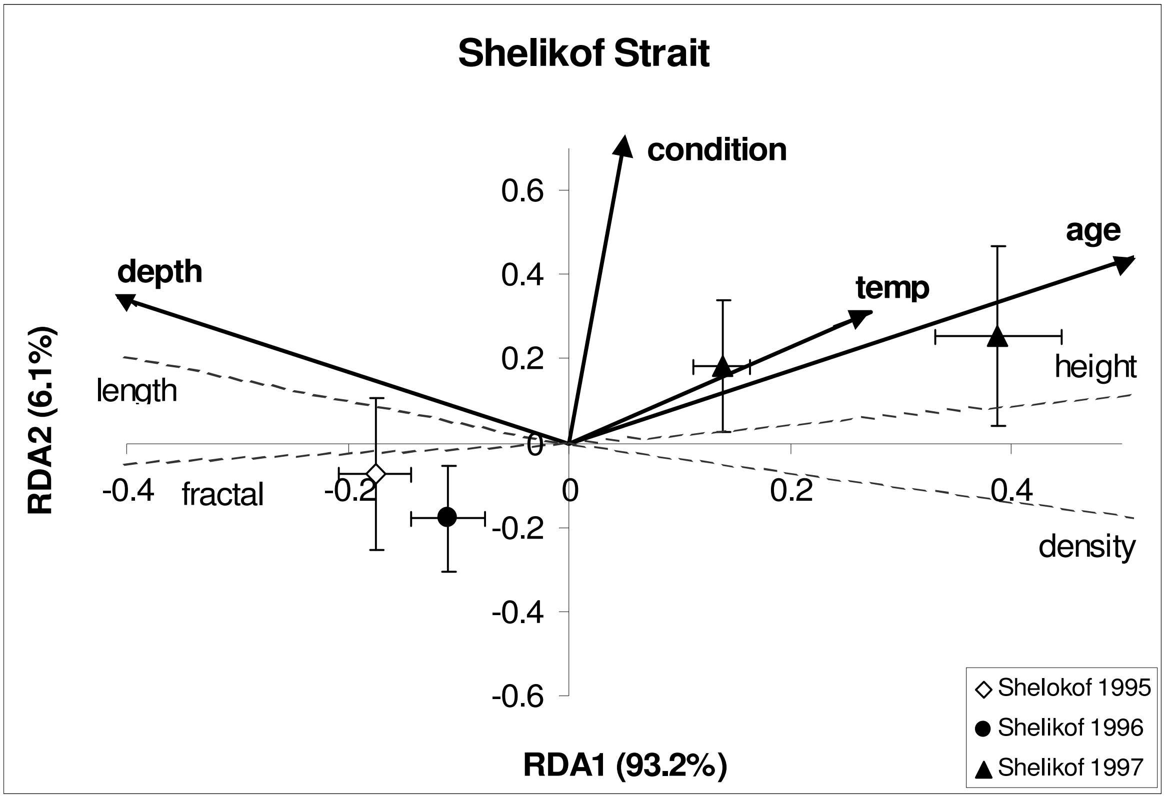

Figure 10. Redundancy analysis diagram showing the estimated distribution center for each Shelikof Strait pass in ordination space. Error bars represent 95% confidence intervals about the mean of each distribution. Identical symbols are indicative of multiple survey passes. The dashed lines represent the fish aggregation descriptor gradients, and the solid lines represent the bio-physical gradients.

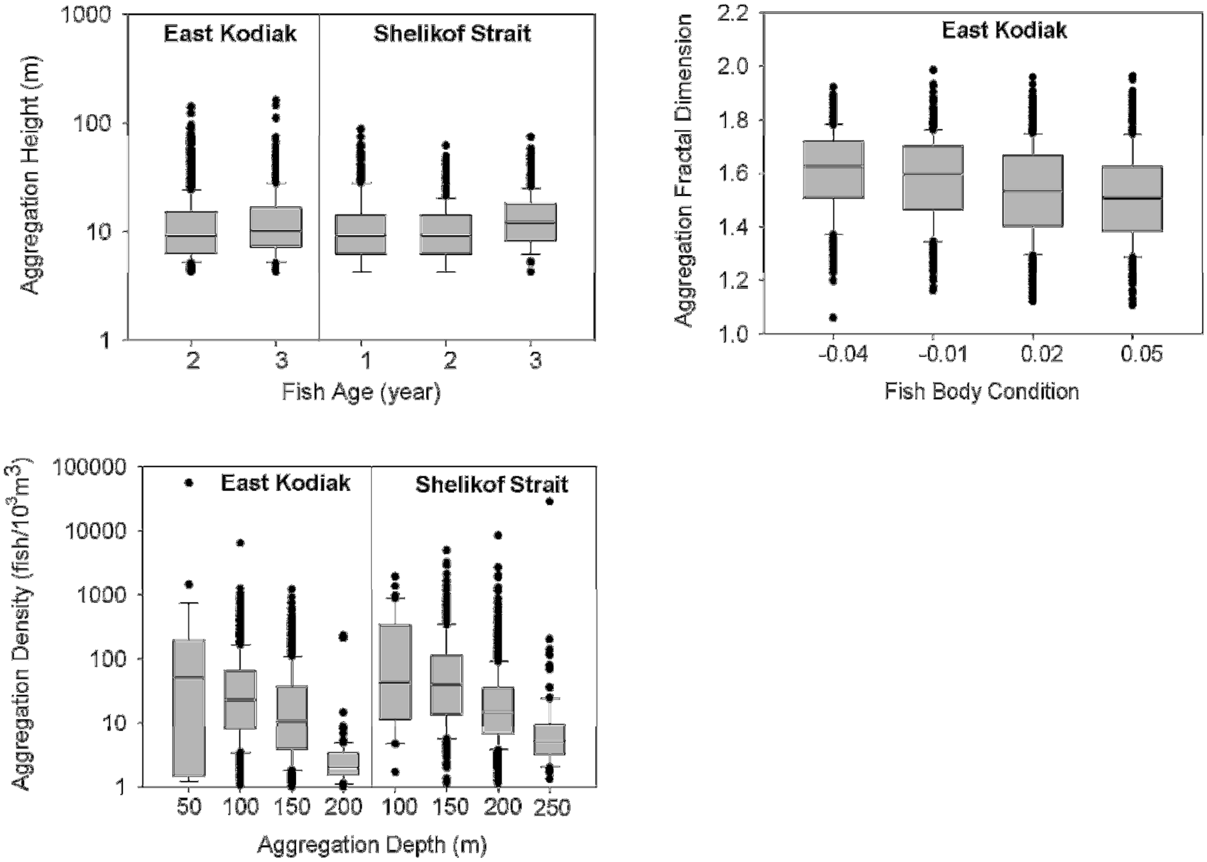

Figure 11. Box plots of the (pre-log-transformed) values of fish aggregation descriptors and bio-physical factors showing the associations between fish age and aggregation height, aggregation depth and aggregation density, and body condition of the fish and aggregation fractal dimension. The box plots show the median, 10th, 25th, 75th, and 90th percentiles. Note the use of a logarithmic scale on the y-axis in two of the plots.

Group responses of juvenile walleye pollock to their environment

Abstract

Size and shape patterns of fish groups are collective outcomes of interactions among members. Consequently, when any member responds to changes in the environment, their internal state, and their external state, group-level patterns are often affected. To determine how groups of fish respond to their environment, and whether the response is influenced by a component of their external state (i.e., fish age), we used a multibeam system to collect three-dimensional grouping characteristics of 5 age classes of juvenile walleye pollock (age 1, age2, age 3, mixed ages 1 and 2, and mixed ages 2 and 3) across the eastern Bering Sea shelf over two consecutive years (2009-2010). Grouping data were expressed as metrics that described group size (length, height), shape (roundness, spread), internal structure (density, internal heterogeneity), and position (depth, distance off bottom). Ecological data (densities of predators and prey – adult walleye pollock and euphausiids, respectively) were collected with a EK60 vertical echosounder, and physical data (water temperature measurements) were collected with temperature-depth probes. The juvenile pollock maintained a relatively constant shape and size-dependent density (fish/fork length^3) among age classes. Unlike the physical environment, the densities of predators and prey did not exert a significant influence on group structure, although they may have influenced the distribution of age classes across the eastern Bering Sea shelf and triggered mixed-age grouping. Mixed-age groups did not exhibit more internal heterogeneity than pure-aged groups. This suggests there is no structural cost to forming mixed-age groups.

Introduction

The aggregation of animals is ubiquitous in nature (Allee 1927). Safety from predators (e.g., Hamilton 1971, Watt et al. 1997, Nøttestad and Axelsen 1999, Ioannou et al. 2012) and increased foraging opportunities and success (Krebs et al. 1972, Pulliam and Millikan 1982, Pitcher et al. 1982, Waite 1982, Baird et al. 1991) are among two of the principal benefits to group living (Rubenstein 1978, Krause and Ruxton 2002). Both these benefits provide a functional advantage to the individuals therein. As group size increases, predators are more likely to be confused by many moving targets (Milinski and Heller 1978, Jeschke and Tollrian 2007), and they are less likely to eat any particular individual (Turner and Pitcher 1986) assuming group detection rate is unaltered (Krause et al. 1998). Additionally, as group membership increases, overall vigilance is increased as there are “many eyes” to scan the environment for predators thereby reducing the vigilance effort of a single individual (Powell 1974, Lima 1995). A decrease in individual vigilance allows members to spend more time on other activities, such as foraging (Pulliam 1973, Morgan and Colgan 1987, Morgan 1988), and increased membership can also lead to faster detection of food (Pitcher et al. 1982).

Natural selection can act on groups that have functional organization (Wilson 1997) by acting on the individual traits and behaviors of the group members. That is, if one group outperforms or outcompetes another group, the fitness of the individuals in the more competitive group is increased, because those individuals survive and reproduce more than individuals in underperforming groups (Sober and Wilson 1998). For example, members benefit from greater group density when a predator is nearby (Pitcher and Parrish 1993). However, individuals reduce distances to their neighbors to increase their personal fitness, not to increase group fitness (Hamilton 1971, Ioannou et al. 2007), although the group's fitness is consequently increased. Likewise, when hungry or in the presence of prey, members often disperse from the safety of their group (Morgan 1988, Godin and Smith 1988) to increase fitness by reducing resource competition (Eggers 1976, Townsend 2008). Shifts toward a more favorable group structure are thus the result, in part, of individuals responding to their particular interpretation of the local environment (Bertrand et al. 2006, Gerlotto et al. 2006).

Individuals with preexisting knowledge about their environment can influence the behavior of conspecifics (e.g., Olla and Samet 1974, Waite 1982, Baird et al. 1991, Ryer and Olla 1991, 1992, Laland and Williams 1997, Lachlan et al. 1998) which in turn influences the behavior of the group (e.g., Romey 1996, Reebs 2000, Brown and Laland 2002, Huse et al. 2002, Reader et al. 2003, Couzin et al. 2005, Mirabet et al. 2008). More specifically, individuals are able to transfer information about their environment through decentralized interactions, and these interactions produce group-level patterns and structure (Couzin and Krause 2003) –i.e., "emergent properties" of the group (Clark et al. 1997) –including group size, shape, and architecture (Parrish and Edelstein-Keshet 1999). In addition to the local environment and behaviors of their neighbors, the reactions of group members are also dependent on individual internal state (e.g., physiology) and external state (e.g., size; Couzin and Krause 2003). Individuals of different ages, sizes, or species likely have different internal states, which can influence large scale grouping patterns or small scale interactions among members. For example, some species of fish form groups when young but individuals lead solitary lives as adults (Keenleyside 1979). In other species, the adults form larger and less dense groups than do the juveniles (Muiño 2003, Wilson et al. 2003). Individuals of different ages, sizes, or species likely have different physical limitations (e.g., average or maximum speed), which can influence the emergent properties of a group (Grünbaum et al. 2005, Viscido et al. 2007). When individuals with different physical limitations are found in the same group, group speed and motion can be altered and sorting can occur (Romey 1996, Hemelrijk and Kunz 2004).

One way to understand whether specific group structures incur functional advantages to its members is to track the moment-to-moment patterns of individuals and quantify these trajectories and associated emergent properties (Parrish et al. 2002). Many simulation studies have connected specific individual behaviors with emergent properties (e.g., Hemelrijk 2000, Couzin et al. 2002, Hemelrijk and Kunz 2004, Viscido et al. 2005, 2007), but it is often difficult to determine which behaviors are biologically relevant. Few laboratory studies have made these connections (but see, e.g., Tien et al. 2004, Viscido et al. 2004, Grünbaum et al. 2005, Stienessen and Parrish 2013) because of the difficulty tracking relatively large, fast animals (e.g., fish or birds) over extended periods of time (Parrish et al. 2002). Quantification of emergent properties –i.e., describing group structure with size (e.g., group length, height), shape (e.g., group perimeter-to-area ratio) and density measurements (e.g., number of individuals/area) - has proved a useful way to characterize *in situ* responses of fish to their environment. Such measurements have been used to depict predator-prey interactions (DeBlois and Rose 1995, Mackinson et al. 1999) and migration patterns (Rose 1993). They have been used to describe group reactions to commercial fisheries (Wilson et al. 2003, Walline et al. 2012) and to changes in the physical environment (Nero and Magnuson 1989, Barange 1994, Swartzman et al. 1994, Soria et al. 2003). Measurements of emergent properties have also been used to delineate sympatric species or age classes, with various degrees of success (Barange 1994, Haralabous and Georgakarakos 1996, Scalabrin et al. 1996, Lawson et al. 2001, Iglesias et al. 2003, Kang et al. 2006). However, emergent properties do not always have a direct relationship to the environment (Swartzman 1997, Soria et al. 2003). For example, the physical environment often influences the grouping of fish at larger regional scales (e.g., clusters of groups or meso-scale fish layers; Swartzman 1997, Swartzman 2001, Bertrand et al. 2005, Trenkel et al. 2009), and emergent properties may reflect the unexpected result of individual responses to a secondary, and even inconsistent, influence (Parrish and Edelstein-Keshet 1999). Without corresponding knowledge of the moment-to-moment reaction of individuals to their neighbors, it is difficult to know whether these types of *in situ* emergent properties are a response to the local environment or are purely epiphenomena (Parrish et al. 2002).

There is evidence to suggest that the distribution of fish density within a group, that is "internal heterogeneity", is indicative of interactions between individual fish (Gerlotto and Paramo 2003, Gerlotto et al. 2006, Paramo et al. 2007), and internal heterogeneity can be observed at the same scale as other measurements of *in situ* emergent properties. As group size increases, individuals are blocked from direct access to most other group members, so they interact with only a few of their closest neighbors (Huse and Wissel 1994, Viscido et al. 2005), often showing preference for those that are familiar, similar-sized, and of the same species (Lachlan et al. 1998, Magurran and Seghers. 1994, Krause et al. 2000, Svensson et al. 2000, Hoare and Krause 2003). This can translate into the formation of subgroups (Hemelrijk and Kunz 2004) and likely areas of high-density nuclei and unfilled vacuoles (Gerlotto and Paramo 2003) within larger cohesive groups. Internal heterogeneity can also be indicative ecological interactions, most notably predator-prey (xx). For example, Gerlotto et al. (2006) were able to detect a 'wave of agitation' that spread through the school when a predator approached and noted the internal school structure was more homogeneous (i.e., had more consistent interfish distances between members) after the disturbance. These findings suggest that group internal heterogeneity can potentially be indicative of interactions between individuals and can be used to quantify ecological or other environmental disturbances.

The goal of this study was to connect *in situ* emergent group properties, including internal heterogeneity, to the local environment. To do this, we took advantage of data collected with an ME70 multibeam system during an ongoing fishery monitoring program of walleye pollock, *Gadus chalcogrammus* (formerly known as *Theragra chalcogramma*; Page et al. 2013) in the eastern Bering Sea. The ME70 multibeam sonar can insonify entire groups *in situ,* effectively allowing us to examine three-dimensional group structure of juvenile walleye pollock as a function of ecological and physical factors. Walleye pollock (hereafter 'pollock') are one of the most abundant and commercially important fish in the Bering Sea (Kim 1990). Although adults are semi-demersal and form aggregations that can extend for miles near the seafloor, juveniles are found throughout the water column in discrete groups with well-defined edges (Wilson et al. 2003, Walline et al. 2012) that allow for readily measured emergent properties (Reid et al. 2000). Additionally, age classes of juvenile walleye pollock move though the population over consecutive years resulting in multiple co-existing cohorts of juvenile pollock (e.g., Stienessen and Wilson 2008, Honkalehto et al., 2010, 2012). This allows for examination of the role that external state (i.e., age, and thus size, differences) plays on the relationship between emergent group properties and basic individual grouping behaviors.

We extracted and quantified emergent properties of juvenile pollock groups from the data collected with the ME70 multibeam sonar to test the following hypotheses: First, given that predator avoidance and foraging success provide two of the main functional benefits to group living, we expected that local predator and/or prey density would affect the short-term responses of fish as evidenced by changes in group external (i.e., size and shape) and internal (i.e., density and internal heterogeneity) structure. Second, because environmental measures have been shown to influence species distribution (e.g., pollock and thermoclines: Traynor 1986, Swartzman et al. 1994) but not group metrics (Swartzman 1997, Soria et al. 2003), we expected that measures of the physical environment (i.e., temperature and shelf depth) would influence group positions rather than group structure. And third, because sorting can occur in groups with different size fish (Hemelrijk and Kunz 2004), we expected that measures of structural heterogeneity would be associated with differences in membership (i.e., fish age/size).

Methods

Study area

Grouping patterns of juvenile pollock were described for the eastern Bering Sea shelf– between approximately 172 °W to 180°W –during the summers of 2009 and 2010 (Fig. 12). The aggregations were observed during acoustic trawl surveys of the area (Honkalehto et al. 2010, 2012). The bottom depths within the surveyed area ranged between 100-150 m. Strong year classes of juvenile pollock were detected, which provided an opportunity to study group patterns of fish as a function of age.

Field methods

Acoustic trawl surveys were conducted onboard the NOAA research ship *Oscar Dyson* and consisted of a series of north-south parallel transects uniformally spaced 20 nmi apart over the Bering Sea shelf from Port Moller, Alaska, across the U.S.-Russia Convention Line to the area around Cape Navarin, Russia (Fig. 12; Honkalehto et al. 2010, 2012). Acoustic data were collected during daylight hours (typically between 6:00 and 24:00 local time) with a Simrad ER60 scientific echo sounding system (Simrad 2004, Bodholt and Solli 1992), which used 5 split-beam transducers (18, 38, 70, 120, and 200 kHz) and with a Simrad ME70 multibeam system (Trenkel et al. 2008). The ME70 multibeam system was configured to operate with 31 symmetrical split-beams, the middle beam being vertically-oriented. The beams in this configuration ranged from a spherical 2.8° nadir beam (steered at 0°) operating at 117 kHz to two 4.5° alongship by 11.0° athwartship ellipsoidal beams steered at ± 66° and operating at 75 kHz (Fig. 13). This configuration reduced the side lobes to around -70 dB while allowing the element beam pattern to minimize grating lobe problems (i.e., it reduced the lobes that are not the main detection lobe; Trenkel et al. 2008). This configuration also allowed for the collection of data with a large signal-to-noise ratio and minimized the pulse duration, which maximized along-beam resolution and minimized the acoustic dead zone (Ona and Mitson 1996). Acoustic data collected with the ER60 were used to obtain shelf depth and juvenile pollock predator and prey densities, and acoustic data collected with the ME70 were used to obtain metrics describing juvenile pollock grouping patterns (Fig.14).

The ME70 system was calibrated at the beginning of the 2009 survey. We were unable to successfully calibrate the 2 outermost beams on each side of the ME70 system. To avoid any confounding effects, data collected by these 4 beams were not used in this study. This effectively made the beam configuration limited to a 110° swath (steered from ±55°), with outer beamwidths of 4.1° alongship by 6.5° athwartship that operated at 80 kHz (Fig. 13). The ER60 system was calibrated at the beginning and end of both surveys, and during the middle of the 2009 survey (Honkalehto et al. 2010, 2012).

The ER60 and ME70 systems transmitted sequentially to avoid system interference. The ping rate for both systems was 1 ping/4 s, and the ship averaged 11 knots. This provided a nominal along track resolution of approximately 1 ping/ 22 m. Only data collected deeper than 16 m and 20 m by the EK60 and ME70, respectively, were used because of the combination of placement of the transducers on the centerboard or hull and the transmit blank zones (Simmonds and MacLennan 2005).

Biological samples were collected with a pelagic trawl (Honkalehto et al. 2010, 2012) to confirm the identity of the species attributed to specific acoustic backscatter (i.e., acoustic reflection, or Sv: the mean volume backscattering strength; MacLennan et al. 2002) of midwater organisms. Biological samples also provided length, weight, and age composition of pollock. Trawl hauls were typically conducted in areas of high backscatter when the backscatter was assumed to be pollock. Catches of pollock were sampled to determine fork length (FL) to the nearest 1.0 cm, body weight to the nearest 2.0 g, and age of the fish. A Methot trawl was used to target midwater macro-zooplankton, age-0 pollock, and other larval fishes (Honkalehto et al. 2010, 2012). Trawl catch information was used to convert acoustic backscatter collected with the EK60 to biomass estimates, which were binned at 0.5 nmi horizontal resolution using standard protocols (Honkalehto et al. 2008 and Ressler et al. 2012).

Temperature profiles were obtained with a temperature-depth probe attached to the trawl headrope. Expendable bathythermograph probes and conductivity-temperature-depth casts were also used to collect water temperature and salinity profile data at selected locations throughout the study area (Honkalehto et al. 2010, 2012).

Defining and isolating a group

Juvenile pollock backscatter (Fig. 14b) collected with the ME70 was isolated from other backscatter using Fledermaus midwater software (http://www.qps.nl/display/fledermaus/main, Version 7.3.2b, Build 443Beta, 64 bit Edition, accessed January 2014). A threshold sensitivity analysis was conducted to determine the most appropriate processing threshold to use when isolating juvenile walleye backscatter (i.e., - 52 dB; Appendix). Once juvenile pollock backscatter was isolated from other backscatter, it was attributed to one of 5 age classes based on haul data: age 1, age2, age3, mixed ages 1-2 (hereafter referred to as 'mix 12'), and mixed ages 2-3 (hereafter referred to as 'mix 23'). To ensure that the correct age of pollock was attributed to the backscatter, only acoustic data that were collected consistently (i.e., no gaps in backscatter lasting more than 0.5 nmi) up to 15 nmi from a haul location where 100% of the trawl contained only one age class were used in this study (Williamson and Traynor 1996, Walline 2007), representing approximately 17% and 11.5% of the transects surveyed in 2009 and 2010, respectively.

Backscatter (Sv) values needed to be adjusted to correct for the effects of fish orientation with respect to the orientation of the ME70 beam-pointing directions (Towler et al. 2003, Hazen and Horne 2004, Cutter and Demer 2007, Holmin et al. 2012). This was done by using average Sv values per beam (Appendix), with the assumption that average Sv should be the same at any horizontal (i.e., athwartship) distance from the ship over the course of the entire survey. We classified the adjusted Sv values (Svc) into juvenile pollock groups based on 4 user-defined input parameters: minimum connected distance, minimum connected size, maximum horizontal linking distance, and maximum vertical linking distance. The distance between two Svc values must be equal to, or less than, the minimum connected distance for the backscatter to be considered part of the same group. A group must have at least the minimum connected size to be considered an actual group. If the distance between any two groups is more than the maximum linking distance, the groups are considered separate from one another. These 4 parameters were examined over a range of values (initial values chosen based on Stienessen and Wilson 2008) and final values were chosen based on their ability to provide the best definition of a juvenile pollock aggregation when compared by eye to the original echogram (10 m, 25 measurements, 25 m, and 5m, respectively). These parameters likely contain substantial and unknown biases, and it has been shown that changing the values can affect the results (Burgos and Horne 2007). However, if they are kept constant, they still provide useful comparative information about the variability of fish group structure (Freon et al. 1996, Reid et al. 2000). Once juvenile pollock adjusted backscatter was classified into groups, we determined if the group had been insonified by either outermost beam of the 110° swath. If so, the group was omitted from further analysis, because of the difficulty verifying whether the group had been wholly insonified. This resulted in 6% of the groups being omitted: 42% of the omitted groups were shallower than 50m, and 56% of the omitted groups were between 50-100 m.

Group metrics

External group structure was described with several size metrics: group length (m), width (m), height (m), surface area (m^2), and volume (m^3; Table 7). Group length, width, surface area, and volume were used to calculate two shape metrics: group roundness and spread (m^{-1}; Table 7). Roundness is the ratio of group length to group width and represents a two-dimensional shape. A smaller roundness value indicates the group is more circular in the horizontal dimension, whereas a larger value indicates that the group is more oblong in the horizontal dimension. Spread is the ratio of group surface area to group volume. For groups with a similar volume, a smaller spread value indicates a rounder shape; conversely, for a given shape, spread is inversely proportional to size. There was a high degree of correlation between group length, width, surface area, and volume ($r > 0.88$ in all cases), and these metrics did not provide any additional information from one another in any of the analyses. Length was thus used as the representative of these four metrics.

Internal group structure was described with group density, both as a function of a fixed volume (fish/m^3) and fish body length (fish/FL^3; accounting for differences in fish fork length, a proxy for fish age: Table 7). The horizontal and vertical density variances were also calculated. To account for the high degree of correlation between density variance and group size ($r = 0.93$ for horizontal variance and group length, and $r = 0.92$ for vertical variance and group height), the horizontal variance was divided by group length and vertical variance was divided by group height to ultimately produce horizontal internal heterogeneity (m) and vertical internal heterogeneity (m), respectively (Table 7). The “corrected” values represent density variance per unit length. A series of modified equations proposed by Diner (2001) were applied to group length, width, roundness, and density measurements to correct for the effects of beam spreading (Appendix), and these corrected metrics were used in further analyses.

Finally, the position of the group in the water column was described with several positional descriptors, based on the group’s density-dependent center of gravity: group depth, distance off bottom, and range from the ship (Table 7). We examined all descriptors as a function of horizontal distance from the vessel (Table 7) via three depth bins: 20-50 m, 50-100 m, and 100-150 m (e.g., Gerlotto and Paramo 2003, Soria et al. 2003, Gerlotto et al. 2004) and determined there was no evidence for vessel avoidance in our data (DeRobertis and Handegard 2012).

Environmental factors

Two categories of environmental factors were examined: the ecological environment (i.e., predator and prey densities) and the physical environment (i.e., water temperature and shelf depth). Predator and estimates were associated with each group of juvenile pollock by matching the position of the group to the nearest (< 0.25 nmi) biomass estimates of adult pollock (sA, the nautical area scattering coefficient, m^2mni^{-2} (MacLennan et al. 2002)), one of the principal predators of juvenile pollock (Bailey 1989). Likewise, prey estimates were associated with each group of juvenile pollock by matching the position of the group to the nearest (< 0.25 nmi) biomass estimates of euphasuiids (kg), one of the main prey items of pollock (Dwyer et al. 1987, Aydin and Mueter 2007). Three water temperature measurements were associated with each group of juvenile pollock (based on the group's density-dependent center of gravity): sea surface temperature, temperature at the depth of the group ("group temperature"), and bottom temperature. Summer sea surface and bottom temperatures are related to the presence or absence of sea ice during the previous winter (Stabeno et al. 2012) and characterize larger-scale temperature patterns over the eastern Bering Sea; whereas group temperature describes the water temperature at the exact depth of the group. These values were determined by matching the surface depth, depth of the group, and depth of the seafloor directly below the group to the corresponding temperatures from the nearest (< 15 nmi) vertical conductivity-temperature profile, which was conducted within a few hours of group insonification.

Statistical analyses

Because walleye pollock are known to exhibit diel grouping patterns (Ryer and Olla 1998, Fréon et al. 1996, Wilson et al. 2003), time of day was used as a covariate in analyses of covariance tests to examine whether juvenile pollock maintained consistent group structures among age classes. One test was performed on each external and internal metric. To test whether juvenile pollock of different age classes were found in similar environments, a single-factor ANOVA was conducted on each positional metric and environmental factor (Zar 1996). Tukey's Honestly Significant Difference tests were then used to check for differences in each group metric and environmental factor based on juvenile pollock age class (Zar 1996).

Because some of the environmental factors in this study (e.g., water temperature) likely influence other environmental factors (e.g., predators) in addition to potentially influencing juvenile pollock group metrics, a path analysis was used to determine the influence of environmental factors on group metrics within an age class. Path analysis is a structural equation model that tests relationships among measured variables (Kline 1998) and determines whether there are any meaningful patterns in the data by examining the overall impact of one variable on another by considering both the direct (e.g., impact of variable 1 on variable 3) and indirect (e.g., impact of variable 1 on variable 3 via variable 2) paths (Streiner 2005). Path analysis is an extension of multiple regression, and it allows some variables (i.e., variables in the middle levels) to be both independent and dependent, and the strength of each of the indirect pathways is calculated as the product of the path-coefficients along that pathway (Streiner 2005). For this study, two *a priori* models were created. The first causal model incorporated four levels of variables. The most basic level involves the depth of the Bering Sea shelf, the second level contains the water temperature, the third level contains the ecological factors (i.e., predator and prey), and the fourth level contains the vertical position of the group in the water column (i.e., group depth and distance off bottom; Fig. 15a). The second causal model incorporated five levels of variables: those levels used in the first model plus a fifth level which contains group metrics. Because school depth and distance off bottom are collinear, only school depth could be included in the fourth level of the model (Fig. 15b). Both models assume that influences move from bottom to top in the diagram and that each lower level variable has a path connecting it to each higher level variable; however, there is no connecting path between variables on the same level. The models assume that temperature values are dependent on water column depth (Coachman and Charnell 1979, Kinder and Schumacher 1981, Schumacher and Stabeno 1998) and in turn influence the distribution of juvenile and adult fish as well as zooplankton (Swartzman et al. 1994, Bertrand et al. 2005, Ressler et al. 2014). Additionally, it assumes that the presence of predators (i.e., adult pollock) and prey (i.e., euphausiids) influence the position of juvenile pollock in the water column (Olla and Davis 1990, Sogard and Olla 1993, Swartzman 2001, Benoit-Bird 2009). Within each age class, the path analysis was done on each group metric.

In all analyses, transformations were first done on group metrics to stabilize the variance. To avoid the assumption that significant associations equate to meaningful associations with such large sample sizes, effect sizes (i.e., total direct + indirect standardized regression coefficients) were used in lieu of t-values and p-values (Cohen 1988, Rosnow and Rosenthal 1996) in the path analyses. Results from Tukey's Honestly Significant Difference tests were considered significant at alpha ≤ 0.05.

Results

Juvenile pollock groups detected in 2009 were classified into age 1 (n = 459), mix 23 (n = 1,259), or age3 (n = 1,256) age classes, and the groups detected in 2010 were classified into age 1 (n = 19), mix 12 (n = 1,334), or age2 age classes (n = 1,406). Although age1 and age2 fish were present both years, there was no appreciable overlap in age classes between the two years. In 2009 age 2 fish were only observed in mix23 groups. In 2010 age 1 fish were only observed in 19 pure-aged groups or as part of mix12 groups; consequently, pure-age 1 groups from 2010 were added to 2009 for all analyses.

Age2 fish formed shallow groups (Fig. 16a) in deep water (Fig. 16b), compared to the other age classes. Age1 fish also tended to aggregate relatively close to the surface (Fig. 16a), but in relatively shallower areas of the shelf (Fig. 16b). The other three age classes –mix12, mix23, and age3 fish – aggregated close to the bottom (Fig. 16c) in deeper water (Fig. 16b).

Effects of predator and prey densities on group structure

Densities of adult pollock and euphausiids had little influence on the short-term patterns of juvenile pollock within an age class based on changes in juvenile group metrics and vertical position in the water column (Table 8, Fig. 17). There were only two instances where an ecological factor had an effect on a group metric (i.e., adult pollock density on mix23 group height and euphausiid density on mix23 group density; Fig. 17b), and only one instance where a biological factor had an effect on group vertical position (i.e., euphausiid density on age2 group depth; Table 8); and in all instances the effect was small. However, densities of adult pollock may have influenced longer-term responses of juvenile pollock. Mix12 groups were found in areas with considerably higher average adult pollock densities ($\bar{x}$ = 2800 Sa) compared to all other age classes ($\bar{x}$ = 200-1200 Sa; Fig. 16d) and they formed significantly bigger groups (Fig. 18a,b,d). In 2009, mix 23 groups were found in areas with the highest densities of adult pollock and formed groups that were significantly more oblong than the other age classes (Fig. 16c).

There is also some evidence that densities of euphausiids influenced the distribution of age classes across the eastern Bering Sea shelf. Older juveniles were detected in areas with significantly higher densities of euphausiids. Mix23 and age3 groups were in areas of higher euphausiid densities than were age1 groups in 2009; and age2 groups were in areas with higher densities of euaphusiids than were mix12 groups in 2010 (Fig. 16e).

Effects of water temperature and shelf depth on group structure

Although juvenile pollock group structure was not different across different densities of adult pollock and euphausiids, it did change in response to the physical environment. Group depth influenced juvenile pollock group structure for all age classes except mix23 fish (Fig. 17b). The group structure of mix23 fish was instead influenced by bottom temperature. Groups became vertically shorter, denser, had more variation in horizontal density as group depth increased (i.e., for age1, mix12, age2, and age3 fish) or bottom temperature decreased (i.e., for mix23 fish), although the degree of this response varied by age class (Fig. 17b).

As expected, the physical environment influenced the location of juvenile walleye pollock groups in the water column. Within an age class, the groups were found further off bottom as the shelf got deeper (Table 8). Fish moved away from the bottom (i.e., age1, mix12, mix23, and age3 fish moved higher in the water column) or surface (i.e., mix12 and mix23 fish moved deeper in the water column) when the respective waters became cooler (Table 8). Additionally, the physical environment influenced the location of age classes: within each year, the older juveniles formed groups in significantly cooler waters compared to the younger fish. Mix23 and age3 groups were in areas with cooler group and bottom temperatures than were age1 groups in 2009; and age2 groups were in areas with cooler surface, group, and bottom temperatures than were mix12 groups in 2010 (Fig. 16f,g,h).

Effects of juvenile pollock age class on group structure

Horizontal internal heterogeneity and volume-dependent density (fish/m^3) were the two metrics that changed as a function of fish age. As fish aged, they formed significantly less dense groups (Fig. 18e), and groups of mix23 and age3 fish had significantly greater estimates of horizontal internal heterogeneity than that of the three younger age classes (Fig. 18g).

There were no obvious linear trends in the other group metrics relative to juvenile pollock age (Fig. 18); however, juvenile pollock maintained a relatively constant shape and size-dependent density (fish/FL^3) among age classes. Roundness was constant across all age groups ($\bar{x}$ = 1.7-1.8; Fig. 18c), except mix 23 ($\bar{x}$ = 1.9), and not correlated to group size (r = 0.35, -0.14, and -0.11, for length, height, and spread, respectively), which suggests a similar horizontal shape. Additionally, the inverse trend that existed between group height and group spread among age classes (r = -0.97) suggests a similar overall shape (Fig. 18b,d). Although volumetric density (fish/m^3) decreased with an increase in age class (Fig. 18e), there were no significant differences in average interfish distances relative to fish body size (i.e., fork length) among all age classes of juvenile pollock (fish/FL^3; Fig. 18f).

Discussion

This work suggests that within an age class, densities of adult pollock and euphausiids had little effect on the short-term patterns of juvenile pollock as evidenced by lack of associated changes in group external structure (i.e., size and shape), internal structure (i.e., density and internal heterogeneity), and vertical position in the water column. Given that predator avoidance and foraging success provide two of the main functional benefits to group living (Hamilton 1971, Krebs et al. 1972), it is surprising that this known predator (Bailey 1989) and important prey species (Dwyer et al. 1987, Aydin and Mueter 2007) had little correlation with the measured group metrics. However, juvenile pollock have other predators (e.g., arrowtooth flounder; Aydin and Mueter 2007, Aydin et al. 2007, Chen et al. 2012) and prey (e.g., copepods; Dwyer et al. 1987) that were not considered for this study. Additionally, pollock undergo a transition from primarily daytime feeding larvae (Canino and Bailey 1995) to nocturnal feeding juveniles (Brodeur et al. 2000). This suggests that the juvenile pollock likely feed on euphausiids at night, which can help to explain the lack of association in our study between euphausiid density and juvenile pollock group structure. We examined groups that were insonified only during daytime hours.

This work does suggest that densities of adult pollock may influence longer-term patterns of juvenile pollock. Relative to the other age classes, mix12 groups were found in areas with the greatest densities of adult pollock, and they formed the largest groups. Large groups are an antipredator tactic often utilized by fish (Pitcher and Parrish 1993). Additionally, mix23 groups were found in areas with the greatest densities of adult pollock in 2009, and they formed the most horizontally oblong groups. An oblong shape can be indicative of a dynamic shift in behavior; that is, it can suggest fish movement. Groups of round sardinella, *Sardinella aurita*, close to a vessel have been shown to display vessel avoidance behavior by forming more horizontally oblong groups compared to those sardinella groups further away from the vessel (Gerlotto and Paramo 2003); and model studies developed for groups of fish in open water show that an oblong shape is characteristic of a moving group (Hemelrijk and Hildenbrandt 2008).

There is also some evidence that densities of euphausiids influenced the distribution of age classes across the eastern Bering Sea shelf, because older juveniles were found in areas with higher densities of euphausiids. There is an association between age of juvenile pollock and euphausiid density, especially within a season. Before their first year, juvenile pollock undergo an ontogentic shift from copepods to euphausiids in their diet (Bailey and Dunn 1979, Merati and Brodeur 1996, Brodeur 1998), showing preference for euphausiids when available (Brodeur 1998). It is thus presumed that all juvenile pollock in our study were capable of preying upon euphausiids. Euphausiid density is higher in areas of the Bering Sea with cooler bottom temperatures (Ressler et al. 2014), and our study showed that within each year, the older juveniles were also found in areas with relatively cooler bottom temperatures. Laboratory studies have demonstrated that smaller walleye pollock and bluefish, *Pomatomus saltarix*, both show a greater avoidance to cooler water than do their larger juvenile cohorts, likely related to their lower tolerance to a thermal change because of their smaller body size (Olla et al. 1985, Olla and Davis 1990, Sogard and Olla 1993). This suggests the older juveniles observed in our study likely had a greater tolerance for cooler temperatures, which potentially allowed them to venture into the cooler waters where higher densities of euphausiids resided.

Contrary to what we predicted, mixed age classes did not form groups with more internal variation in density compared to their pure-aged cohorts. The horizontal internal heterogeneity of mix12 groups was similar to that of age1 and age2 groups per unit length, even though mix12 fish formed considerably larger groups. Additionally, the horizontal internal heterogeneity of mix23 groups was similar to that of age3 groups. This suggests some consistency in the internal structure of younger juvenile pollock groups, regardless of group size. Studies have shown that the internal structure of fish groups can be highly consistent within a species (Paramo et al. 2007), regardless of the aggregation type (i.e., group or layer; Gerlotto et al. 2004). This also suggests that there are no structural costs to forming mixed-age groups. Instead, there may be benefits. Mix12 groups were larger than age1 or age2 groups, and mix23 groups were larger than age2 groups. The larger group size theoretically offers more safety for the members (Pitcher and Parrish 1993), and being in a mixed group can provide an advantage for the smaller, more preyed upon fish (Theodorakis 1989), especially when mixed-age groups are found near relatively higher densities of predators, as observed in our study.

Although juvenile pollock group structure did not change in response adult pollock and euphausiid densities, it did change in response to the physical environment. Deeper groups of age1, mix12, age2, and age3 fish were vertically shorter, denser, and had more variation in horizontal density. In the Bering Sea, demersal predators of juvenile walleye pollock such as adult pollock and arrowtooth flounder increase with proximity to the seafloor (Bailey 1989, Aydin and Mueter 2007). Group compaction, an antipredator tactic (Pitcher and Parrish 1993, Sogard and Olla 1997), might be favored by juvenile pollock when they are closer to such demersal predators. Our study determined that densities of adult pollock had no effect on juvenile pollock group structure, but it did not measure whether the vertical proximity of adult pollock had an effect. It is possible that age1, mix12, age2, and age3 groups became more compact closer to the bottom as a defense against the closer proximity to predators that reside there.

As expected, the physical environment influenced the location of juvenile walleye pollock groups in the water column. Age1, mix12, mix23, and age3 fish reacted to cooler bottom water by moving shallower in the water column, and mix12 and mix23 fish reacted to cooler surface water by moving deeper in the water column. This behavior agrees with laboratory studies that have shown the importance of thermal stratification on the vertical distribution of juvenile pollock. Juvenile pollock generally avoid cold water, swimming upward in the tank to evade an introduced thermocline (Olla and Davis 1990). Additionally, water stratification can act as a boundary dictating the distribution of fish, and it can affect movement patterns of pollock, often as a function of fish age. For example, young-of-the-year pollock tend to concentrate above the thermocline and adult pollock below it (Traynor 1986, Swartzman et al. 1994). This trend for older fish to venture into colder water is further verified by our results which demonstrate an *in situ* proclivity by older pollock for cooler waters each year *within* the juvenile stage (but see Stienessen and Wilson 2003).

Juvenile pollock maintained a relatively constant size-dependent density (fish/FL^3) and group shape among age classes. Consistency in both metrics is not unique to juvenile pollock. Other species of fish have been reported to maintain consistent interfish spacing based on body length (Pitcher and Partridge 1979, Viscido et al. 2004, Newlands and Porcelli 2008) and a consistent group shape irrespective of fish age or size (Abrahams and Colgan 1985, Coetzee 2000, Muiño et al., 2003). Perhaps juvenile pollock group spacing and shape are ubiquitous because they provide benefits to the individuals. It has been determined that optimal spacing exists within some species of fish (Newlands and Porcelli 2008). Brierley and Cox (2010) found the spread (i.e., surface area –to-volume) measurements of Antarctic krill shoals to be relatively constant and also similar to spread measurements of various clupeid fish groups found in tropical regions of the Atlantic and Pacific. They postulated that because the emergent shape property was common, it might provide a benefit to the krill and clupeids, and they showed this shape potentially reflected a tradeoff between predator avoidance and oxygen acquisition. Although juvenile pollock do not maintain a constant spread –they form such low density groups relative to other fish (Simmonds et al. 1992) that oxygen acquisition is a nonissue (Domenici et al. 2002.) –they did form groups with a similar shape, which suggests that there could be a species-specific group shape for juvenile pollock that is optimal and offers advantages to the individuals therein (e.g., Fréon and Misund 1999).

Because group structure was not associated with changes in adult pollock and euphausiid densities, and because the associations between the physical environment and group structure differed between age classes, our work suggests that juvenile pollock group metrics would not be a good indicator to characterize the condition of the environment (ICES 2001). However, the reported values of juvenile pollock group metrics may provide helpful to future efforts looking to discriminate the juveniles from co-occurring species. Examining if/how juvenile pollock group metrics compare to those of other species found in the eastern Bering Sea would be an informative next step. Another, and important, avenue for further investigation would be to determine if the vertical proximity of predators and prey, rather than absolute densities, influence the short-term response of juvenile pollock group structure.

Acknowledgements

I thank the scientists and crew of the NOAA ship *Oscar Dyson* for their hard work in helping with the data collection. I thank James Ha for his multivariate input Chris Wilson, Julia Parrish, Tom Weber, and Alex De Robertis for valuable comments and remarks on earlier drafts of this paper.

Table 7. Names, symbols, and definitions of Group Metrics and the various indices, intermediary equations, and scattering quantities used to calculate them.

	Symbol	Name (and unit)	Definition or Algorithm
Group Metrics	L	Length (m)	Maximum distance between all points in η_{2D}
	W	Width (m)	Greatest horizontal distance perpendicular to group length in the Θ_{L+90° direction
	H	Height (m)	$z_{max(i)} - z_{min(i)}$
	R	Roundness	L/W
	V	Volume (m^3)	η_{3D}
	SA	Surface Area (m^2)	$\sum_1^f (v1 * v2 + v2 * v3 + v3 * v1)/2$ for all k_{3D}
	Sp	Spread (m^{-1})	SA/V
	d/m^3	Density (fish/m^3)	$sv/\overline{\sigma}_{bs}$
	d/FL^3	Density (fish/fork length^3)	$d/m^3 * 1/(FL/100)$
	D	Depth (m)	$\frac{\sum_1^n z_i * d_i}{\sum_1^n d_i}$
	DB	[4]Distance off Bottom (m)	Bottom depth – D
	IH_h	Horizontal Internal Heterogeneity (m)	$\frac{\sum_1^n \sqrt{(x_i - C_x)^2 + (y_i - C_y)^2} * d_i}{\sum_1^n d_i} / L$
	IH_v	Vertical Internal Heterogeneity (m)	$\frac{\sum_1^n (z_i - C_z)^2 * d_i}{\sum_1^n d_i} / H$
	R	Range from the ship (m)	$\sqrt{(S_x - C_x)^2 + (S_y - C_y)^2 + {C_z}^2}$,
	HD	Horizontal distance from the ship (m)	$\sqrt{(S_x - C_x)^2 + (S_y - C_y)^2}$

Indices	n		Total number of measurements within a group
	i		Each measurement within a group
	k		Number of indices defining η_k
	a		One of 2 measurements in η_k used to define L
	b		One of 2 measurements in η_k used to define L
	p		Total number of pings

Positional Intermediaries	x,y	Horizontal position (m,m)	Universal Transverse Mercator (UTM) coordinate position of the Sv measurement
	z	Depth position (m)	Depth of the Sv measurement
	s_x, s_y	Ship position (m,m)	UTM coordinate position of the vessel
	S_x, S_y	Mean ship position (m,m)	$\frac{\sum sx_i}{p}, \frac{\sum sy_i}{p}$
	C_x, C_y, C_z	Density –dependent center of gravity (m,m,m)	$\frac{\sum_1^n x_i * d_i}{\sum_1^2 d_i}, \frac{\sum_1^n y_i * d_i}{\sum_1^2 d_i}, \frac{\sum_1^n z * d_i}{\sum_1^2 d_i}$

	η_k	Convex hull	$= \left\{ \sum_{j=1}^{n} \lambda_j p_j \mid \lambda_j \geq 0 \text{ for all j and } \sum_{j=1}^{n} \lambda_j = 1 \right\}$
	η_{2D}	2D convex hull	The smallest convex polygon that contains every one of the n data points ($x_1, y_1 \ldots x_n, y_n$) within the group

Geometrical Intermediaries	η_{3D}	3D convex hull	The smallest convex volume that contains every one of the n data points ($x_1,y_1,z_1....x_n,y_n,z_n$) within the group
	Θ_L		arctan ($\lvert x_a-x_b\rvert$ / $\lvert y_a-y_b\rvert$)
	f		Number of triangle facets
	v1,v2,v3		The vertices of each triangle facet

Scattering quantities	sv	[1]Volume backscattering coefficient (m^{-1})	$10^{*Svc/10}$
	FL	[2]Fish length (cm)	Mean fork length
	TS	[3]Target strength (dB re 1 m^2)	TS = 20*log(FL) – 66
	σ_{bs}	[1]Backscattering cross section (m^2)	$10^{*TS/10}$

[1] McLennan et al. (2002)

[2] Based on the population length composition from the nearest (< 15 nmi) haul location

[3] TS to FL_{cm} model for walleye pollock from Foote and Traynor (1988)

[4] Bottom depth was taken from the nearest (< 15 nmi) haul location

Table 8. Total effects (direct + indirect) of environmental factors on juvenile walleye pollock position in the water column within each age class. No effects are in gray, small effects are in black, medium effects are bolded, and large effects are filled.

	Age 1		**Mix 12**		**Age 2**		**Mix 23**		**Age 3**	
Biophysical Factor	Group Depth	Off Btm	Group Depth	Off Btm	Group Depth	Off Btm	Group Depth	Off Btm	Group Depth	Off Btm
Shelf depth	1.35	0.62	0.91	0.79	-0.34	0.68	-0.51	1.28	**0.39**	1.47
Surface temp	0.11	-0.15	-0.31	0.33	0.04	0.03	-0.59	0.60	-0.10	0.15
Group temp	**-0.37**	0.50	0.07	-0.07	-0.04	0.03	-0.32	0.33	**-0.36**	0.52
Bottom temp	**0.48**	-0.65	0.31	-0.34	-0.29	0.24	0.23	-0.23	0.58	-0.85
Adult pollock	-0.12	0.16	0.08	-0.09	0.00	0.00	-0.00	0.00	-0.08	0.12
Euphausiids	-0.06	0.08	0.05	-0.06	0.20	-0.17	-0.08	0.08	-0.07	0.10

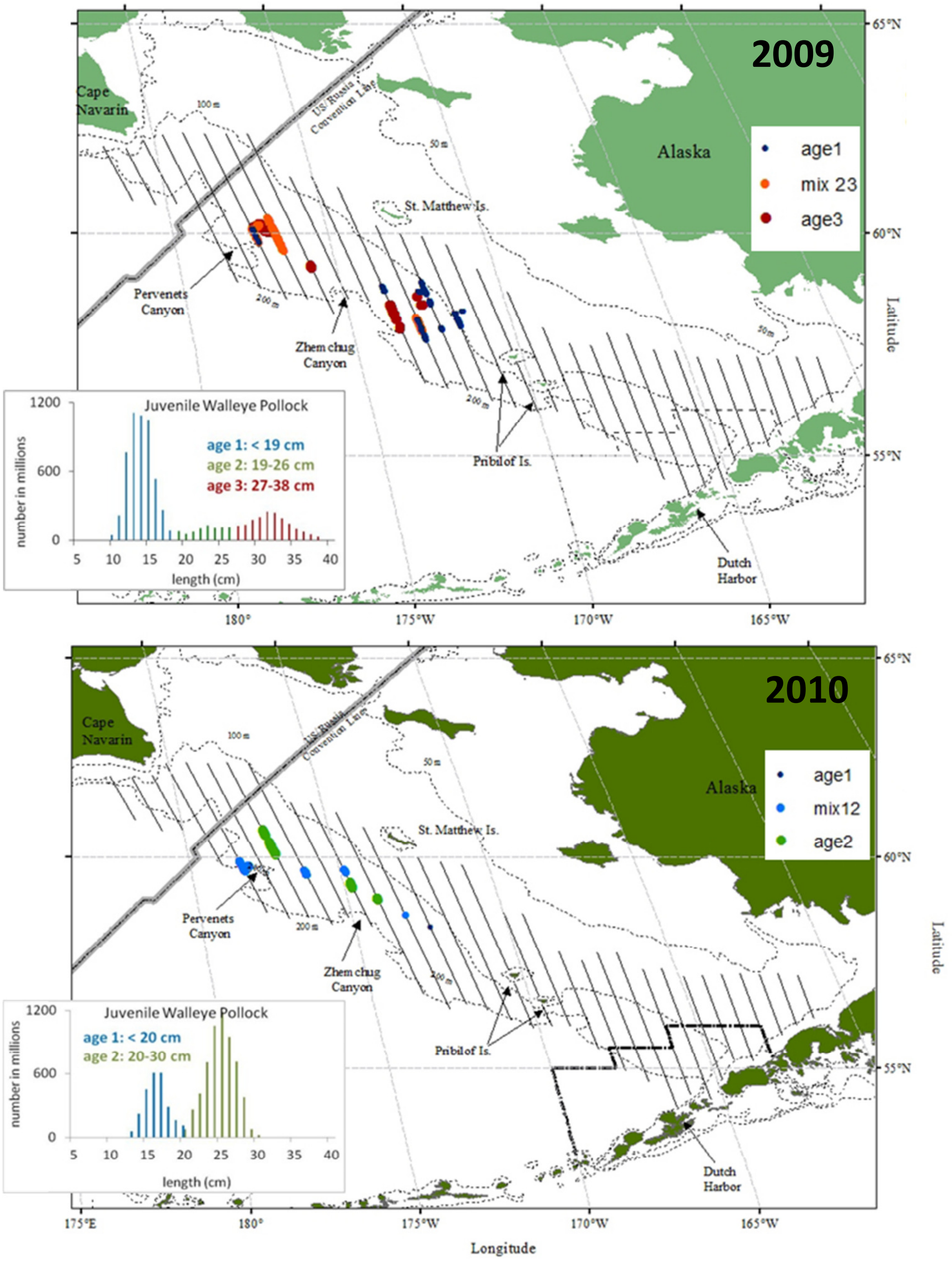

Figure 12. The study area in the eastern Bering Sea during 2009 (top) and 2010 (bottom). Both plots show the survey tracklines by age class, where mix12 are groups that contain both age1 and age2 fish, and mix23 are groups that contain both age2 and age3 fish.

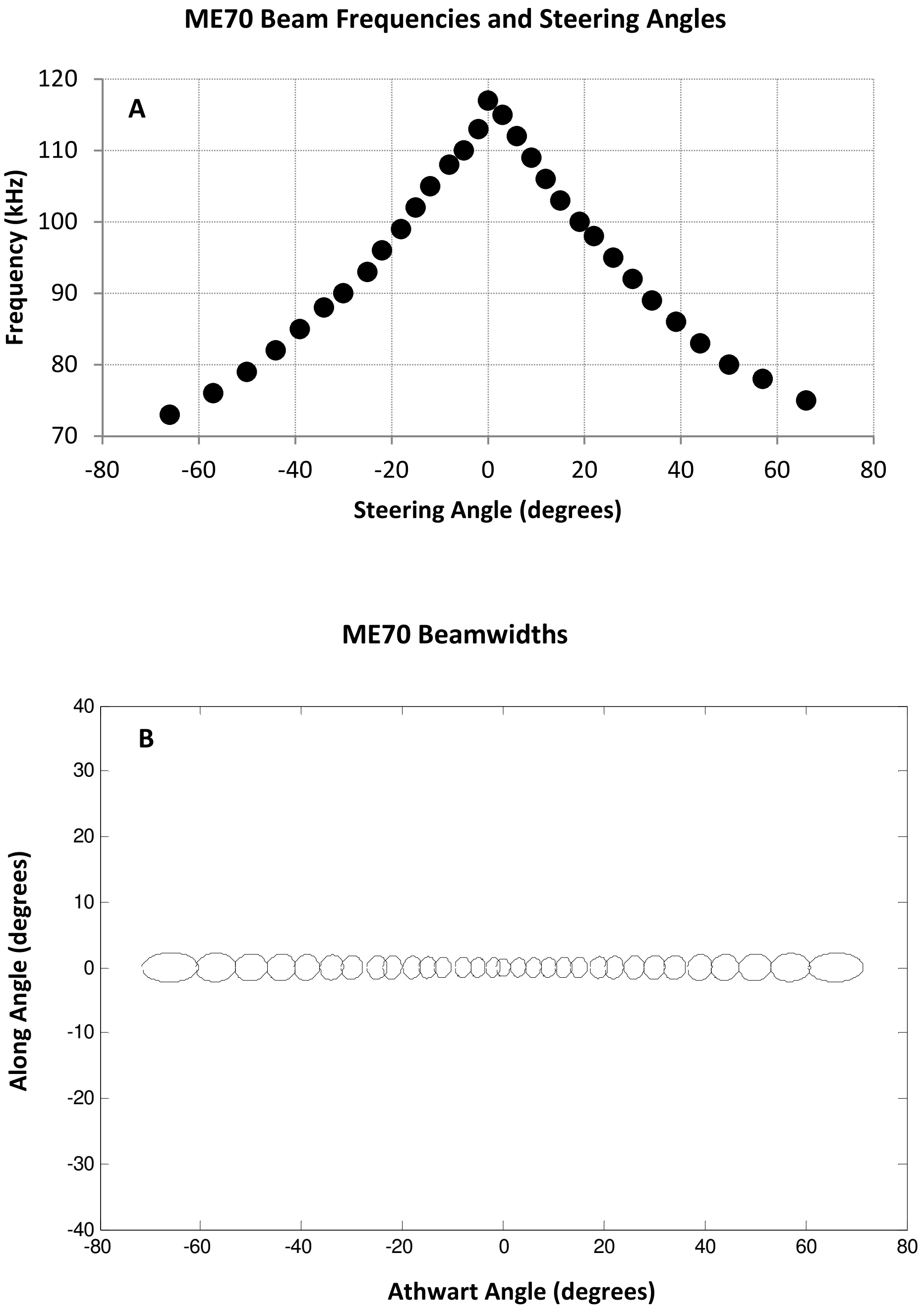

Figure 13. The ME70 beam configuration, showing A) the steering angle-frequency combination for each beam, and B) the beamwidths (beam opening values refer to the one-way received beams). Note the athwart angle axis in Fig. 2B is double that of the along angle axis. Data collected in 4 outermost beams were not used. This resulted in an effective fan width of ±55°.

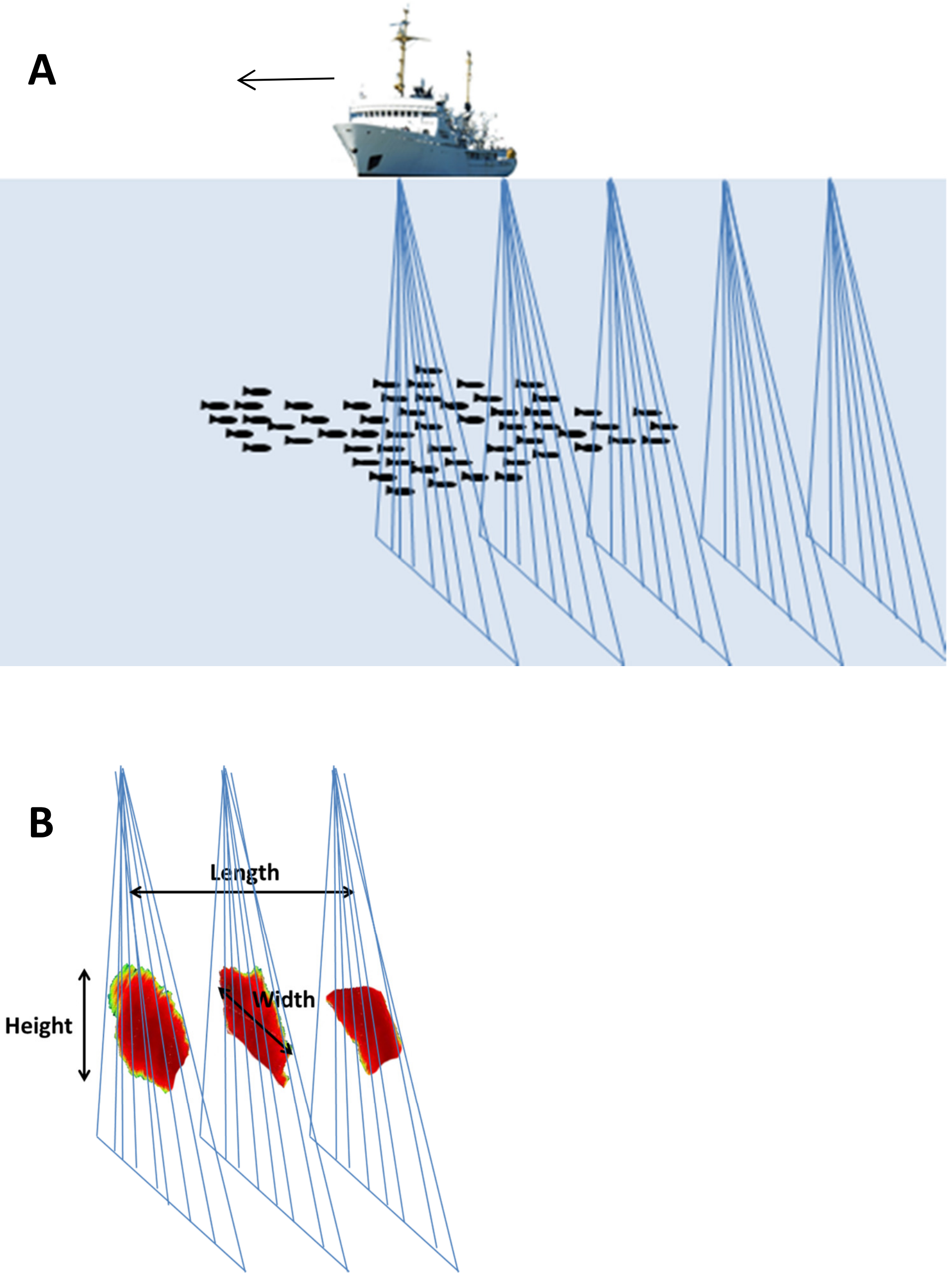

Figure 14. A) Schematic of the insonification of a fish group with a 7-beam multibeam sonar. In this depiction, part of the group has been insonified over three consecutive transmitted acoustic signals (i.e., pings). B) The associated backscatter characterizes the three-dimensional structure of the insonified part of the group. The color scale green-to- dark red represents low to high backscatter values, respectively.

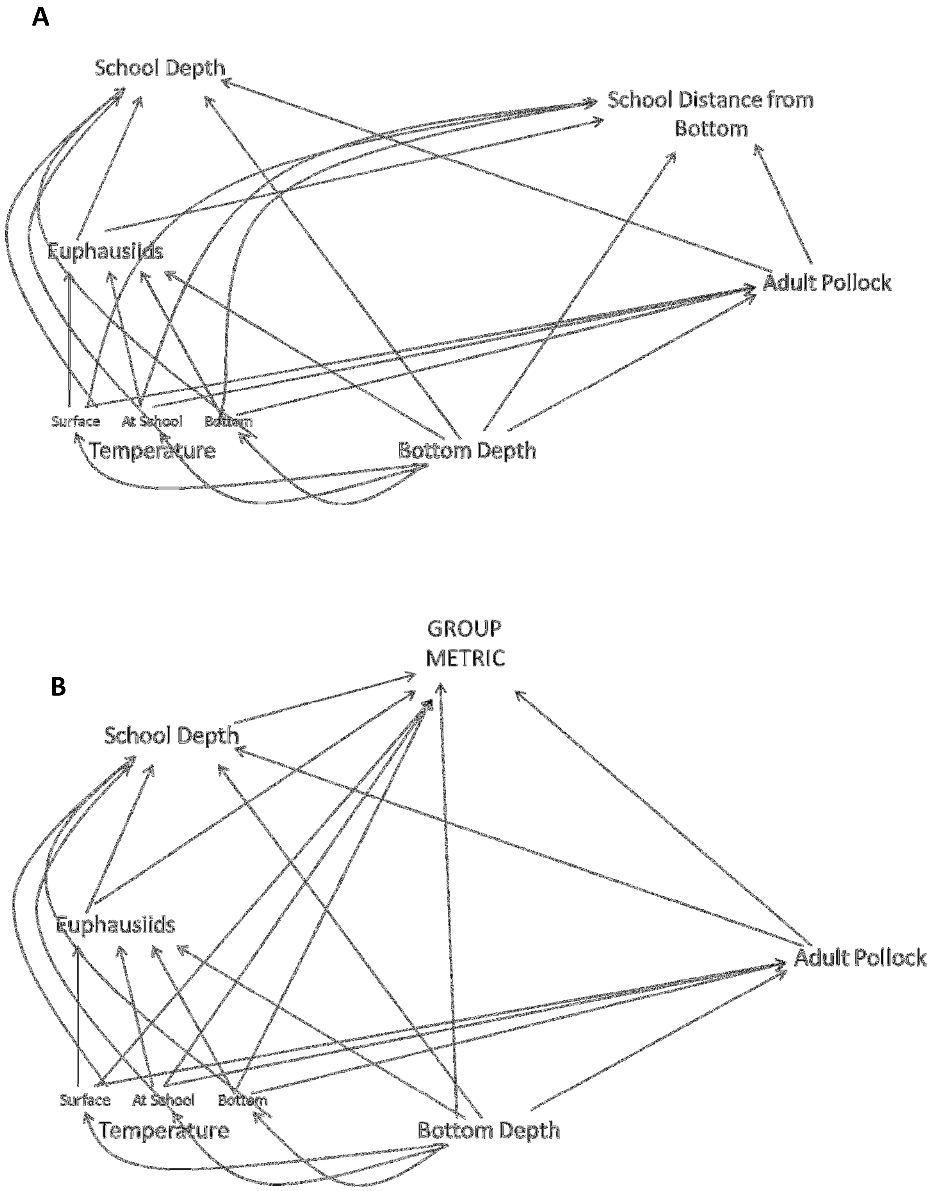

Figure 15. A) The causal model used to examine the influences of physical and biological factors on group position in the water column within each age class, and B) the causal model used to examine the influences of physical and biological factors on group metrics within each age class.

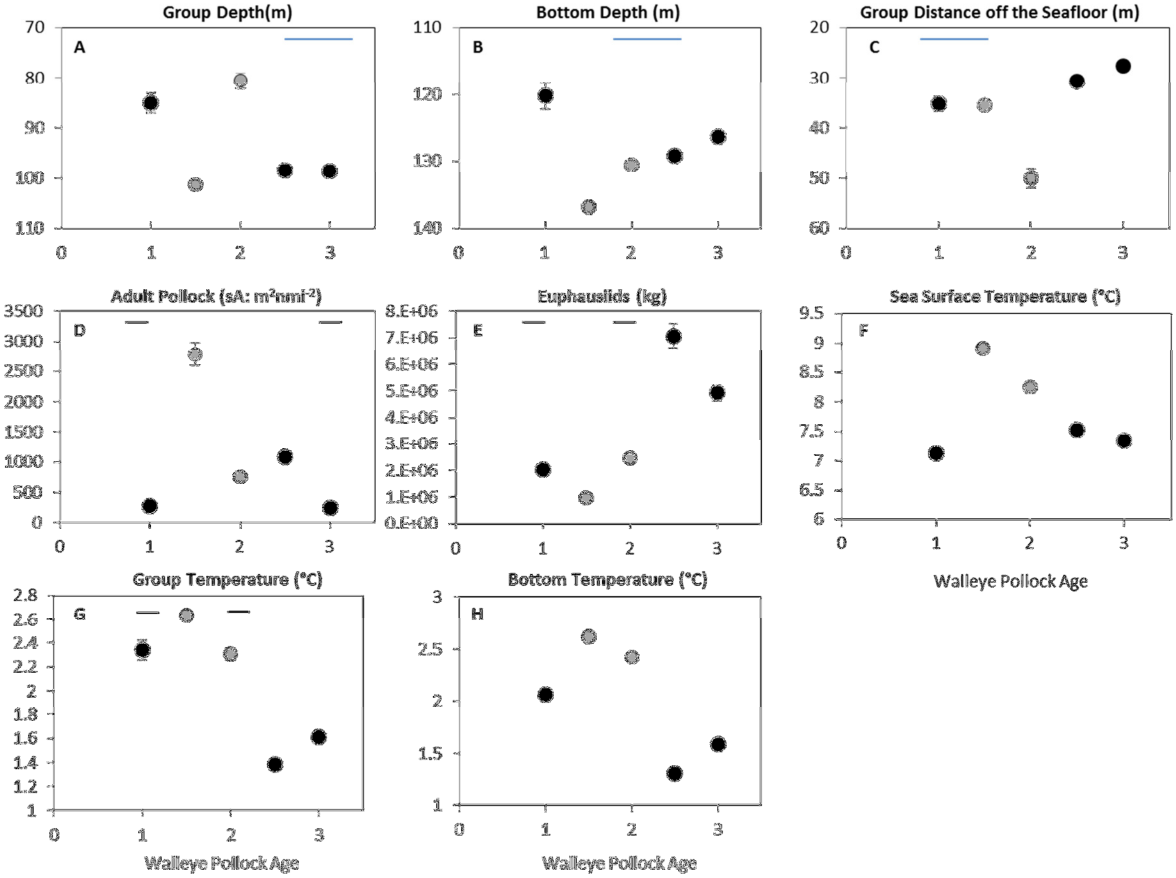

Figure 16. The local environment for each age class of juvenile walleye pollock (A, group depth; B, shelf depth ; C, group distance off the seafloor; D, adult pollock density; E, euphausiid density; F, sea surface temperature; G, group temperature; and H, bottom temperature). The error bars represent 95% confidence intervals about the mean and are sometimes obscured by the symbol. Note that the black circles represent means from 2009, and the gray circles represent means from 2010. Mix 12 results are plotted between age 1 and age 2, and mix 23 results are plotted between age 2 and age 3. Lines above the symbols indicate no statistically significant differences were detected between those age groups based on Tukey's multiple comparison tests.

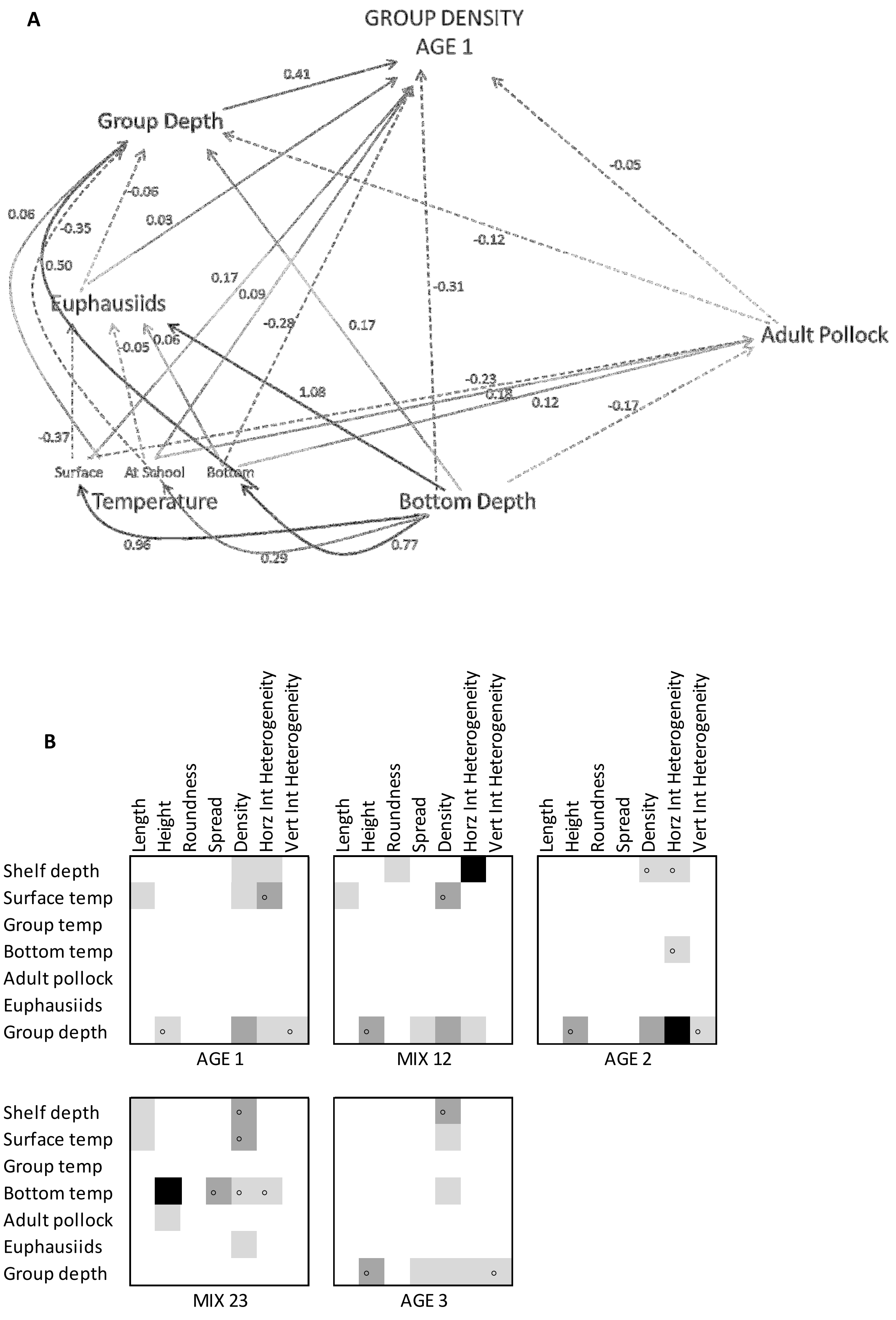A
GROUP DENSITY
AGE 1
Group Depth
Euphausiids
Adult Pollock
Surface
At School
Bottom
Temperature
Bottom Depth
0.41
-0.05
-0.06
0.06
-0.35
0.03
-0.12
0.50
0.17
0.09
-0.31
-0.29
0.17
-0.05
0.06
1.08
-0.23
0.18
0.12
-0.17
-0.37
0.96
0.29
0.77
B
Length
Height
Roundness
Spread
Density
Horz Int Heterogeneity
Vert Int Heterogeneity
Shelf depth
Surface temp
Group temp
Bottom temp
Adult pollock
Euphausiids
Group depth
AGE 1
MIX 12
AGE 2
MIX 23
AGE 3

Figure 17. A) Direct effects of environmental factors on group density of age1 pollock. This result is intended as an illustrative example of how direct effects culminate into total effects. Similar results for the other 34 path analyses are not shown. Larger effects are indicated by more bold arrows. Solid arrows represent positive effects and dashed arrows represent negative effects.

B) Total effects (direct + indirect) of environmental factors on size, shape, and internal structure of age1, mix12, age2, mix23, and age3 groups of juvenile walleye pollock. No effects (0-0.20) are indicated by white fill, small effects (0.20-0.35) are indicated by light gray fill, medium effects (0.35-0.50) are indicated by dark gray fill, and large effects (>0.50) are indicated by black fill. Positive effects are indicated by a solid fill, and negative effects are indicated by an open circle '◦'within the fill.

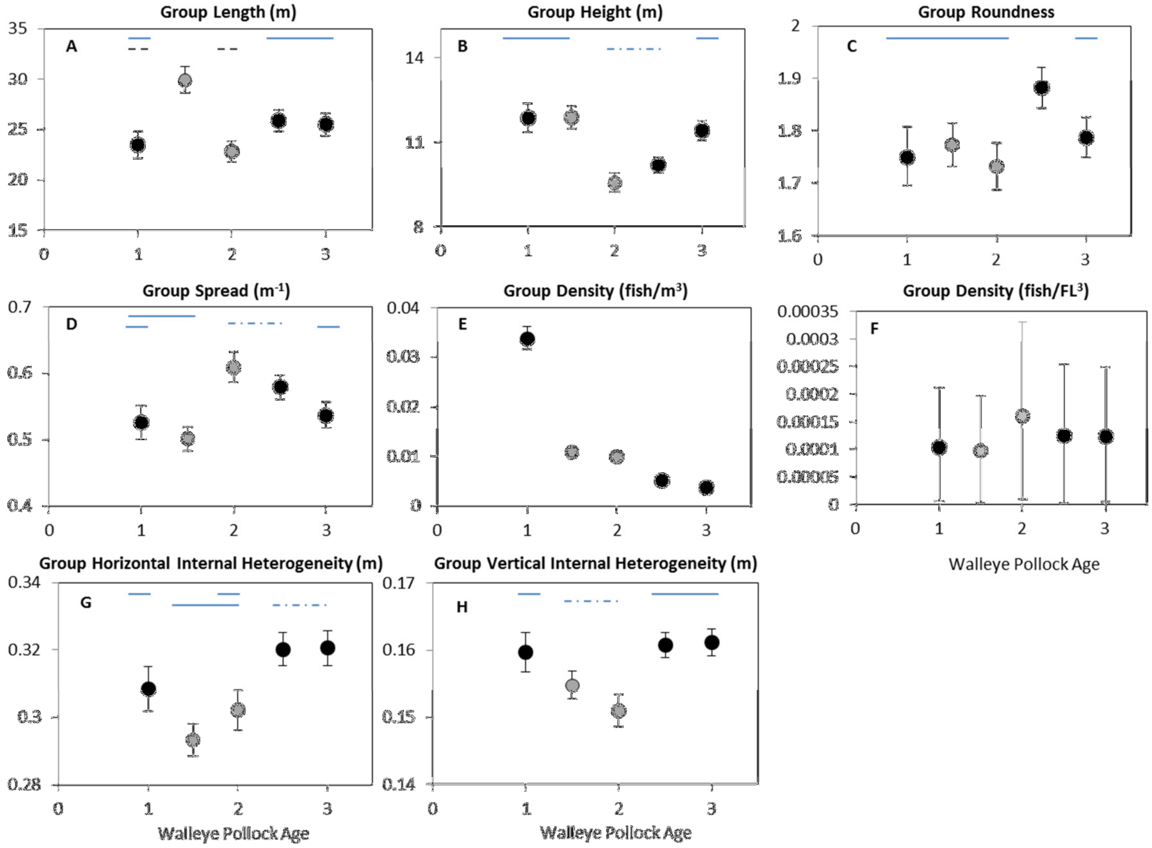

Figure 18. Effects of juvenile pollock age on group metrics (A, length; B, height; C, roundness; D, roughness; E, volumetric density; F, density based on fork length; G, horizontal internal heterogeneity; and H, vertical internal heterogeneity). The error bars represent 95% confidence intervals about the mean and are sometimes obscured by the symbol. Note that the black circles represent means from 2009, and the gray circles represent means from 2010. Mix 12 results are plotted between age 1 and age 2, and mix 23 results are plotted between age 2 and age 3. Lines above the symbols indicate no statistically significant differences were detected between those age groups based on Tukey's multiple comparison tests.

The following appendix accompanies chapter 4

Appendix . Expansion on methods used to define and isolate a group and derive the associated metrics.

Threshold Sensitivity Analysis

Various processing thresholds, ranging from -66 to -48 dB Sv, were applied to a subset of the data divided into 12 areas (6 areas from each year). The backscatter in each area was classified into groups, and 4 basic metrics were calculated: number of groups, average group Sv, average group length, and average group depth (Table 1). The results of the sensitivity analysis indicated that the number of groups stabilized at processing thresholds greater than -55 dB Sv (Fig. A1a), and average group length stabilized at processing thresholds greater than -58 dB Sv (Fig. A1c). Average group depth was fairly constant (Fig. A1d) across all processing thresholds, and average group Sv generally decreased with a decrease in processing threshold (Fig. A1b). Together, the results of the sensitivity analysis indicate that thresholds of -55 dB Sv to at least -48 dB Sv produced similar metrics. We chose -52 dB Sv for the processing threshold, because -52 dB Sv fell near the center of that range.

Sv correction

Average Sv values of juvenile pollock backscatter differed among beams. The measured backscatter values decreased as the steering angle increased (Fig. A2). This is likely the result of the angular response of insonified juvenile pollock (Towler et al. 2003, Hazen and Horne 2004, Cutter and Demer 2007, Holmin et al. 2012) and, to a much lesser extent, the bandwidth and frequency differences between beams (Fig. 2; DeRobertis et al. 2010). We presumed the fish were not aligned geographically; and because there is no evidence that the pollock were responding to the vessel; we assumed that over the course of a survey the average Sv should be the same at any horizontal (i.e., athwartship) distance from the ship. To correct for the effects of fish orientation and beam directivity on all Sv measurements, average Sv-by-beam curves were calculated for each age class of juvenile pollock (Fig. A2):

$$\overline{Sv_b} = 10*\log\left(\frac{\sum_1^n 10^{Sv_{i,b}/10}}{n}\right)$$

where i = each Sv measurement of juvenile pollock backscatter extracted by Fledermaus software, n = total measurements, and b = beam number.

Within each age class, the vertically-oriented beam (i.e., the middle beam) was used to create an adjustment factor (ΔSv) for the other beams:

$$\Delta Sv_b = \overline{Sv_m} - \overline{Sv_b} \qquad (1)$$

where m = middle beam. Adjusted Sv values were then applied to the data:

$$Svc_{i,b} = Sv_{i,b} + \Delta Sv_b \qquad (2)$$

where Svc = adjusted Sv value.

This method of adjustment produced similar average Svc values across beams. A shortcoming of using a range of steered beams to collect acoustic data is that in some instances low Sv values detected by vertical beams may not be detected by the more steered beams. Unfortunately, this is something that cannot be adjusted for.

Adjustments for beam spreading effects

A group of fish insonified by sonar will appear longer and less dense the deeper it is in the water column because of the beam spreading effect (Diner 2001). This result is exacerbated as processing threshold decreases or beam width increases. To correct for the beam spreading effect, Diner developed a series of equations generated from a simulated dataset. The groups of juvenile pollock in our study had an ellipsoidal shape and relatively homogeneous density (a basic assumption of Diner's equations), so we applied Diner's equations to our data. Diner's equations utilize a form of corrected school length increase, dL, which is a function of nominal beamwidth (bw)

$$dL = 2 * depth * \tan(bw/2),$$
(3)

and many of the equations involve constants generated from a simulated dataset. Diner's equations are applicable for vertically steered beams, so we had to make modifications to the equations to account for steered beams. This was done by calculating the footprint for each steered beam at a fixed depth using basic geometry (Fig. A3). It was then assumed the footprint was produced by a vertical, non-steered, beam and the corresponding, or effective beamwidth (ebw), was calculated:

$$\mathrm{ebw} = 2 * \tan^{-1}(\mathrm{footprint}/(2*\mathrm{depth})). \quad (4)$$

Effective beamwidths were used instead of the actual beamwidths, and group range (Table 1) was used instead of group depth, in all of Diner's equations. For example:

$$\mathrm{dL} = 2 * \mathrm{range} * \sin(\mathrm{ebw}/2). \quad (5)$$

For each group, three sets of beams were identified: 1) the two beams which bounded group length, 2) the two beams which bounded group width, and 3) the two beams which bounded the entire group. The effective beamwidth of the two beams were used in the calculation of length, width, and density corrections, respectively. For a given metric, the final correction value was obtained by summing half the correction value generated by each of the two bounding beams. A limitation to using Diner's corrections is that the group dimensions need to be large compared to the beamwidth. Therefore, we only applied the corrections when the normalized group length, relative to beamwidth, was larger than 1.5 (Diner 2001). Additionally, the corrections were only applicable for group length, width, and density (and applied to morphological isotropy); therefore, the other morphological metrics in our study were not corrected.

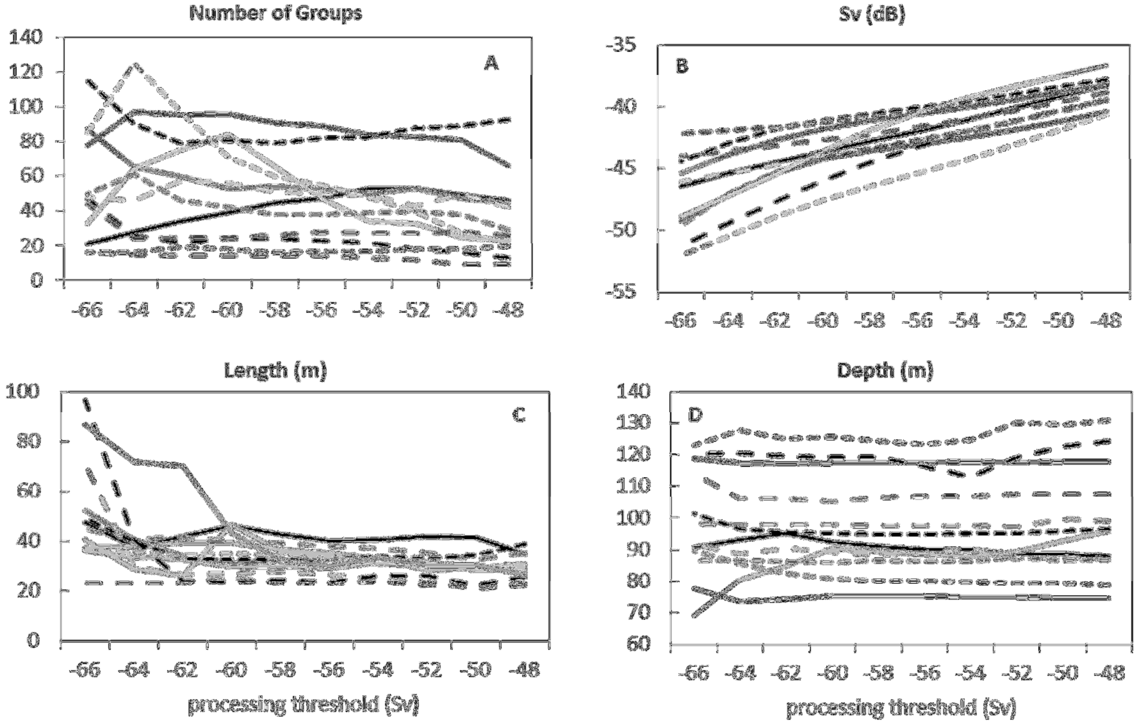

Figure A1. The results of the threshold sensitivity analysis showing A) number of groups, B) average group Sv, C) average group length, and D) average group depth as a function of various processing thresholds. Each line represents a subset area of the original dataset.

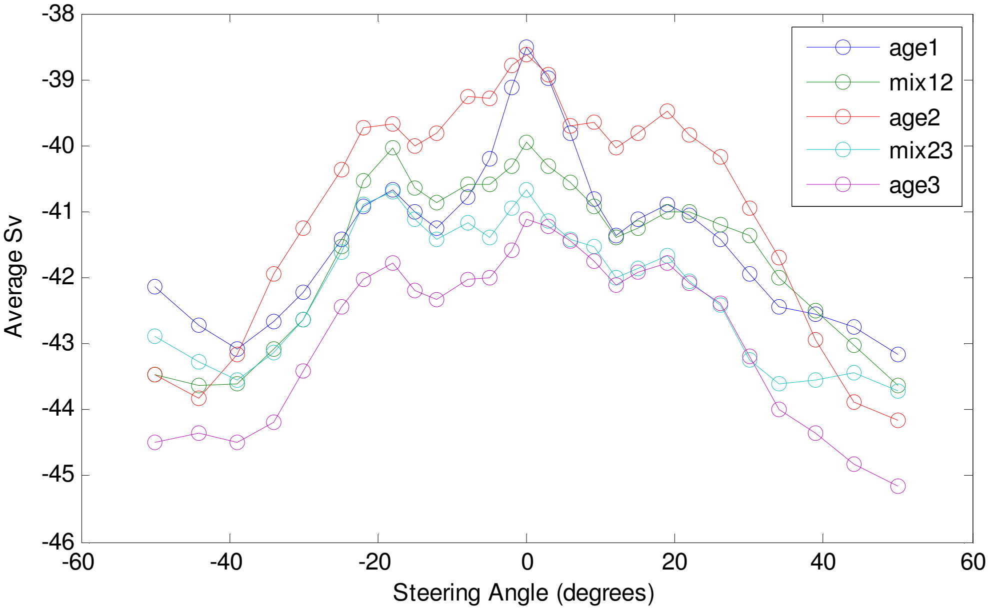

Figure A2. Mean volume backscattering, Sv, values for each age class of walleye pollock.

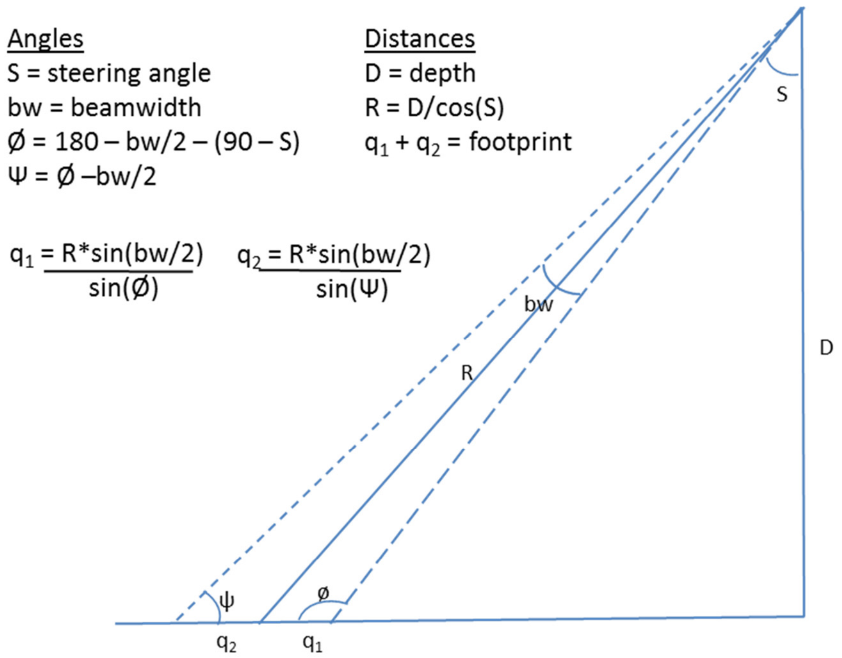

Figure A3. Angles and distances involved in calculating the footprint of steered beams.

References

Abdi H, Valentin D. 2007. Multiple Factor Analysis. In: Salking, N, editor. Encyclopedia of Measurement and Statistics. Dallas, Texas: The University of Texas at Dallas. p. 1-14.

Abrahams, M. V., and P. W. Colgan. 1985. Risk of predation, hydrodynamic efficiency and their influence on school structure. Environmental Biology of Fishes, 13: 195-202.

Alexander, R.D. 1974. The evolution of social behavior. Ann. Rev. Ecol. Sys, 5: 325-383.

Allee, W.C., 1927. Animal Aggregations. Quarterly Review of Biology, 2: 367-398.

Aoki, I. 1982. A simulation study on the schooling mechanism in fish. Bull Jpn Soc Sci Fish 48: 1081-1088.

Aoki, I. 1980. An analysis of the schooling behaviour of fish: Internal organization and communication process. Bull. Ocean Res. Inst. Univ. Tokio, 12: 1-65.

Aoki, I., T. Inagaki, and L. Van Long. 1986. Measurements of the three-dimensional structure of free-swimming pelagic fish schools in a natural environment. Bulletin Japanese Society for Science of Fisheries, 52: 2069-2077.

Axelsen, B.E., T. Anker-Nilssen, P. Fossum,C. Kvamme, L. Nøttestad. 2001. Pretty patterns, but a simple strategy: predator-prey interactions between juvenile herring and atlantic puffins observed with multi-beam sonar. Canadian J. of Zoology, 79: 1586-1596.

Axelsen, B.E., L. Nøttestad, A. Fernõ, A. Johannessen, and O.A. Misund. 2000. ‘Await’ in the pelagic: dynamic trade-off between reproduction and survival within a herring school splitting vertically during spawning. Marine Ecology Progress Series, 205: 259-269.

Aydin, K., S. Gaichas, I. Ortiz, D. Kinze, and N. Friday. 2007. A comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands large marine ecosystems through food web modeling. U.S. Department of Commerce, NOAA Technical Memo. NMFS-AFSC-178.

Aydin, K., and F. Mueter. 2007. The Bering Sea—a dynamic food web perspective. Deep Sea Research Part II: Topical Studies in Oceanography, 54(23-26): 2501-2525. doi:10.1016/j.dsr2.2007.08.022.

Bailey, K.M. 1989. Interaction between the vertical distribution of juvenile walleye pollock *Theragra chalcogramma* in the eastern Bering Sea, and cannibalism. Marine Ecology Progress Series, 53: 205-213.

Bailey, K.M, and J. Dunn. 1979. Spring and smmer foods of walleye pollcok, Theragra chalcogramma, in the Eastern Bering Sea. Fisheries Bulletin, 77: 304-308.

Baird, T.A., C.H. Ryer, and B.L. Olla. 1991. Social enhancement of foraging on an ephemeral food source in juvenile walleye pollock, *Theragra chalcogramma*. Environmental Biology of Fishes, 31: 307-311.

Bakun A, Cury P. 1999. The “school trap”: a mechanixm promoting large-amplitude out-of-phase population oscillations of small pelagic fish species. Ecol Lett. 2:349-351.

Ballerini, M., N. Cabibbo, R. Candelier, A. Cavagna, E. Cisbani, I. Giardina, V. Lecomte, A. Orlandi, G. Parisi, A. Procaccini, M. Viale, and V. Zdravkovic.2008a. Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study. Proc Nat Acad Sci, 105:1232–1237.

Ballerini, M., N. Cabibbo, R. Candelier, A. Cavagna, E. Cisbani, I. Giardina, A. Orlandi, G. Parisi, A. Procaccini, M. Viale, and V. Zdravkovic. 2008b. Empirical investigation of starling flocks: a benchmark study in collective animal behaviour. Animal Behaviour, 76: 201-215.

Barange, M. 1994. Acoustic identification, classification and structure of biological patchiness of the edge of the Aguhas Band and its relation to frontal features. S. Afr. J. mar. Sci. **14**: 333-347.

Benoit-Bird, K.J. 2009. Dynamic 3-dimensional structure of thing zooplankton layers is impacted by foraging fish. Marine Ecology Progress Series, 369: 61-76.

Berger, J. 1977. Organizational systems and dominance in feral horses in the Grand Canyon. Behav Ecol Sociobiology, 2: 131-146.

Bertram, B.C.R. 1978. Living in groups: predators and prey. In: J.R. Krebs and N.B. Cavies (eds.), Behavioural ecology, first edition. Blackwell, Oxford, UK, pp. 64-93.

Bertrand, A., M. A. Barbieri, F. Gerlotto, F. Leiva, and J. Córdova. 2006. Determinism and plasticity of fish schooling behavior as exemplified by the South Pacific Jack mackerel *Trachurus murphyi*. Marine Ecology Progress Series, 311: 145-156.

Bertrand, A., M. Guitérrez, S. Bertrand, P. Espinoza, F. Gerlotto, J. Ledesma, R. Quesquén, L. Alza, S. Peraltilla, A. Chipollini, and F. Chavez. 2005. How fish habitat suitability does shape the 3D spatial organization of anchovy across scales? ICES Annual Conference, Aberdeen, UK, 20-24/09/2006, ICES CM/U:10, 23 pp.

Biggs, M.A., P.F. Olesiuk, G.M. Ellis, J.K.B. Ford, and K.C. Blacomb III. 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Report of the International Whaling Commission Special Issue 12, 383-405.

Bilde, T., K.S. Coates, K. Birkhofer, T. Bird, A. A. Maklakov, Y. Lubin, and L. Avilés. 2007. Survival benefits select for group living in a social spider despite reproductive costs. J. Evol. Biol, 20: 2412-2426.

Bodholt, H. and H. Solli. 1992. Split beam techniques used in Simrad EK500 to measure target strength, p. 16-31. *In* World Fisheries Congress, May 1992, Athens, Greece.

Bourke, A.F.G., and N.R. Franks. 1995. Social evolution in ants. Princeton University press, Princeton, NJ.

Brierley, A.S., and M. J. Cox. 2010. Shapes of krill swarms and fish schools emerge as aggregation members avoid predators and access oxygen. Current Biology, 20: 1-5.

Brodeur, R.D. 1998. Prey selection by age-0 juvenile walleye pollock, Theragra chalcogramma, in nearshore waters of the Gulf of Alaska. Environmental Biology of Fishes, 51: 175-186.

Brodeur, R.D., and M.T. Wilson. 1996a. A review of the distribution, ecology, and population dynamics of age-0 walleye pollock in the Gulf of Alaska. Fish. Oceanogr. 5(Suppl. 1): 148-166.

Brodeur, R.D., and M.T. Wilson. 1996b. Mesoscale acoustic patterns of juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. Can. J. Fish. Aquat. Sci. 53:1951-1963.

Brodeur, R.D., M.T. Wilson, and L. Ciannelli. 2000. Spatial and temporal variability in feeding and condition of age-0 walleye pollock (Theragra chalcogramma) in frontal regions of the Bering Sea. ICES Journal of Marine Science, 57: 256-264.

Brown, C., and K. N. Laland. 2002. Social learning of a novel avoidance task in the guppy: conformity and social release. Animal Behaviour, 64: 41-47.

Brown, C., and K.N. Laland. 2003. Social learning in fishes: a review. Fish and Fisheries, 4: 280-288.

Brown, C., and K. Warburton. 1999. Social mechanisms enhance escape responses in shoals of rainbowfish, *Melanotaenia duboulayi*. Environmental Biology of Fishes, 56: 455-459.

Buhl J, et al. 2006. From disorder to order in marching locusts.Science312:1402–1406.

Budgey, R. 1998. The three-dimensional structure of bird flocks and its implicaitons for birdstrike tolerance in aircraft. International Bird Strike Committee Proceedings, 24: 207-220.

Bumann, D. J. Krause, and D. Rubenstein. 1997. Mortality risk of spatial positions in animal groups: the danger of being in the front. Behaviour 134: 1063-1076.

Burgos, J.M., and J.K. Horne. 2007. Sensitivity analysis and parameter selection for detecting aggregations in acoustic data. ICES Journal of Marine Science, 64: 160-168.

Canestrari, D., J.M. Marcos, and V. Baglione. 2007. Preproductive success sin creases with group size in cooperative carrion crows, *Corvus corone corone*. Animal Behaviour, 75: 403-416.

Canino, M.F., and K.M. Bailey. 1995. Gastric evacuation of walleye pollock, *Theragra chalcogramma* (Pallas) in Shelikof Straight, Gulf of Alaska. Journal of Fish Biology, 46: 389-103.

Capello, M., M. Soria, P. Cotel, J-L Deneubourg, and L. Dagorn. 2011. Quantifying the interplay between environmental and social effects on aggregated-fish dynamics. PLos ONE 6(12): e28109.

Caraco, T., and M.C. Bayham. 1982. Some geometric aspects of house sparrow flocks. Animal Behaviour, 30: 1255-1256.

Caron, D.M. 1999. Honey bee biology and beekeeping. WicwasPress, Cheshire, Conn.

Chen, K., K-S Chan, K. M. Bailey, K. Aydin, and L. Ciannelli. 2012. A probabilistic cellular automata approach for predator–prey interactions of arrowtooth flounder (*Atheresthes stomias*) and walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. Canadian Journal of Fisheries and Aquatic Sciences, 69: 259-272). doi:10.1139/F2011-1.

Churnside, J., Willson, J. and Tatarskii, V. 1997. Lidar profiles of fish schools. Appl. Opt. 36: 6011-6020.

Clark, P.J., K. Irwig, and W. Wobke. 1997. Emergent properties of teams of agents in the Tileworld. Lecture Notes in Computational Science, 1209: 164-176.

Clay, C.S., and Heist, B.G. 1984. Acoustic scattering by fish: acoustic models and a two-parameter fit. J. Acoustc. Soc Am, 75: 1077-1083.

Coachman, L.K., and R.L. Charnell. 1979. On laternal water mass interaction –a case study, Bristol Bay, Alaska. Journal of Physical Oceanography, 9: 278-297.

Coetzee, J. 2000. Use of a shoal analysis and patch estimations system (SHAPES) to characterize sardine schools. Aquatic Living Resources, 13: 1-10.

Cohen, J. 1988. Statistical power analysis for the behavioral sciences (2nd ed.). Hillsdale, New Jersey: Lawrence Erlbaum Associates.

Conradt L, Roper TJ. 2003. Group decision-making in animals. Nature. 421:155-158.

Conradt L, Roper TJ. 2005. Consensus decision making in animals. Trends Ecol Evol. 20:449-456.

Conradt L, and T.J. Roper TJ. 2007. Democracy in animals: the evolution of shared group decisions. Proc R Soc B-Biol Sci. 274:2317-2326.

Conradt L, Roper TJ. 2009. Conflicts of interest and the evolution of decision sharing. Proc R Soc Lond Ser B Biol Sci. 364:807-819.

Conradt, L., J. Krause, I.D. Couzin, T.J. Roper. “Leading according to need” in self-organizing groups. The American Naturalist, 173: 304-312.

Coolen I, van Bergen Y, Day RL, Laland KN. 2003. Species difference in adaptive use of public information in sticklebacks. Proc R Soc Lond Ser B Biol Sci. 270:2413-2419.

Couzin ID, and J. Krause. 2003. Self-organization and collective behavior in vertebrates. Advanced Studies in Behavior, 32:1–75.

Couzin, I. D., J. Krause, N. R. Franks, and S. A. Levin. 2005. Effective leadership and decision-making in animal groups on the move. Nature 433: 513-516.

Couzin, I. D., J. Krause, R. James, G. D. Ruxton, and N. R. Franks. 2002. Collective memory and spatial sorting in animal groups. Journal of Theoretical Biology, 218: 1-11.

Couzin, I.D., and M.E. Laidre. 2009. Fission-fusion populations. Current Biology, 19: r633-r635.

Croze, H., C. Mari, and R.D. Este. 2000. Serengeti's Great Migration. Abbeville Press.

Crozier, R.H., and P. Pamilo. 1996. Evolution of social insect colonies. Oxford University Press, Oxford.

Curio, E, Ernst, U, Vieth, W. 1978. The adaptive significance of avian mobbing II. Cultural transmission of enemy recognition in blackbirds: effectiveness and some constraints. Z Tierpsychol. 48:184-202.

Cutter, G. R. and D. A .Demer. 2007. Accounting for scattering directivity and fish behavior in multibeam-echosounder surveys. ICES Journal of Marine Science, 64(9):1664-1674.

Day RL, MacDonald T, Brown C, Laland KN, Reader SM. 2001. Interactions between shoal size and conformity in guppy social foraging. Anim Behav. 62:917-925.

DeBlois, E.M., and G.A. Rose. 1995. Effect of foraging activity on the shoal structure of cod (*Gadus morhus*). Canadian Journal of Fisheries and Aquatic Sciences, 52: 2377-2387.

Deneubourg, J. L., S. Goss, N. R. Franks, and J. M. Pasteels. 1989. The blind leading the blind: modeling chemically mediated army ant raid patterns. J. Insect Behav. 2: 719-725.

DeRobertis, A., and N. O. Handegard. 2012. Fish avoidance of research vessels and the efficacy of noise-reduced vessels: a review. ICES Journal of Marine Science,70: 34-45. doi:10.1093/icesjms/fss155

DeRobertis, A., D.R. McKelvey, and P.H. Ressler. 2010. Development and application of an empirical multifrequency method for backscatter classification. Canadian Journal of Fisheries and Aquatic Science, 67: 1459-1474.

Dewey MR, Zigler SJ. 1996. An evaluation of fluorescent elastomer for marking bluegills in experimental studies. Prog Fish Cult. 58:219-220.

Dill LM. 1983. Adaptive flexibility in the foraging behavior of fishes. Can J Fish Aquat Sci. 40:398-408.

Diner, N. 1998. Correction on school geometry and density. ICES C.M. 1998/B:1. 51 pp.

Diner, N. 2001. Correction on school geometry and density: approach based on acoustic image simulation. Aquatic Living Resources, 14: 211-222.

Domenici, P., R.S. Ferrari, J. F. Steffensen, and R. S. Batty. 2002. The effects of progressive hypoxia on school structure and dynamics in Atlantic herring *Clupea harengus*. Proceedings of the Royal Society B: Biological Sciences, 269: 2103-2111.

Domenici, P., C. Lefrançois, and A. Shingles. 2007. Hypoxia and the antipredator behaviours if fishes. Philosophical Transactions of the Royal Society B, 362: 2105-2121.

Drews C. 1993. The concept and definition of dominance in animal behaviour. Behaviour 125: 283–313.

Dwyer, D.A., K. M. Bailey, and P.A. Livingston. 1987. Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, with special reference to cannibalism. Canadian Journal of Fisheries and Aquatic Sciences, 44: 1972-1984.

Edwards. S., Pratt, S. 2009. Rationality in collective decision-making by ant colonies. *Proceedings of the Royal Society B,* 276: 3655-3661.

Eggers, D.M. 1976. Theoretical effect of schooling by planktivorous fish predators on rate of prey consumption. Journal of the Fisheries Research Board of Canada, 33: 1964–1971.

Escofier B, Pagès J. 1994. Multiple factor analysis. Comput Stat Data An. 18:121-140.

Farmer, D., Trevorrow, M., and Pedersen, B. 1999. Intermediate range fish detection with a 12-kHz sidescan sonar. J. Acoust. Soc. Am. 106(5): 2481-2490.

Fisher RA (1930) The Genetical Theory of Natural Selection. Clarendon Press, Oxford

Foote, K.G., 1980. Importance of the swimbladder in acoustic scattering by fish: a comparison of gadoid and mackerel target strengths. J. Acoustc. Soc. Am, 67: 2084-2089.

Foote, K.G. and J.J. Traynor. 1988. Comparison of walleye pollock target-strength estimates determined from in situ measurements and calculations based on swimbladder form. Journal of the Acoustical Society of America, 83: 9-17.

Frederick JL. 1997. Evaluation of fluorescent elastomer injection as a method for marking small fish. Bull Mar Sci. 61:399-408.

Fréon, P., F. Gerlotto, and M. Soria. 1996. Diel variability of school structure with special reference to transition periods. ICES Journal of Marine Science, 53: 459-464.

Fréon, P., and O.A. Misund. 1999. Dynamics of pelagic fish distribution and behavior: effects on fisheries and stock assessment. Blackwell Science, Oxford. 360 pp.

Gerlotto, F., S. Bertrand, N. Bez, and M. Gutiérrez. 2006. Waves of agitation inside anchovy schools observed with multibeam sonar: a way to transmit information in response to predation. ICES Journal of Marine Science, 63: 1405-1417.

Gerlotto, F., J. Castillo, A. Saavedra, M.A. Barbieri, M. Espejo, and P. Cotel. 2004. Three-dimensional structure and avoidance behavior of anchovy and common sardine schools in central southern Chile. ICES Journal of Marine Science, 61: 1120-1126.

Gerlotto, F. and J. Paramo. 2003. The three-dimensional morphology and internal structure of clupeid schools as observed using vertical scanning multibeam sonar. Aquatic Living Resources, 16: 113-122.

Giardina, I. 2008. Collective behavior in animal groups: theoretical models and empirical studies. HFSP Journal, 2 (4): 205-219.

Godin, J.G.J. and S.A. Smith. 1988. A fitness cost of foraging in the guppy. Nature (London), 333: 69-71.

Grant, S.M. and J.A. Brown. 1999. Variation in condition of coastal Newfoundland 0-group Atlantic cod (*Gadus morhua*): field and laboratory studies using simple condition indices. Mar. Biol. 133:611-620.

Griffiths SW, Magurran AE. 1997. Familarity in schooling fish: how long does it take to acquire? Anim Behav. 53:945-949.

Grünbaum, D. 1998. Schooling as a strategy for taxis in a noisy environment. Evol Ecol. 12:503-522.

Grünbaum D, Viscido SV, Parrish JK. 2005. Extracting interactive control algorithms from group dynamics of schooling fish. Lecture Notes in Control and Information Sciences, 309:103-117.

Gueron, S., and S. A. Levin. 1993. Self-organization of front patterns in large wildebeest herds. Journal of Theoretical Biology, 165: 541-552.

Gueron S., Levin S.A., Rubenstein D.I. 1996. The dynamics of herds: from individuals to aggregations. Journal of Theoretical Biology, 182:85-98.

Guhl, A.M.The social order of chickens . Scientic American, Vol. 194(2), pp. 42{46,1956.

Guttal, V., and I.D. Couzin. 2010. Social interactions, information use, and the evolution of collective migration. Proceedings of the National Academy of Sciences, 107: 16172-16177.

Guttormsen, M.A., C.D. Wilson, and S. Stienessen. 2002. Echo integration-trawl survey results for walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska during February and March, 2002. In:
Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pac. Fish. Manage. Council, Anchorage, AK, Appendix D:1-47.

Hamilton, W. D.. 1971. Geometry for the selfish herd. Journal of Theoretical Biology, 31: 295-311.

Handegard, N.O. and K. Williams. 2008. Automated tracking of fish in trawls using the DIDSON (Dual frequency IDentifican SONar). ICES J Mar Biology, 65: 636-644.

Haralabous, J., and Gerogakarakos, S. 1996. Artificial neural networks as a tool for species identification of fish schools. ICES Journal of Marine Science, 53: 173-180.

Hare et al. 2000. Chimpanzees know what conspecifics do and do not see. Animal Behaviour, 59: 771-785.

Hart PJB. 1993. Teleost foraging: facts and theories. In: Pitcher, JT, editor. Behavior of Teleost Fishes, 2nd ed. London, England: Chapman and Hall. p. 253-284.

Hart, A.G., and F. L. W. Ratnieks. 2005. Crossing the taxonomic divide: conflict and its resolution in societies of reproductively totipotent individuals. Jorunal of evolutionary biology, 18: 383-395.

Hartley, R., and A. Zisserman. 2003. Multiple view geometry in computer vision. Cambridge University Press, Cambridge.

Hazen, E.L. and J.K. Horne. 2004. Comparing the modelled and measured target-strength variability of walleye pollock, Theragra chalcogramma. ICES Journal of Marine Science, 61: 363-377.

Helfman GS. 1984. School fidelity in fishes: the yellow perch pattern. Anim Behav. 32:663-672.

Helfman, G.S., and E.T. Schultz. 1984. Social tradition of behaviorural traditions in a coral reef fish. Animal Behaviour, 32: 379-384.

Hemelrijk, C. K., 2000. Towards the integration of social dominance and spatial structure. Animal Behaviour, 59: 1035-1048.

Hemelrikj, C.K., and H. Hidenbrandt. 2008. Self-organised shape and frontal density of fish schools. Ethology, 114: 245-254.

Hemelrijk, C.K., and H. Kunz. 2004. Density distribution and size sorting in fish schools: an individual-based model. Behavioral Ecology, 16: 178-187.

Hiramatsu, K., S. Shikasho, and K. Mori. 2000. Mathematical modeling of fish schooling of Japanese medaka using basic behavioral patterns. J. Fac. Agric. Kyushu Univ. 45: 237-253.

Hoare, D. J., I. D. Couzin, G. J. Godin, and J. Krause. 2004. Context-dependent group size choice in fish. Animal Behaviour, 67: 155-164.

Hoare, D.J., and J. Krause. 2003. Social organization, shoal structure and information transfer. Fish and Fisheries, 4: 269-279.

Hollowed, A.B., J.N. Ianelli, and P.A. Livingston. 2000. Including predation mortality in stock assessments: a case study for Gulf of Alaska walleye pollock. ICES J. Mar. Sci. 57:279-293.

Hoare, D.J., G.D. Ruxton, J.-G. J. Godin, and J. Krause. 2000. The social organization of free-ranging fish shoals. Oikos, 89: 546-554.

Holland, R.A., M. Wikelski, and D. S. Wilcove. 2006. How and why do insects migrate? Science , 313(5788):794-796

Holmin, A.J., N. O. Handegard, R.J. Korneliussen, and D. Tjøstheim. 2012. Simulations of multi-beam sonar echos from schooling individual fish in a quiet environment. Journal of the Acoustical Society of America, 132(6): 3720-3734.

Honkalehto, T., A. McCarthy, P. Ressler, K. Williams, and D. Jones. 2012. Results of the acoustic-trawl Survey of Walleye Pollock (Theragra chalcogramma) on the U.S. and Russian Bering Sea Shelf in June – August 2010 (DY1006). AFSC Processed Report 2012-01, 57p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

Honkalehto, T., A. McCarthy, P. Ressler, S. Stienessen, and D. Jones. 2010. Results of the acoustic-trawl Survey of Walleye Pollock (*Theragra chalcogramma*) on the U.S. and Russian Bering Sea Shelf in June – August 2009 (DY0909). AFSC Processed Report 2010-03, 57p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

Honkalehto, T., N. Williamson, D. Jones, A. McCarthy, and D. McKelvey. 2008. Results of the echo integration-trawl survey of walleye pollock (*Theragra chalcogramma*) on the U.S. and Russian Bering Sea shelf in June and July 2007. U.S. Department of Commerce, NOAA Technical Memo. NMFS-AFSC-190, 53 p.

Huntingford, F.A. and A. K Turner. 1987. Animal conflict. *Chapman and Hall Animal Behaviour Series*. Chapman and Hall, London, 448 pp

Huse G, Railsback S, Fernö A. 2002. Modelling changes in migration pattern of herring: collective behavior and numerical domination. J Fish Biol. 60:571-582.

Huth, A., and Wissel, C. 1994. The simulation of fish schools in comparison with experimental data. Ecological Modelling, 75:135 – 146.

Huth, A. and C. Wissel. 1992. The simulation of the movement of fish schools. J. Thero. Biol., 156: 365-385.

ICES. 2001. Report of the ICES Advisory Committee on Ecosystems. ICES Cooperative Research Report, 249. 75 pp.

Iglesias, M., P. Carrera, and R. Muino. 2003. Spatio-temporal patterns and morphological characterization of multispecies pelagic fish schools in the North-Western Mediterranean Sea. Aquatic Living Resources, 16: 541-548.

Ioannou, C.C., V. GUttal, and I.D. Couzin. 2012. Predatory fish select for coordinated collective motion in virtual prey. Science, 337: 1212-1215.

Ioannou, C.C., C.R. Tosh, L. Neville, and J. Krause. 2007. The confusion effect –from neural networks to reduced predation risk. Behavioral Ecology, 21: 126-130.

Israeli, D. and E. Kimmel. 1996. Monitoring the behavior of hypoxia-stressed *Carrasius auratus* by computer vision. Aquaculture Engineering, 15: 423-440.

Jaffe, J., Moore, K., McLean, J., and Strand, M. 2001. Underwater optical imaging: status and prospects. Oceanography 14(3): 64-75.

Jakob, E.M., S.D. Marshall, and G.W. Uetz. 1996. Estimating fitness: a comparison of body condition indices. Oikos 77:61-67.

Janson CH, Goldsmith ML (1995) Predicting group size in primates: foraging costs and predation risks. Behav Ecol 6:326–336

Jeschke, J.M. and R. Tollrian. 2007. Prey swarming: which predators become confused and shy? Animal Behaviour, 74(3): 387-393.

Kang, M., S. Honda, and T. Oshima. 2006. Age characteristics of walleye pollock school effects. ICES Journal of Marine Science, 63: 1465-1476.

Keenleyside, M.H.A. 1979. Social organization. In: M.H.A. Keenleyside (ed .), Diversity and adaptation in fish behaviour. Springer-Verlag, New York, pp. 149-177.

Kendal JR, Rendell L, Pike T, Laland KN. 2009. Nine-spined sticklebacks deploy a hill-climbing social learning strategy. Behav Ecol. 20:238-244.

Kendal RL, Coolen I, Laland KN. 2004. The role of conformity in foraging when personal and social information conflict. Behav Ecol. 15:269-277.

Kerr JP. 1963. Grouping behavior of the zebrafish as influenced by social isolation. Am Zool. 2:532-533.

Kim, S. 1990. Status of fishery and science of Bering Sea walleye pollock: 1. History and importance of fisheries. Ocean Research, 12: 117-128.

Kinder, T.H., and J.D. Schumacher. 1981. Hydrographic structure over the continental shelf of the Southeast Bering Sea. In: D.W. Hood, J.A. Calder (Eds.), The Eastern Bering Sea Shelf: Oceanography and Resources, University of Washington Press, Seattle, WA , pp. 31–52.

Kline, R.B. 1998. Principles and Practice of Structural Equation Modeling. New York: The Guilford Press.

Kloppmann, M.H.F., H. Hillgruber and H. Von Westernhagen. 2002. Wind-mixing effects on feeding success and condition of blue whiting larvae in the Porcupine Bank area. Mar. Ecol. Prog. Ser. 235:236-277.

Kolmer, K. and J. Heinze. 2000. Rank orders and division of labour amoung unrelated cofounding ant queens. Proceedings of the Royal Society B, 267: 1729-1734.

Kotwicki, S., T.W. Buckley, T. Honkalehto, and G. Walters. 2005. Variation in the distribution of walleye pollock (*Theragra chalcogramma*) with temperature and implications for seasonal migration. Fish. Bull. 103:574-587.

Krause, J., R. K. Butlin, N. Peuhkuri, and V. L. Pritchard. 2000. The social organization of fish shoals: a test of the predictive power of laboratory experiments for the field. Biol. Rev. 75: 477-501.

Krause, J., J.-G.J. Godin, and D. Brown. 1996. Size-assortativeness in multi-species fish shoals. Journal of Fish Biology, 49: 221-225.

Krause, J., D. J. Hoare, D. Croft, J. Lawrence, A. Ward, G.D. Ruxton, J.G.J. Godin, and R. James. 2000. Fish shoal composition: mechanisms and constraints. Proceedings for the Royal Society of London B, 267: 2011-2017.

Krause, J. and Ruxton, G. D. 2002. *Living in Groups*. Oxford University Press, Oxford, England. 228 pp.

Krause, J., G. Ruxton, G., and D. Rubenstein. 1998. Is there always an influence of shoal size on predator hunting success? Journal of Fish Biology 52, pp 494-501.

Krause, J., G. Staaks, and T. Mehner. 1998. Habitat choice in shoals of roach as a function of water temperature and feeding rate. J. Fish Biol. 53:377-386.

Krebs, J.R., M.H. MacRobers, and J.M. Cullen. 1972. Flocking and feeding in the great tit *Parus major* –an experimental study. Ibis 114: 507-534.

Kummer H, Goodall J. 1985. Conditions of innovative behavior in primates. Phil Trans R Soc Lond B Bio Sci. 308:203-214.

Lachlan, R., L. Crooks, and K.N. Laland. 1998. Who follows whom? Sholaing preferences and social learning of foraging information in guppies. Animal Behaviour, 56: 181-190.

Laland KN, Atton N, Webster MW. 2011. From fish to fashion: experimental and theoretical isights into the evolution of culture. Phil Trans R Soc Lond B Bio Sci. 366:958-968.

Laland, K.N, and K. Williams. 1997. Shoaling generates social learning of foraging information in guppies. Animal Behavior, 53: 1161-1169.

Laland KN, Williams K. 1998. Social transmission of maladaptive information in the guppy. Behav Ecol. 9:493-499.

Lawson, G. L., Baranbe, M., and Freon, P. 2001. Species identification of pelagic fish schools on the South African continental shelf using acoustic descriptors and ancillary information. ICES Journal of Marine Science, 58: 275-287.

Le Boeuf BJ. 1974. Male-male competition and reproductive success in elephant seals. *Amer. Zool.* **14**: 163–176.

Lima, S. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. Animal Behaviour, 49(1): 11-20.

Longuet-Higgins, H.C., 1981. A computer algorithm for reconstructing a scene from two projections. Nature, 293: 133-135.

Mackinson, S., L. Nøttestad, S. Guénette, T. Pitcher, O.A. Misund, and A. Fernö. 1999. Cross-scale observations on distribution and behavioural dynamics of ocean feeding Norwegian spring-spawning herring (*Clupea harengus* L.). ICES Journal of Marine Science, 56: 613-626.

MacLennan, D.N., P.G. Fernandes, and J. Dalen. 2002. A consistent approach to definitions and symbols in fisheries acoustics. ICES Journal of Marine Science, 59: 365-369.

Magurran, A. E., W. Oulton, and T. J. Pitcher. 1985. Vigilant behaviour and shoal size in minnows. Zeitschrift für Tierpsychologie, 67: 167-178.

Magurran, A.E., and B.H. Seghers. 1994. Predator inspection behaviour covaries with schooling tendency amongst wild guppy, *Poecilia reticulate*, populations in Trinidad. Behaviour, 128: 121-134.

Majolo, B., A.B., Vizioli, andG. Schino. 2008. Costs and benefits of group living in primates: group size effects on behaviour and demography. Animal Behaviour, 76: 1235-1247

Major, P.F., and L.M. Dill. 1978. The three-dimensional structure of airbourne bird flocks. Behavioral Ecology and Sociobiology, 4: 111-122.

Makarenkov, V. and P. Legendre. 2002. Nonlinear redundancy analysis and canonical correspondence analysis based on polynomial regression. Ecology 83: 1146-1161.

Makris, N.C., Ratilal, P., Symonds, D., Jagannathan, S., Lee, S., and Nero, R. 2006. Fish population and behavior revealed by instantaneous continental shelf-scale imaging. Science 311 (5761): 660-663.

McCann, T. S. "Aggression and Sexual Activity of Male Southern Elephant Seals, Mirounga Leonina." Journal of Zoology 195 (1981): 295-310. Web.

Mech, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Doubleday Publishing Co., New York.

Mech, L. David. 1999. Alpha status, dominance, and division of labor in wolf packs. Canadian Journal of Zoology 77:1196-1203.

Megrey, B.A. 1989. Exploitation of walleye pollock resources in the Gulf of Alaska, 1964-1988: portrait of a fishery in transition. In: Proceedings of an international symposium on the biology and management of walleye pollock. Alaska Sea Grant, University of Alaska, Fairbanks, Vol.89-1, pp. 33-58.

Milinski M, and R. Heller. *1978*. Influence of a predator on the optimal foraging behaviour of sticklebacks *(Gasterosteus aculeatus L.).* Nature, 275*:* 642-*644.*

Miller, R.S. and W.J.D. Stephen. 1996. Spatial relationships in flocks of sandhill cranes (Grus Canadensis). Ecology, 47: 323-327.

Mirabet, V., P. Fréon, and C. Lett. 2008. Factors affecting information transfer from knowledgeable to naïve individuals in groups. Behavioral Ecology and Sociobiology 63: 159-171.

Misund, O. A. 1997. Underwater acoustics in marine fisheries and fisheries research. Reviews in Fish Biology and Fisheries, 7: 1-34.

Misund, O.A., and A. Aglen. 1992. Swimming behviour of fish schools in the North Sea during acoustic surveying and pelagic trawl sampling. ICES J. Mar. Sci. 49:325-334.

Misund, O. A., and Coetzee, J. 2000. Recording fish schools by multi-beam sonar: potential for validating and supplementing echo-integration recordings of schooling fish. Fisheries Research, 47: 149-159.

Misund, O.A., H. Vilhjalmsson, S.H. Jakupsstovu, I. Rottingen, S. Belikov, O. Asthorsson, J. Blindheim, J. Jonsson, A. Krysov, S.A. Malmberg, and S. Sveinbjornsson. 1998. Distribution, migration and abundance of Norwegian spring spawning herring in relation to the temperature and zooplankton biomass in the Norwegian Sea as recorded by coordinated surveys in Spring and Summer. Sarsia 83:117-127.

Molloy, P.P., I.M. Côté, and J.D. Reynolds. 2011. Why spawn in aggregations? In: Y. Sadovy de Mitcheson and P.L. Colin (eds). Reef fish spawning aggregations: biology, research and management. Springer Dordrecth Heidelberg London New York, pp. 57-84.

Morgan, M. J. 1988. The influence of hunger, shoal size and predator presence on foraging in bluntnose minnows. Animal Behaviour, 36: 1317-1322.

Morgan, M. J., and P. W. Colgan. 1987. The effects of predator presence and shoal size on foraging in bluntnose minnows, *Pimephales notatus*. Environmental Biology of Fishes, 20: 101-111.

Muiño, R., P. Carrera, and M. Iglesias. 2003. The characterization of sardine (*Sardina pilchardus* Walbaum) schools off the Spanish-Atlantic coast. ICES Journal of Marine Science, 60: 1361-1372.

Muir, W. M. 2009. Genetic selection and behaviour. Canadian Journal of Animal Science 89 (1): 182–182.

Nero, R.W. and Magnuson, J.J. 1989. Characterization of patches along transects using high-resolution 70-khz integrated acoustic data. Canadian Journal of Fisheries and Aquatic Sciences 46: 2056-2064.

Neill, S.R.StJ., and J.M. Cullen. 1974. Experiments on whether schooling by their prey affects the hunting behaviour of cephalopod and fish predators. J. Zool. Lond. 172:549-469.

O'Connor, E., and J. Krause. 2003. Effect of light intensity on the shoaling behaviour of the guppy (*Poecilla reticulata*). J. Fish. Biol. 63(Suppl. 1): 254.

Newlands, N.K., and T.A. Porcelli. 2008. Measurement of the size, shape and structure of Atlantic Bluefin tuna schools in the open ocean. Fisheries Research, 91: 42-55.

NMFS 1996. Preliminary cruise results NOAA ship Miller Freeman cruise 96-05: Echo integration-trawl survey of walleye pollock in Shelikof Strait. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE., Seattle, WA 98115-0070. 6 p. Online, http://www.afsc.noaa.gov/RACE/surveys/cruise_archives/cruises1996/results_MF1996-05.pdf.

Nøttestad, L. and B.E. Axelsen. 1999. Herring schooling manoeuvres in response to killer whale attack. Canadian Journal of Zoology, 77: 1540-1546.

Nøttestad, L., B.E. Axelsen, A. Beltestad, A. Fernõ, A. Johannessen, and O.A. Misund. 1996. Schooling dynamics of Norwegian spring spawning herring (*Clupea harengus* L.) in a coastal spawning area. Sarsia, 80: 277-284.

Nowell, K., and P. Jackson. 1996. Panthera Leo. In: *Wild Cats: Status Survey and Conservation Action Plan*. Gland, Switzerland: IUCN/SSC Cat Specialist Group. pp. 17–21.

O’Connor, E., and J. Krause. 2003. Effect of light intensity on the shoaling behaviour of the guppy (*Poecilla reticulata*). J. Fish. Biol. 63(Suppl. 1): 254.

O'Gorman, R., Wilson, D. S.; Sheldon, K. M. 2008. For the good of the group? Exploring group-level evolutionary adaptations using multilevel selection theory. Group Dynamics-Theory Research and Practice 12 (1): 17–26.

Olla, B.L. and M.W. Davis. 1990. Behavioral responses of juvenile walleye pollock *Theragra chalcogramma* Pallas to light, thermoclines and food: possible role in vertical distribution. Journal of Experimental Marine Biology and Ecology, 135: 59-68.

Olla, B.L. and C. Samet. 1974. Fish-to-fish attraction and the facilitation of feeding behavior as mediated by visual stimuli in striped mullet, Mugil cephalus. Journal of the Fisheries Research Board of Canada, 31: 1621-1630.

Olla, B.L., A.L. Studholme, and A.J. Bejda. 1985. Behavior of juvenile bluefish *Pomatomus saltarix* in vertical thermal gradients: influence of season, temperature acclimation and food. Marine Ecology Progress Series, 23: 165-175.

Ona, E. and R. B. Mitson. 1996. Acoustic sampling and signal processing near the seabed: the deadzone revisited. ICES Journal of Marine Science, 53: 677-690.

Osborn, J. 1997. Analytical and digital photogrammetry. In: Animal Groups in Three Dimensions (Ed by J.K. Parrish and W. M. Hammer), pp. 36-60. Cambridge: Cambridge University Press.

Page, L.M., H. Espinosa-Pérez, L.T. Findley,C.R. Gilbert and others. 2013. Common and scientific names of fishes from the United States, Canada, and Mexico, 7th edition. Spec Publ Am Fish Soc No. 34, Bethesda, MD.

Pais, D., and N.E. Leonard. 2013. Adaptive network dynamics and evolution of leadership in collective migration. Physica D: Nonlinear Phenomena, 267: 81-93.

Paramo, J., Bertrand, S., Villalobos, H., and Gerlotto, F. 2007. A three-dimensional approach to school typology using vertical scanning multibeam sonar. Fisheries Research, 84: 171–179.

Parrish, J.K., and L. Edelstein-Keshet. 1999. Complexity, pattern, and evolutionary trade-offs in animal aggregations. Science, 284: 99-101.

Parrish, J.K. and W. M. Hamner, editors. Animal Groups in Three Dimensions. Cambridge University Press, 1997

Parrish, J. K., S. V. Viscido, and D. Grünbaum. 2002. Self-organized fish schools: an examination of emergent properties. Biol. Bull. 202: 296-305.

Partridge, B.L. 1980. The effect of school size on the structure and dynamics of minnow schools. Anim Beahv, 28: 68-77.

Partridge, B.L. 1981. Internal dynamics and interrelations of fish in schools. J. Comp. Physiol., 144: 313-325.

Patridge, B.L, T. Pitcher, J.M Cullen, and J. Wilson. 1980. The three-dimensional structure of fish schools. Behavioral Ecology and Sociobiology, 6: 277-288.

Pedersen, T. and M. Jobling. 1989. Growth rates of large, sexually mature cod, *Gadus morhua*, in relation to condition and temperature during an annual cycle. Aquaculture 81:161-168.

Petit O, Gautrais J, Leca J-B, Theraulax G, Deneubourg J-L. 2009. Collective decision-making in white-faced capuchin monkeys. Proc R Soc Lond Ser B Biol Sci. 276:3495-3503.

Pike TW, Laland, KN. 2010. Conformist learning in nine-spined sticklebacks' foraging decisions. Biol Lett. 6:466-468.

Pillot M, Gautrais J, Arrufat P, Couzin ID, Bon R, Deneubourg J-L. 2011. Scalable rules for coherent group motion in a gregarious vertebrate. PLoS ONE 6(1): e14487. doi:10.1371/journal.pone.0014487.

Pitcher, T., A. Magurran, and I. Winfield. 1982. Fish in larger shoals find food faster. Behavioral Ecology and Sociobiology, 10:149-151.

Pitcher, T.J. 1982. Fish in larger shoals find food faster. Behavioral Ecology and Sociobiology, 10: 149-151.

Pitcher TJ, and Parrish JK. 1993. Functions of shoaling behavior in teleosts. In: Pitcher, JT, editor. Behavior of Teleost Fishes, 2nd ed. London, England: Chapman and Hall. p. 363-439.

Pitcher, T.J., and B.L. Partridge. 1979. Fish school density and volume. Marine Biology, 54: 383-394.

Pitman, R. L. and J. W. Durban. 2011. Coopeative hunting behavior, prey selectivity and prey handling by pack ice killer whales (Orcinus orca), type B, in Antarctic Peninsula waters. Marine Mammal Science,

Powell, G. V. N. 1974. Experimental analysis of the social value of flocking by starlings (Sturnus vulgaris) in relation to predation and foraging. Anim. Behaviour, 22: 501–505.

Pulliam, H. R. 1973. On the advantages of flocking. Journal of Theoretical Biology, 38: 419–422.

Pulliam, H.R., and G.C. Millikan. 1982. Social organization in the nonreproductive season. In: D.S. Farner, J.R. King and K. C. Parkes (eds). Avian Biology, vol. 6. Academic Press, London, pp. 169-197.

Pusey, AE., and C. Packer. 1997. The ecology of relationships. In: Krebs JR, Davies NB, editors. Behavioral ecology. An evolutionary approach. 4th ed. Oxford: Blackwell; 1997. p. 254-283.

Reader, S. M., J. R. Kendal, and K. N. Laland. 2003. Social learning of foraging sites and escape routes in wild Trinidadian guppies. Anim. Behav. 66: 729-739.

Reebs S. 2000. Can a minority of informed leaders determine the foraging movements of a fish shoal? Anim Behav. 59:403-409.

Reid, D.G. 2000. Report on echo trace classification. ICES Coop. Res. Rept. 238 107.

Reid, D., C. Scalabring, P. Petigas, J. Masse, R. Aukland, P. Carrera, and S. Gerogakarakos. 2000. Standard protocols for the analysis of school based data from echo sounder surveys. Fisheries Research, 47: 125-136.

Reid, D.G., and E.J. Simmonds. 1993. Image analysis techniques for the study of fish school structure from acoustic survey data. Can. J. Fish. Aquat. Sci. 50: 886-893.

Reader, S.M., J.R. Kendal, and K.N. Laland. 2003. Social learning of foraging sites and escape route in wild Trinidadian guppies. Animal Behavior, 66: 729-739.

Reebs, S. 2000. Can a minority of informed leaders determine the foraging movements of a fish shoal? Anim. Behav. 59: 403-409.

Ressler, P.H., A. DeRobertis, and S. Kotwicki. 2014. The spatial distribution of euphausiids and walleye pollock in the eastern Bering Sea does not imply top-down control by predation. Marine Ecology Progress Series, 503: 111-222. doi:10.3354/meps10736

Ressler, P. H., A. DeRobertis, J.D. Warren, J.N.Smith, and S. Kotwicki. 2012. Developing an acoustic survey of euphausiids to understand tropic interactions in the Bering Sea ecosystem. Deep-Sea Research II, 65-70: 184-195.

Romey WL. 1996**.** Individual differences make a difference in the trajectories of simulated schools of fish. Ecological Modelling, 92:65-77.

Rose, G.A. 1993. Cod spawning on a migration highway in the northwest Atlantic. Nature, 366: 458-461.

Rosnow, R.L. and R. Rosenthanl. 1996. Meta-analytic procedures for combining studies with multiple effect sizes. Psychological Bulletin, 99: 400-106.

Rubenstein, D.I., 1978. On predation, competition, and the advantages of group living. Perspectives in Ethology, 3: 205-231.

Rusby, J., Somers, M., Revie, J., McCartney, B., and Stubbs, A. 1973. An Experimental survey of a herring fishery by long-range sonar. Marine Biology 22: 271-292.

Ryer, C.H., and B.L. Olla. 1991. Information transfer and the facilitation and inhibition of feeding in a school of fish. Environ. Biol. Fish. 30: 317-323.

Ryer, C.H., and B.L. Olla. 1992. Social mechanisms facilitating exploitation of spatially variable ephemeral food patches in a pelagic marine fish. Animal Behavior, 59: 403-409.

Ryer, C.H., and B.L. Olla. 1998*a*. Effect of light on juvenile walleye pollock shoaling and their interaction with predators. Marine Ecology Progress Series, 167: 215-226.

Ryer, C.H., and B.L. Olla. 1998b. Shifting the balance between foraging and predator avoidance: the importance of food distribution for a schooling pelagic forager. Environ. Biol. Fish. 52:467-475.

Scalabrin, C., Diner, N., Weill, A., Hillion, A., and Mouchot, M. 1996. Narrowband acoustic identification of monospecific fish shoals. ICES J. Mar. Sci. 53: 181-188.

Schellinck, J. and T. White. 2011. A review of attraction and repulsion models of aggregation: methods, findings and a discussion of model validation. Ecological Modelling, 222: 1897-1911.

Schumacher, J.D., and P.J. Stabeno. 1998. The continental shelf of the Bering Sea. In: A.R. Robinson, K.H. Brink (Eds.), The Sea: The Global Coastal Ocean: Regional Studies and Synthesis, John Wiley and Sons, New York (1998), pp. 789–822.

Searcy, W. A. 1979. Female choice of mates: a general model for birds and its application to Red-winged Blackbirds (Agelaius phoeniceus). Am. Nat. 114: 77-100.

Schilder MBH, and PL Boar. 1987. Ethological investigations on a herd of plains zebra in a safari park time-budgets, reproduction and food competition. Appl Anim Behav Sci, 18: 45-56.

Seely, T.D. When is self-organizasiton used in biological systems? The Biological Bulletin, 202: 314-318.

Seeley, T. D., Visscher, P.K. 2004. Quorum sensing during nest-site selection by honeybee swarms. Behavioral Ecology and Sociobiology 56: 594-601.

Seyfarth R.M. and Cheney, D.L. Grooming, alliances and reciprocal altruism in vervet monkeys . Nature, Vol. 308, pp. 541{543, 1984

Shrader, A.M., S. Ferreira, and R. van Aarde. 2006. Digital photogrammetry and laster rangefinder technizues to measure African elephants. South African Journal of Wildlife Research, 36: 1-7.

Similä, T. and F. Ugarte. 1993. Surface and underwater observations of cooperatively feeding killer whales in northern Norway. Canadian Journal of Zoology, 71: 1494-1499.

Simmonds, E., N.J. Williamson, F. Gerlotto, and A. Aglen. 1992. Acoustic survey design and analysis procedures: a comprehensive review of current practice. ICES Cooperative Research Report, 187: 112 pp.

Simmonds, J. and D. MacLennan. 2005. Underwater Sound. In: Fisheries Acoustics Theory and Practice, 2nd ed. Oxford, England: Blackwall Science. p. 20-69.

Simrad. 2004. Simrad ER60 scientific echo sounder operator manual. Simrad Subsea A/S, Strandpromenaden 50, Box 111, N-3191 Horten, Norway.

Sober, E., & Wilson, D.S. 1998. Unto others: The evolution and psychology of unselfish behavior. Cambridge, MA: Harvard University Press.

Sogard, S.M. and B.L. Olla. 1993. Effects of light, thermoclines and predator presence on vertical distribution and behavioral interaction of juvenile walleye pollock, *Theragra chalcogramma* Passas. Journal of Experimental Marine Biology and Ecology, 167: 179-195.

Sogard, S.M., and B.L. Olla. 1997. The influence of hunger and predation risk on group cohesion in a pelagic fish, walleye pollock, Theragra chalcogramma. Environmental Biology of Fishes, 50: 405-413.

Sogard, S.M., and B.L. Olla. 2000. Endurance of simulated winter conditions by age-0 walleye pollock: effects of body size, water temperature and energy stores. J. Fish. Biol. 56:1-21.

Soria, M. T. Bahri, and F. Gerlotto. 2003. Effect of external factors (environment and survey vessel) on fish school characteristics observed by echosounder and multibeam sonar in the Mediterranean Sea. Aquatic Living Resources, 16: 145-157.

Spence R, Gerlach G, Lawrence C, Smith C. 2008. The behavior and ecology of the zebrafish, Danio rerio. Biol Rev Camb Philos. 83:13-34.

Stabeno, P.J., N.B. Kachel, S.E. Moore, J.M. Napp, M. Sigler, A. Yamaguchi, and A.N. Zerbini. 2012. Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem.

Steeves, Tanner K., Shannon B. Kearney-McGee, Margaret A. Rubega, Calvin L. Cink and Charles T. Collins. 2014. Chimney Swift (Chaetura pelagica), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/646 doi:10.2173/bna.646

Stienessen, S.C. and J.K. Parrish. 2013. The effect of disparate information on individual fish movement and emergent group behavior. Behavioral Ecology, 24(5): 1150-160. doi: 10.1093/beheco/art042.

Stienessen, S.C. and C.D. Wilson. 2008. Juvenile Walleye Pollock Aggregation Structure in the Gulf of Alaska. ***In***: Kruse, G.H. *et al.* (Ed.) (2008). *Resiliency of gadid stocks to fishing and climate change: 24th Lowell Wakefield Fisheries Symposium.* pp. 271-287. Alaska Sea Grant College Program, University of Alaska Fairbanks: Fairbanks. ISBN 978-1-56612-126-2. 364 pp.

Streiner, D.L. 2005. Finding Our Way: An Introduction to Path Analysis. The Canadian Journal of Psychiatry, 50(2): 115-122.

Sumpter DJT, Krause J, James R, Couzin ID, Ward AJW. 2008. Consensus decision making by fish. Curr Biol. 18:1773-1777.

Sumpter DJT, Pratt, SC. 2009. Quorum responses and consensus decision making. Phil Trans R Soc Lond B Bio Sci. 364:743-753.

Svensson, P.A., I. Barber, and E. Forsgren. 2000. Shoaling behviour of the two-spotted goby. Journal of Fish Biology, 56: 1477-1487.

Svensson, B.G., and E. Petersson. 1992. Why insects swarm: testing the models for lek mating systems on swarming empis borealis females. Behavioral Ecology and Sociobiology: 31: 253-261.

Swaney W, Kendal J, Capon H, Brown C, Laland KN. 2001. Familiarity facilitates social learning of foraging behavior in the guppy. Anim Behav. 62:591-598.

Swartzman, G. 1997. Analysis of the summer distribution of fish schools in the Pacific Eastern Boundary Current. ICES Journal of Marine Science, 54: 105-116.

Swartzman, G. 2001. Spatial patterns of Pacific hake (*Merluccius productus*) shoals and euphausiid patches in the California current ecosystem. . ***In***: Kruse, G.H. *et al.* (Ed.) (2001). *Spatial Processes and Management of Marine Populations.* pp.495-512. Alaska Sea Grant College Program, University of Alaska Fairbanks: Fairbanks. ISBN 978-1-56612-268-3. 720 pp.

Swartzman, G., W. Stuetzle, K. Kulman, and M. Powojowski. 1994. Relating the distribution of pollock schools in the Bering Sea to environmental factors. ICES Journal of Marine Science, 51: 481-492.

Swedell, L. 2011. African Papionins: Diversity of Social Organization and Ecological Flexibility. IN *Primates in Perspective, Second Edition* (Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf, RM, eds). New York: Oxford University Press, pp. 241-277.

Tegeder, R.W., and J. Krause. 1995. Density-dependence and numerosity in fright stimulated aggregation behaviour of shoaling fish. Philosophical Transactions of the Royal Society of London, Series B, 350: 381-390.

Tella, J. L. 2002. The evolutionary transition to coloniality promotes higher blood parasitism in birds. J. Evol. Biol, 15: 32.-41.

Theberge, J.B. and J. Bruce Falls. 1967. Howling as a means of communication in timber wolves. Amer Zool, 7: 331-338.

Theodorakis, C.W. 1989. Size segregation and the effects of oddity on predation risk in minnow schools. Animal Behaviour. 38: 496-502.

Tien, J. H., S. A. Levin, and D. I. Rubenstein. 2004. Dynamics of fish shoals: identifying key decision rules. Evol. Ecol. Research 6: 555-565.

Towler, R.H., J M. Jech, and J. K. Horne. 2003. Visualizing fish movement, behavior, and acoustic backscatter. Aquatic Living Resources, 16: 277-282.

Traynor, J.J. 1986. Midwater abundance of walleye pollock in the eastern Bering Sea, 1979 and 1982. International North Pacific Fish Commission Bulletin, 45: 121-135.

Trenkel, V.M., L. Berger, S. Bourguignon, M. Doray, R. Fablet, J. Massé, V. Mazauric, C. Poncelet, G. Quemener, C. Scalabrin, and H. Villalobos. 2009. Overview of recent progress in fisheries acoustics made by Ifremer with examples from the Bay of Biscay. Aquatic Living Resources, 22: 433–445.

Trenkel, V.M. , V. Mazauric, and L. Berger. 2008. The new fisheries multibeam echosounder ME70: description and expected contribution to fisheries research. ICES Journal of Marine Science, 65:645-655.

Turner, G. and T. Pitcher. 1986. Attack abatement: a model for group protection by combined avoidance and dilution. American Naturalist, 128:228-240.

van Bergen Y, Coolen I, Laland, KN. 2004. Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. Proc R Soc Lond Ser B Biol Sci. 271:957-962.

Viscido, S. V., J. K. Parrish, and D. Grünbaum. 2004. Individual behavior and emergent properties of fish schools: a comparison of observation and theory. Mar. Ecol. Prog. Ser. 273: 239-249.

Viscido SV, Parrish, JK, Grünbaum D. 2005. The effect of population size and number of influential neighbors on the emergent properties of fish schools. Ecological Modelling, 183:347-363.

Viscido SV, Parrish JK, Grünbaum D. 2007. Factors influencing the structure and maintenance of fish schools. Ecological Modelling, 206:153–165.

Wade, M. J., Bijma, P., Ester, E. D., & Muir, W. M. 2010. Group selection and social evolution in the domesticated animals. *Evolutionary Applications, 3*(5-6), 453-465.

Waite, R.K. 1982. Local enhancement for food finding by rooks, (*Corvus frugilegus*) foraging on grassland. Z. Tierpsychology, 57: 15-36.

Watt, P.J., S.F. Nottingham, and S. Young. 1997. Toad tadole aggregation behavior: evidence for a predator avoidance function. Animal Behaviour: 54: 865-872.

Walline, P.D. 2007. Geostatistical simulations of eastern Bering Sea walleye pollock spatial distributions, to estimate sampling precision. ICES Journal of Marine Science, 64:559-569.

Walline, P.D., C.D. Wilson, A.B. Hallowed, and S.C. Stienessen. 2012. Short-term effects of commercial fishing on the distribution and abundance of walleye pollock (*Theragra chalcogramma*). Canadian Journal of Fisheries and Aquatic Science, 69: 354-368.

Ward, A.J.W, and J. Krause. 2001. Body length assortative shoaling in the European minnow, *Phoxinus phoxinus*. Animal Behaviour, 62: 617-621.

Ward AJW, Sumpter DJT, Couzin ID, Hart PJB, Krause J. 2008. Quorum decision-making facilitates information transfer in fish shoals. Proc Nat Acad Sci. 105:6498-6953.

Warburton K. 2003. Learning of foraging skills in fish. Fish and Fish. 4:203-215.

Watt, P.J., S.F. Nottingham, and S. Young. 1997. Toad tadole aggregation behavior: evidence for a predator avoidance function. Animal Behaviour: 54: 865-872.

Weber, T.C., D. Grünbaum, and T.K. Stanton. 2014. Obervations of fission/fusion processes in fish aggregations using a multibeam echosounder. J. Acoust. Soc. Am, 135: 2153.

Webster, T., S. Dawson, and E. Slooten. 2010. A simple laser photogrammetry technizue for measuring Hector's deolphins (Cephalorhynchus hectori) in the field. Marine Mammal Science, 26: 296-308.

Weston, D. and Revie, J. 1989. A 5-day long-range sonar record of an extensive concentration of fish. J. Acoust. Soc. Am. 86(4): 1608-1611.

Wikelski, M., C. Carbone, and F. Trillmich. 1996. Lekking in marine iguanas: female grouping and male reproductive strategies. Animal Behaviour, 52: 581-596.

Wilkinson, G.S. Reciprocal food sharing in the vampire bat . Nature, Vol. 308, pp. 181{184, 1984.

Williams GC. 1966. Adaptation and Natural Selection. Oxford University Press.

Williamson, N. and J. J. Traynor. 1996. Application of a one-dimensional geostatistical procedure to fisheries acoustic surveys of Alaskan pollock. ICES Journal of Marine Science, 53:423-428.

Wilson, C.D., A.B. Hollowed, M. Shima, P. Walline, and S. Stienessen. 2003. Interactions between commercial fishing and walleye pollock. Alaska Fisheries Research Bulletin, 10: 61-77.

Wilson, D. S. 1997. Altruism and organism: disentangling the themes of multilevel selection theory. The American Naturalist, *150*(S1), S122-S134.

Winston, M.L. 1987. The biology of the honey bee. Harvard University Press, Cambridge, Mass.

Yamamura, O., S. Honda, O. Shida, and T. Hamatsu. 2002. Diets of walleye pollock *Theragra chalcogramma* in the Doto area, northern Japan: ontogenetic and seasonal variations. Mar. Ecol. Prog. Ser. 238:187-198.

Zar, J.H. 1996. Biostatistical analysis, 3rd ed., Prentice Hall. Upper Saddle River, NJ, USA, 662 pp.

Zimen, E. 1975. Social dynamics of the wolf pack. In The wild canids: their systematics, behavioral ecology and evolution. Edited by M. W. Fox. Van Nostrand Reinhold Co., New York. pp. 336-368.

Zimen, E. 1982. A wolf pack sociogram. In Wolves of the world. Edited by F. H. Harrington, and P. C. Paquet. Noyes Publishers, Park Ridge, NJ. pp. 282-322.