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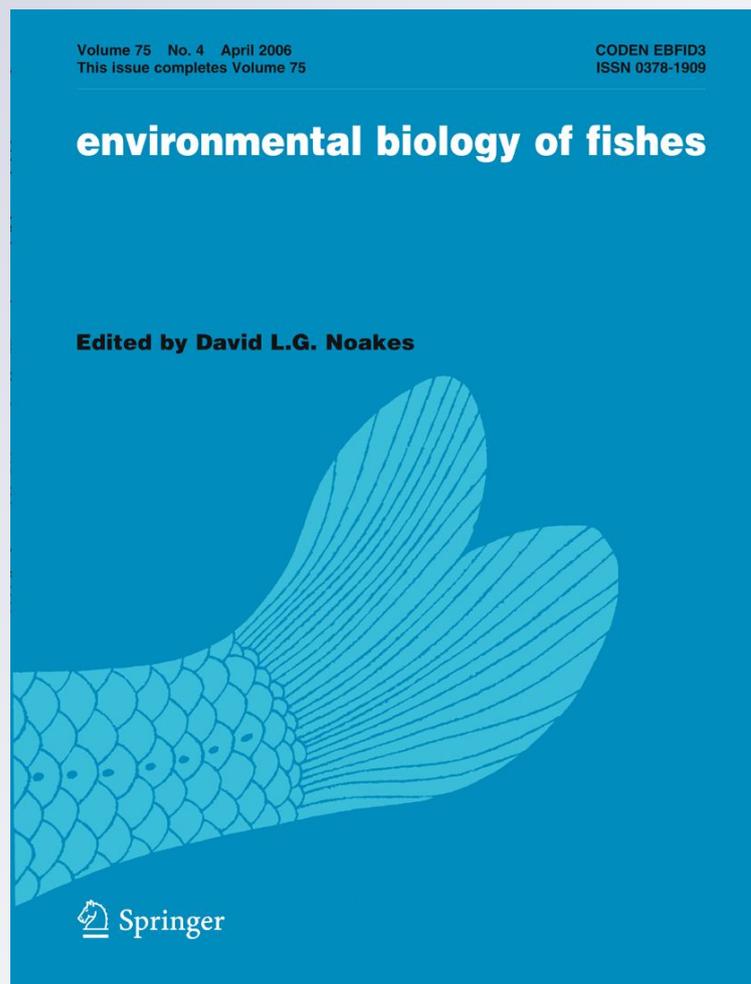
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Abstract Animals swimming in tidal environments continuously interact with water currents which may either hinder or aid their movement. It is difficult to observe the orientation of an organism relative to the current when it is swimming in the wild without specialized telemetry; however, using the total recorded movement vector and the current vector, one can use vector analysis to calculate the actual movement of the animal. Here, we apply this method to six tracks of green sturgeon (*Acipenser medirostris*) in the San Francisco Estuary, using current vectors derived from a hydrodynamic model. Three movements were near the surface in deeper, high-current regions of the bay and three were near the bottom in shallow, low-current areas. The total displacement over ground was faster at the surface (0.9 m sec^{-1} versus 0.5 m sec^{-1}) and occurred in stronger currents (0.7 m sec^{-1} versus 0.4 m sec^{-1}), but the swimming speeds of the fish were similar between surface and bottom movements (0.5 m sec^{-1} versus 0.6 m sec^{-1}). All surface movements were in the direction of the current, and two of the fish also oriented closely to the flow. In contrast, none of the three benthic movements were in the direction of the current, and two were oriented opposite to the flow. It seems plausible that green sturgeon orient to and make use of water currents to efficiently move through tidal habitats, riding the flow in high-current areas, and moving independently of, or even into, the flow in slower currents.

Keywords Rheotaxis · Orientation · Selective tidal stream transport · Vector analysis

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Introduction

Water currents, whether in the form of large-scale oceanic gyres, wind-generated surface currents, tidal flows, or running rivers, are a factor in the daily lives of most animals that swim (Arnold 1981). These currents may be both an impediment and an asset to an organism. Currents may deflect moving animals off course, requiring compensatory orientation and movement. Additionally, moving in opposition to a current increases the energetic cost of transport since the animal has to exert additional effort to compensate for the retrograde movements of the water mass in which it is swimming. Alternatively, currents can be beneficial. They may carry food items on which to

feed, chemical cues on which to home, or the animal itself, facilitating an individual's movement and reducing energetic costs. Given such costs and benefits, swimming animals can be expected to have evolved means to both detect currents and use them when possible to move efficiently, thus minimizing energy expenditure (Bernatchez and Dodson 1987).

Perhaps the best example of the influence of currents on movement and directionality is 'selective tidal stream transport' (STST), a behavior first described in elvers of European eel (*Anguilla anguilla*) by Creutzberg (1961), and later defined by Greer Walker et al. (1978) in their studies of the migration of European plaice (*Pleuronectes platessa*) in the English Channel. STST can be envisioned as a 'ratchet' in which the organism makes forward progress by moving into the water column to take advantage of tidal currents heading in a particular direction, and returns to the substrate to wait out currents moving in the opposite direction. During the period of mid-water transport, the organism may either drift passively, gaining all of its net movement from the current, or it may swim while aligned in the direction of the flow, thus adding its own forward movement to that of the water mass (Arnold 1981). STST has since been described in adults of such diverse species as cod (*Gadus morhua*; Arnold et al. 1994), sole (*Solea solea*) and dogfish (*Scyliorhinus canicula*; Greer Walker et al. 1980), American eel (*Anguilla rostrata*; Parker and McCleave 1997), and sockeye salmon (*Oncorhynchus nerka*; Levy and Cadenhead 1995). It is also widely reported in the planktonic larval stages of fishes such as European flounder (*Platichthys flesus*; Jager 1999), menhaden (*Brevoortia tyrannus*; Hettler and Barker 1993), spot (*Leistomus xanthurus*) and pinfish (*Lagodon rhomboide*; Forward et al. 1998).

Studies of STST in adult fishes to date have generally focused on the role of the behavior in migration through tidally-dominated habitats, such as plaice moving through the English Channel (Greer Walker et al. 1978); however, currents are ubiquitous and have broader relevance in the lives of most fishes. Energy not spent on activity is instead available for growth and reproduction (Harden Jones 1980); therefore, a fish could shift the energy budget in its favor by opportunistically using predictable, local currents in its environment to assist movement. Indeed, Weihs (1978) argued that following the flow would be most beneficial on short journeys because the cost of the time spent not moving would be minimized relative to the benefit gained from swimming with the flow. The ability to detect and utilize currents should be particularly relevant to those species that routinely move in complex current environments such as diadromous fishes that inhabit such diverse habitats as the open ocean, tidal estuaries, and the mono-directional flow of rivers during the course of their lives (Arnold 1981).

It is extremely challenging to examine the orientation behavior of a free-swimming animal. One needs to know the heading and speed of both the water current and the animal at all times, yet continuous direct observations are rarely possible for any length of time. While it is simple enough to track the movements of an animal in the wild with positional telemetry, this only tells us the overall movements of that animal over ground which is a combination of both the movements of the animal and the water in which the animal is swimming. From these observations alone, we do not know how the animal is orienting with respect to the current, or how much of the overall movement we have observed has been contributed by the animal. Are the animals simply being carried in the water column, or are they actively swimming with the current? To address this, a few researchers have been able to use specialized tags designed to detect the actual compass heading of swimming animals (e.g. Greer Walker et al. 1978; Klimley 1993). Alternatively, one can use vector analysis to calculate the movement of the animal relative to the surrounding parcel of water if one knows both the total movements of the animal and the movements of the water current throughout the track. This method has been used in the past to examine STST in long-distance migration studies of fishes using coarse-scale tidal current measurements (e.g. Greer Walker et al. 1978; Metcalfe et al. 1990); however, vector analysis may be used to look at movements related to currents at any scale and in any habitat. Preferably, the movement of the water would be recorded simultaneously with the movement of animal; however, in instances where that is not feasible, or where the analysis of the role of currents is post hoc, it may also be possible to use a hydrodynamic model to estimate current conditions during the movement.

Here we employ the vector analysis method in an investigation of the influence of currents in the daily, non-migratory movements of green sturgeon (*Acipenser medirostris*) in the San Francisco Bay Estuary. These

tracks were collected in 2001–2002 during a study of the daily movement patterns and distribution of the species in the bay (Kelly et al. 2007). The fish tracked in this study occasionally made lengthy, highly-oriented directional movements. Based on observations in the field, it appeared that 1) green sturgeon moved in the same direction as the tidal flow in the deeper, swift-current regions of the bay, but moved on the bottom and without apparent relation to the direction of the current in the shallow, low-current expanses of the bay; and 2) that the green sturgeon were detecting the direction of flow and swimming in that direction, rather than simply being carried passively by the current. These tracks provide both an example of the application of vector analysis to examine the small-scale behaviors of an animal with respect to current, and the first description of a swimming behavior not previously reported in the ancient acipenserid lineage of fishes.

Materials and methods

Study species

The green sturgeon is one of two acipenserid species native to the temperate waters of the west coast of North America (Moyle 2002). The southern Distinct Population Segment (DPS), which spawns solely in the Sacramento River watershed in California, is listed as threatened under the US Endangered Species Act, while the northern DPS is a species of concern. Green sturgeon, which may grow in excess of three meters (Nakamoto et al. 1995), are anadromous and iteroparous, making long distance migrations to spawn in their natal river every 2 to 5 years (Erickson and Webb 2007). The species has an extended oceanic phase, and are thought to be the most oceanic of the acipenserids (Lindley et al. 2008; Moyle 2002); however, individuals of different age classes routinely reside in estuaries (Lindley et al. 2008). Juvenile green sturgeon are thought to migrate from the river to the estuary in their first year and remain there for approximately 3 years before entering the ocean (Nakamoto et al. 1995). Adults may also inhabit these areas before and after spawning migrations, and sub-adult and non-spawning adults are found in estuaries during the summer and fall months (Kelly et al. 2007; Moser and Lindley 2007).

Study region

Green sturgeon were tracked in the San Francisco Bay Estuary (Fig. 1), the largest coastal embayment on the west coast of the United States and one of the country's largest estuaries (Cheng et al. 1993). The region is highly tidal, with a large tidal range relative to mean depth, and is influenced by semi-diurnal mixed tides with a period of 24 h 50 min (Conomos et al. 1985). The estuary is generally shallow with a mean depth of 6.1 m (median=2 m) (Conomos and Peterson 1977). Large expanses of shallow flats predominate in the northeastern regions of San Pablo and Suisun Bays, though deep channels (average 10–20 m), through which flow swift tidal currents, pass through the area (Conomos et al. 1985). There is no measurable precipitation in the region in the summer and early fall, and freshwater input from rivers during this time is strictly regulated by agricultural and municipal diversions. The northern portions of the bay where the study was primarily conducted are described as well-mixed in summer with little vertical stratification (Conomos et al. 1985; Kelly et al. 2007).

Telemetry

Six green sturgeon were captured September-October 2001 and 2002 in the San Pablo Bay region of the estuary using trammel nets (15.25 cm, 17.75 cm, and 20.25 cm stretched mesh) deployed from the *R/V Striper II* operated by the California Department of Fish and Game (CDFG). Nets were set for 1 h in daytime in shallow water (<3 m). After capture, fish selected for tagging were transferred without delay to our research boat. In 2001, captured sturgeon were placed in an insulated, aerated tank and transported to the San Francisco State University Romberg Tiburon Center (RTC) in Tiburon, CA. Telemetry tags were implanted at this location, and the fish allowed to recover for 3 days in 3-m diameter circular holding tanks, supplied by flow-through bay water, before being transported again by boat for release at the point of capture. Green sturgeon (GS) 1 and GS2 were handled in this manner. In 2002, tags were implanted on our research boat and the fish (GS3-6) released immediately after tagging, in the manner of Moser and Lindley (2007). GS3, GS4, and GS6 were released at the point of capture. We were unable to

Fig. 1 Map of study area showing directional movements conducted by tagged green sturgeon in the San Francisco Bay Estuary. *Circles* indicate the position of the fish at 5-min intervals (*black* = bottom 50% of water column, *white* = top 50% of water column). Position of label (e.g. GS1) indicates the start of the directional movement. AI = Angel Island, GG = Golden Gate, RS = Raccoon Strait, RTC = Romberg Tiburon Center (SFSU), SC = Southampton Cove. Inset map shows location of study region in California
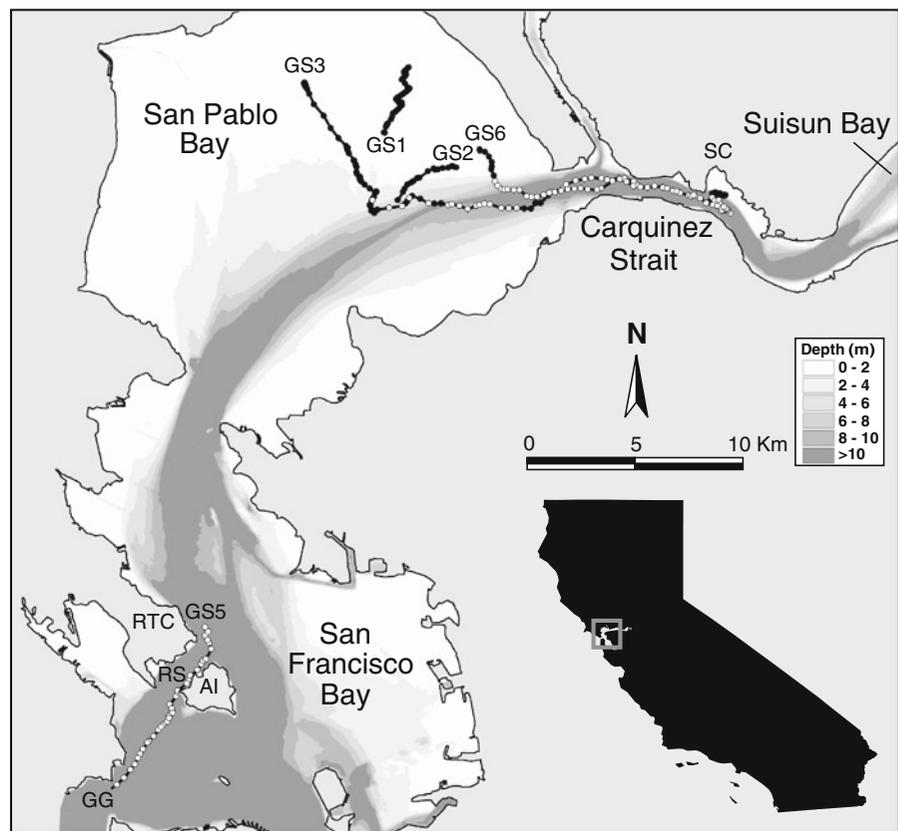
start tracking when GS5 was captured, so the fish was transported to RTC, held overnight, and tagged and released near that location the next day. In all cases, tags were surgically implanted into the peritoneum and the incision was closed with three or four individual knotted monofilament sutures. Full details of the tagging procedure are described in Kelly et al. (2007).

In 2001, sturgeon were implanted with depth-sensing ultrasonic telemetry transmitters (Sonotronics, DT-97) with a weight of 19 g and an expected battery life of 360 days. To improve performance and range, fish in 2002 were implanted with high power, depth-sensing transmitters (Vemco Ltd., V22XP) with a weight of 40 g and an expected battery life of 10 days. In all instances, tag weight was less than 0.7% of body weight. The tagged fish were localized with a directional hydrophone (Vemco Ltd., VH11) and an ultrasonic receiver (Vemco Ltd., VR60) that were interfaced with a laptop computer and differentially corrected GPS (Magellan, NAV5000 DLX).

Active tracking commenced immediately upon release of the green sturgeon using the 'ground zero' method described by Nelson (1987) for tracking

highly mobile organisms ranging over large areas. The fish was localized by rotating the hydrophone to find the direction from which the signal strength was strongest and the boat was moved closer to the fish by moving in that direction while reducing the gain of the amplifier yet maintaining a high level to the signal. The arrival of the boat over the fish was evident by a constant signal when the hydrophone was rotated 360º. The tagged sturgeon were tracked continuously as long as conditions permitted, and when possible were relocated on subsequent days. Positions and measurements of depth were automatically recorded at 10-second intervals throughout the duration of each track.

Bathymetry, currents and tides

The geographic coordinates from each tracked fish were entered into a geographical information system (GIS) (ESRI, ArcView 3.2) and projected over a 5-meter grid digital elevation model of the bathymetry of the San Francisco Bay Estuary (California Department of Fish and Game, Bathymetry Project, Information Technology

Division, GIS Service Center, Sacramento, California). The bathymetry in this model is based on the Mean Lower Low Water (MLLW) datum, from National Ocean Service (NOS) Hydrographic Survey Data (v. 4.0). The bottom depths over which the fish swam were determined based on this bathymetry map and adjusted with tide heights recorded at the nearest NOS tide station in the bay.

A consideration of the role of currents was not part of the original tracking study in which these data were collected, so the direction and magnitude of the current vectors were not directly recorded in the field. Fortunately, tidal dynamics in the San Francisco Bay region are well studied and understood (e.g. Conomos et al. 1985). Since there was no precipitation in the region when this study was conducted, and freshwater input from rivers was also closely controlled by water regulators during this time, the majority of the forces influencing tidal currents were highly predictable (R.T. Cheng, Senior Research Scientist, US Geological Survey, pers. comm.). Therefore, in order to estimate the current vector experienced by the fish during each track, we used a hydrodynamic current prediction model (Local Knowledge, Inc., Force 2) developed for vessel navigation and racing in San Francisco Bay. The Force 2 model computes tide and current conditions at any position and time using NOS reference and subordinate station data, a basin bounding function, and hydrodynamic modeling. The spatial resolution of the model in the San Francisco Bay region is stated by the developer as 100 m or better (D. Brayshaw, Local Knowledge, Inc., pers. comm.).

To test the validity of the current model, we measured current directions and speeds from an anchored boat at haphazardly selected locations in eastern San Pablo Bay and the Carquinez Strait, the region in which most of the directional swimming was recorded. Current direction was determined with a subsurface float on a monofilament line and measured by compass. Current speed, averaged over 10 s, was measured at a depth of 1 m with a staff-mounted flow meter (Marsh-McBirney, Flo-mate 2000). Three flow measurements were taken at each location and the average of those measurements used in subsequent calculations.

Data treatment and analysis

Prior to analysis, the data were filtered to remove poor or incomplete detections. Detections recorded using added gain from the receiver (indicating weaker signals) were omitted. To reduce spatial error due to boat position and GPS errors, the data were smoothed by filtering at a time interval sufficient to reduce error while still retaining valid positional information. A time interval of 5 min between locations was selected using the method described by Klimley et al. 2005. Briefly, a curve of the coefficient of concentration of the directions moved between successive positions, plotted for intervals of 1–15 min, formed an asymptote at an interval of 5 min. The spatial error between the boat's position and that of the tracked animal was minimized relative to the distance moved over this time interval.

Movement vectors representing both heading (direction relative to north, 0°) and magnitude (speed) were calculated between each 5-min position using the great circle method. These vectors represent the total movement of the fish over ground (total vector, t), and thus are a combination of the vectors of both the actual swimming movement of the fish (fish vector, f) and the movement of the water mass in which the fish is located (current vector, c). The actual orientation of the fish and the speed at which it was swimming can be calculated as follows using the law of cosines if the heading and magnitude of the current at each position is known.

When plotted, the 't' and 'c' vectors form two sides of an oblique triangle originating from point A_n (Fig. 2). The difference between the bearings of c and t is the angle between the two sides (α). The third side of the triangle represents 'f', the net movement of the fish needed to compensate for the current and arrive as detected at point B_{n+1}. We can calculate the magnitude of f using the following equation:

$$f = \sqrt{c^2 + t^2 - 2ct\,\cos(\alpha)} \qquad (1)$$

We can also plot f originating from point A_n to better illustrate the different contributions of the fish and current to the total movement. The heading of the fish relative to the heading of the total movement over ground t is described by the angle γ, which is also the angle between sides f and t of the triangle. Knowing the magnitudes of each vector, we may then calculate γ using:

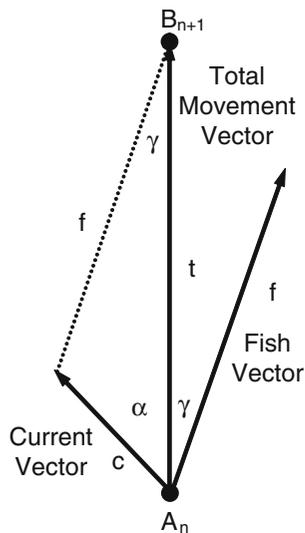$$\gamma = \arccos\left(\frac{f^2 + c^2 - t^2}{2fc}\right) \qquad (2)$$

Fig. 2 Vector components of movement. Line t is the total movement vector between two consecutive recorded positions, points A and B. As a vector, it has both direction (heading) and magnitude (speed). Line c is the current vector experienced by the fish at point A, which is at angle α to the total vector. The fish vector (line f) at point A may also be drawn originating from the end of the current vector (point C, line f'), where it meets point B to complete an oblique triangle. Angle γ is the angle of the fish vector relative to the total vector, and angle $\alpha + \gamma$ is the angle of the fish relative to the current. Given t, c, and α, f and γ can be calculated using the law of cosines

The bearing of the fish with respect to the current is then the sum of angles α and γ.

Circular statistics, calculated by Oriana 2.00 software (Kovach Computing Services), were used to describe and assess the degree of orientation of the track of each fish. These statistical tests are analogous to traditional linear statistics, but are applicable to scales such as compass bearings or time where there is no true zero and high and low values are arbitrary (Zar 1998). Rayleigh's concentration coefficient (r) was used to describe the angular concentration of the vectors. The value for 'r' ranges from '1', when all headings are precisely the same, to '0' when the headings are uniformly distributed in all directions. Rayleigh's Test was used to determine if the headings were distributed uniformly or were significantly concentrated around a mean angle. We defined 'directional movement' as travel in which the recorded movement vectors were concentrated around a mean heading that was found to be significant using Rayleigh's Test. The V test, a modified version of the Rayleigh test (Zar 1998), was used to test if the observed headings were concentrated in a predicted mean direction such as in the direction of, or opposite

to, the current. For example, if the fish were indeed following the current, the difference between the fish's vectors and the current vectors should be zero so we may test the observed difference in vectors against the predicted value of 0°. The Watson-Williams test is an F-test for circular data, and was used to determine if distributions of headings differed significantly. In all tests, significance was accepted when $\alpha < 0.05$.

Results

Testing current model predictions

Twenty measurements of current speed and direction were made between 11:30 and 14:40 on 11 June 2007, divided between flood tide ($n=10$) and ebb tide ($n=10$). For each field sampling location and time, matching data were predicted using the Force 2 model. The current measurements were divided by tide stage and F-statistics calculated with the Watson-Williams test. There was no significant difference in current heading between field observations and the model predictions (flood: $P=0.463$; ebb: $P=0.191$). The difference between the field and model headings for all points were then calculated. For all points, the mean difference between the angles was 7.2° and the results were tightly concentrated (Fig. 3a). This was highly significant by both Rayleigh's test for concentration ($P=<0.001$) and also by V test against a predicted mean difference of 0° ($P=<0.001$), indicating that the model closely predicted the real-world current heading at most times.

Upon further examination of the data, it was apparent that there were two heading points that did not closely agree between field and model. These points were consecutive, spaced 10-min apart, and both occurred in the period of slack tide. In both cases, the measured current in the field was very slow (<0.15 m sec^{-1}) and matched the direction of the prevailing winds. It seems likely that since the tide was essentially zero at that point, these were measurements of wind-driven surface currents and not the larger, tidal movement of the water mass. Since we could not be confident that the model predictions during these periods accurately represented the conditions experienced by the fish in the wild, and since according to Schoellhamer (2001), "slack tide in northern San Francisco Bay typically is only a few
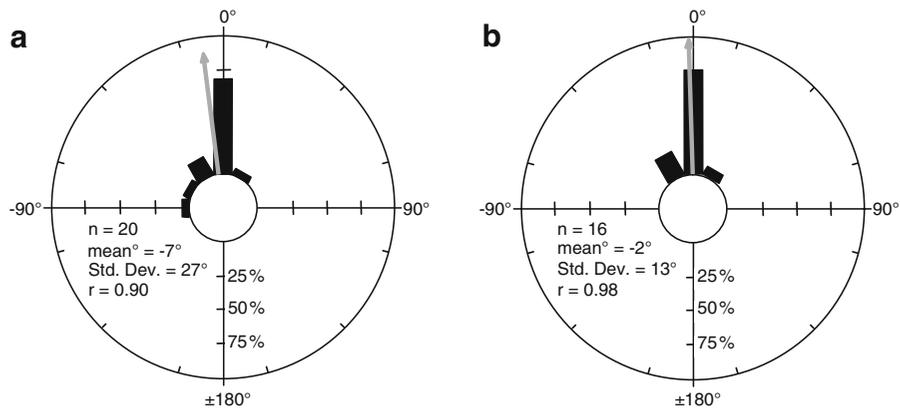
Fig. 3 Circular histograms illustrating the distribution of the differences between current vectors measured in the field versus predicted by the Force 2 model (*black bars*) for (**a**) all points, and (**b**) omitting measurements ±20 min of slack tide. Degree of concentration (r) is indicated by the length of the arrow between the inner and outer ring

minutes in duration," we omitted data collected 20-min before and after slack tide and reanalyzed the remaining points (Table 1). As before, there was no significant difference between the field observations and the model predictions. The mean difference between measured and simulated angles was 1.6°, and the coefficient of concentration was very high (Fig. 3b). This result was highly significant by both Rayleigh's test for concentration ($P=<0.001$) and also by V test against the predicted mean difference of 0° ($P=<0.001$). Lastly, there was no

significant difference between the speeds of the current measured in the field compared to those predicted by the model (paired *t*-test, $P=0.336$).

Fish orientation to current

Six fish were tagged and tracked during 2000 (GS1 and GS2) and 2001 (GS3-GS6) for tracking periods ranging from 1 to 15.25 h per day for up to 9 d within a 12-day span. Based on total length, five of the fish (GS1-GS4, GS6) were sub-adults while one (GS5) was believed to be an adult. The sex of each fish was not apparent during the tagging procedure and is unknown. There was no indication that handling altered the behavior of the fish in any predictable way. A stressed individual might be expected to accelerate away from the site of release; however, GS1-3 moved minimally for several hours after release before initiating directional movement, GS4 also moved minimally for the duration of the initial track but was relocated 2 days later almost 12 km from the last point of contact, and GS5-6 both started directional movement immediately after release. Furthermore, it is unlikely that any sturgeon died as a result of the operation. In a later study of the species' movements region-wide, 96 green sturgeon were tagged using similar tagging procedures with no known mortality (Heublein et al. 2009). A description of the entire tagging study, including analysis of observed green sturgeon distribution and movements with respect to environmental parameters such as depth, temperature, salinity, and dissolved oxygen,

Table 1 Results of comparison of measured San Francisco Bay tidal flows to those predicted by current model. Current directions and speeds were recorded at haphazardly selected locations in eastern San Pablo Bay ("Field") on a flood and ebb tide on 11 June 2007, and were compared to current vectors predicted for the same time and locations by the Force 2 model ("Model"). Watson-Williams F-test was used to determine if the predicted vectors differed from the measured vectors

	Flood Tide		Ebb Tide	
Sample period start	11:34		13:07	
Sample period end	12:31		14:40	
	Field	Model	Field	Model
N	8	8	10	10
Mean bearing	83°	77°	227°	233°
R	0.995	0.997	0.970	0.998
Circular Std Dev.	6°	4°	14°	3°
Rayleigh's test (p)	<0.001	<0.001	<0.001	<0.001
Watson-Williams F	4.167		1.844	
Watson-Williams (p)	0.061		0.191	

has previously been published (Kelly et al. 2007). We report here just on the directional movements of these fish, relating the observed swimming behavior to local water currents.

The total amount of time spent actively tracking during this study was 80 h 9 min. The majority of the tracks consisted of non-directional movements in close proximity to the substrate, consistent with foraging behavior as described in Kelly et al. (2007); however, five of the six fish also engaged in directional movements for a total of 26 h 7 min (Table 2, Fig. 1). While GS4 moved widely within San Pablo Bay between tracking events, it was not actively tracked while doing so and was not included in this analysis. GS1 was recorded making a directional movement lasting 3 h 16 min, but the activity occurred in the extremely shallow northwestern reaches of San Pablo Bay and encompassed a change in tide. The currents in this region during this track were slow and complex and the winds very strong. Based on the results of the current model validation, we were not sufficiently confident of the model predictions to include this track in the vector analysis.

The depth distribution of the directional movements was bimodal (Fig. 4): 57.3% of directional movements were recorded in the upper half of the water column, whereas 42.7% were recorded in the bottom half. Two fish, GS3 and GS6, were recorded making both surface- and benthic-oriented movements, GS5 was recorded making only surface movements, and GS2 was only observed making benthic movements (Table 2). In contrast, over 95% of observations of non-directional movements occurred in close proximity to the bottom (Kelly et al. 2007).

The track of GS3 is illustrative of both surface and benthic movement (Fig. 5). This fish was captured, tagged, and released in the shallow north-central region of San Pablo Bay on 18 September 2002. The fish moved non-directionally for 2 h 10 min before initiating a southeasterly directional movement (mean heading=149°, r=0.68, P<0.001) starting at 15:45. This movement occurred during the ebb tide which peaked at 16:04 in that region of the estuary. The mean current heading during this tide was 219° at a mean current speed of 0.2 m sec^{-1}. Around the time of slack tide (19:00), and for the early parts of the building flood tide, the fish continued to move along the same course, though its overall speed slowed and the fish occasionally stopped. During this first phase of the track, the fish remained in the lower half of the water column, on or very close to the substrate, over a mean bottom depth of 3.0 m. A section of this movement is expanded in Fig. 6a. Note that the vectors of the movement of the fish in the water mass (gray lines) are similar in length to the vectors of the movement over ground (black lines between points) indicating that the majority of the recorded movement was the result of the fish's swimming. The average speed of GS3 over ground during this section was 0.7 m sec^{-1}, and the mean calculated swimming speed of the fish was also 0.7 m sec^{-1}. Note also the large difference between the distribution of current vectors (black bars) and fish vectors (white bars), indicating that the fish was not following the flow of the water (Fig. 6c), but rather maintaining a mean bearing of 112° (r=0.71, P<0.001).

This green sturgeon then dramatically changed its behavior, beginning to exhibit behavior consistent

Table 2 Summary of the observed benthic and surface oriented directional movements of green sturgeon in the San Francisco Estuary indicating the size of fish (cm), and the duration and Rayleigh's coefficient of concentration (r) for each movement. GS4 was not observed making directional movements and was omitted

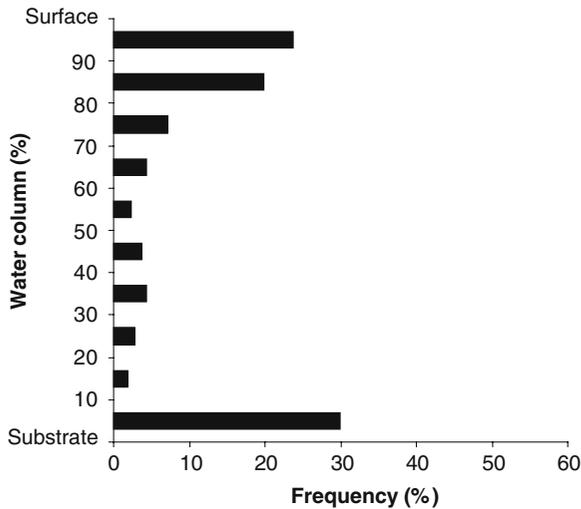| Fish ID	Total Length (cm)	Benthic		Surface	
		Time (h:mm)	r	Time (h:mm)	r
GS1	105	3:16	0.75[a]	–	–
GS2	105	1:45	0.79[a]	–	–
GS3	101	10:26	0.46[a]	4:55	0.62[a]
GS5	153	–	–	3:05	0.90[a]
GS6	106	0:40	0.68	2:00	0.93[a]

[a] significant (Rayleigh's test, p<0.05)

Fig. 4 Fraction of water column in which green sturgeon were recorded during directional movements in the San Francisco Bay Estuary

with STST. An examination of a sample of this movement illustrates this pattern (Fig. 7a). GS3 entered the top half of the water column at 21:20 coincident with the strengthening flood tide. During this period of time, GS3 swam at a mean depth of 4.1 m while over an average bottom depth of 23.3 m. The fish swam on a mean heading of 105° ($r=0.54$, $P<0.001$), similar to the direction of flow of the main tidal current passing through the deep water channel into the narrows of the Carquinez Straits. The mean current heading during this tide was 94°, and the mean current speed was 0.5 m sec^{-1}. Notice that

during this time, the vectors of the water current (black lines) and fish movement (gray lines) are closely associated and of similar length, showing that GS3 was swimming in the direction of the flow and that the water current contributed significantly to its movement. The average speed over ground was 0.9 m sec^{-1}, and the average swimming speed of the fish was 0.5 m sec^{-1}. GS3 continued to move near the surface in a highly directional manner until 02:20, coinciding with slack tide, at which point it reversed direction and moved on a meandering path until settling to the shallow bottom of Southampton Cove on the north side of the Strait at 03:15, where it remained until tracking ended at 04:25 on 19 September.

The surface movements of all the green sturgeon combined differed from tracks recorded of movement near the substrate (Table 3). Surface movements typically occurred over deeper water (mean=22.0 m) though the tracked fish swam at a mean depth of 2.7 m. The total speed of the fish over ground averaged 0.9 m sec^{-1}, while the mean current speed was 0.7 m sec^{-1}. The swimming speed of the fish at the surface was 0.5 m sec^{-1}. In contrast, during benthic movements, green sturgeon swam close to the bottom, at a mean depth of 4.3 m, and in shallow water, over a mean bottom depth of 4.4 m. The total speed over ground was slower, 0.6 m sec^{-1}, and the movements occurred in lower current speeds, averaging 0.4 m sec^{-1}; however, the swimming speed of the fish during benthic movements was slightly faster than in surface movements, averaging 0.6 m sec^{-1}.
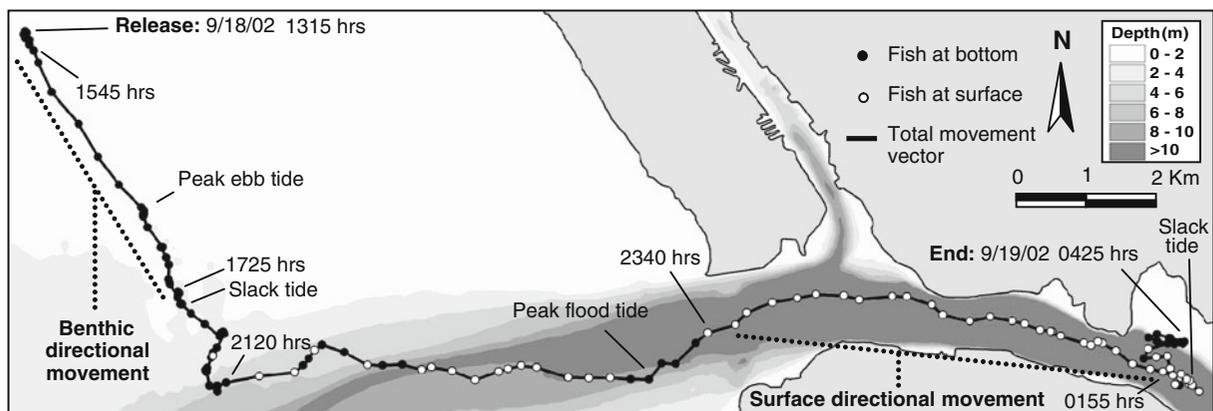

Fig. 5 Example of benthic versus surface oriented swimming during a directional movement. The dark line indicates the recorded track of fish GS3 as it swam from San Pablo Bay into the Carquinez Strait, circles indicate the position of the fish at 5 min intervals (*black* = benthic, *white* = surface). Dotted line indicates benthic and surface movements expanded in Fig. 6 and 7
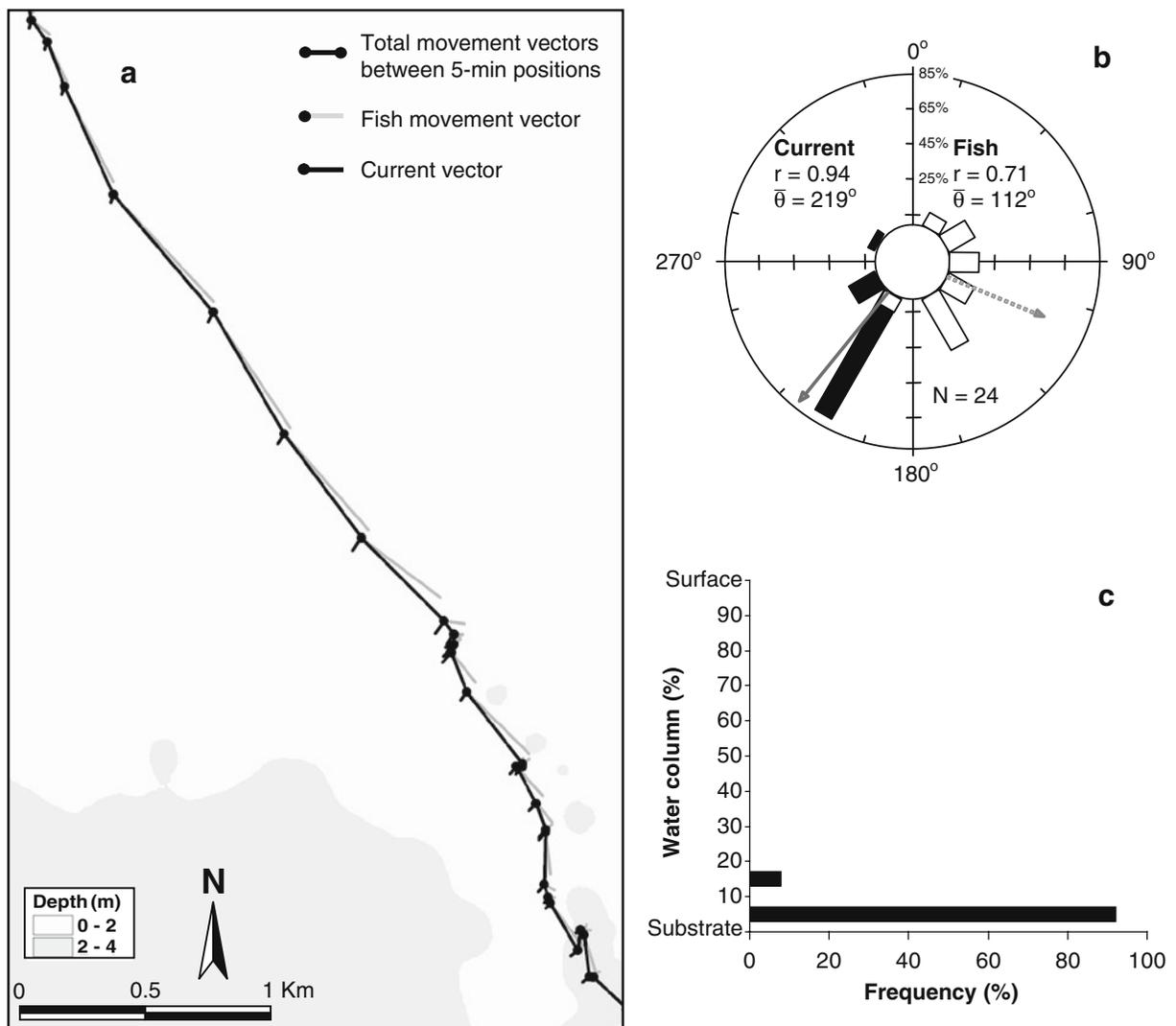
Fig. 6 Expanded section of benthic directional movement conducted by GS3 consisting of 24 points (**a**) illustrating the movement vector contributed by the tidal current (*black line*) and the movement vector contributed by the fish (*gray line*) that sum to the observed total movement vector (*black line* between points). Circular histogram (**b**) illustrates the mean heading (*arrows*) and degree of concentration (length of arrows) and distribution of the bearings (*bars*) of the current versus the fish (*solid arrow/black bars* and *dotted arrow/white bars*, respectively) during the illustrated movement. Bearings are grouped in bins of 30° (e.g. 346°–15°, 16°–45°, etc.). Histogram (**c**) summarizes the fraction of water column in which the fish was moving during this period

The movement vectors of two of the three fish recorded at the surface (GS3 and GS6) were oriented in the direction of the current (Fig. 8, Table 4). The mean difference between the heading of GS3 and the current was 35°. The r coefficient of the headings was 0.47, which was significantly different than a uniform distribution by Rayleigh's Test ($P<0.001$). It was also significantly different from a uniform distribution assuming a predicted mean angle of 0° by V Test ($P<0.001$) indicating that the fish was oriented in the direction of the current. The movement of GS6 was also oriented to the current. The mean difference between the headings of this sturgeon and the current was 48° ($r=0.51$), which was significant both by Rayleigh's Test ($P=0.001$) and V Test (predicted angle=0°, $P=0.009$). In contrast, the mean difference between the headings of GS5 and the current was 221° ($r=0.21$) which was neither significant by Rayleigh's Test ($P=0.185$) and nor by V Test (predicted angle=0°, $P=0.916$). However, the mean headings of both the total movement (206°,

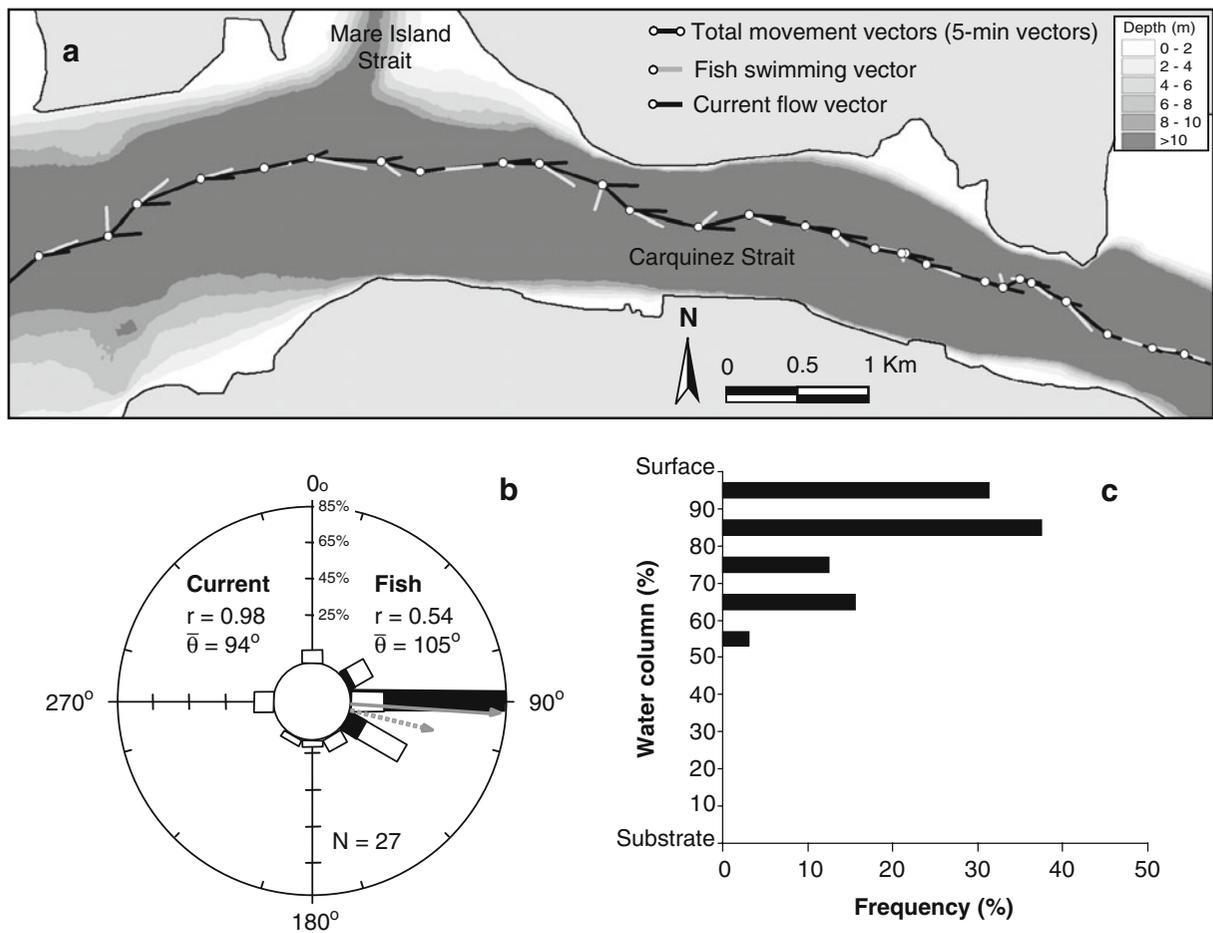**Fig. 7** Expanded section of surface directional movement conducted by GS3 consisting of 27 points (**a**) illustrating the movement vector contributed by the tidal current (*black line*) and the movement vector contributed by the fish (*gray line*) that sum to the observed total movement vector (*black line* between points). Circular histogram (**b**) illustrate the mean heading (*arrows*) and degree of concentration (length of arrows) and distribution of the bearings (*bars*) of the current versus the fish (*solid arrow/black bars* and *dotted arrow/white bars*, respectively) during the illustrated movement. Bearings are grouped in bins of 30° (e.g. 346°–15°, 16°–45°, etc.). Histogram (**c**) summarizes the fraction of water column in which the fish was moving during this period

r=0.91) and the current (211°, r=0.91) were very similar indicating that GS5 was moving in the direction of the prevailing current.

The orientation of the fish to the current when moving near the bottom differed among individuals (Fig. 8). The movements of GS3 and GS6 were

Table 3 Comparison of all surface and benthic directional movements (n = number of 5-min track segments)

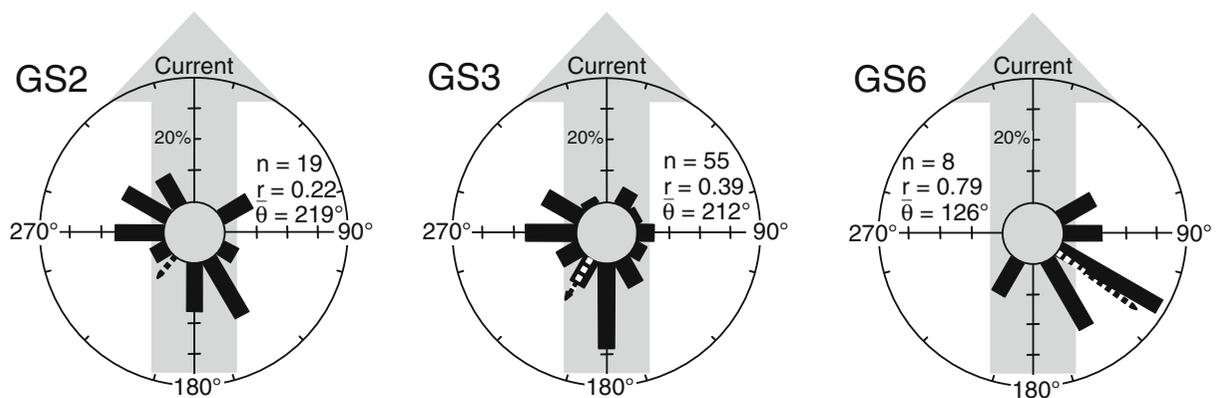| Parameter	Benthic (*n*=82)		Surface (*n*=112)	
	Mean (SD)	Range	Mean (SD)	Range
Fish depth (m)	4.3 (2.9)	1.1–16.9	2.7 (2.2)	0.3–15.0
Bottom depth (m)	4.4 (4.6)	1.0–23.8	22.0 (11.2)	5.6–58.4
Total speed (m sec-1)	0.6 (0.5)	0.0–2.1	0.9 (0.4)	0.1–1.9
Current speed (m sec-1)	0.4 (0.2)	0.1–0.9	0.7 (0.2)	0.2–1.0
Fish speed (m sec-1)	0.6 (0.5)	0.1–2.1	0.5 (0.3)	0.0–1.6

Surface movements
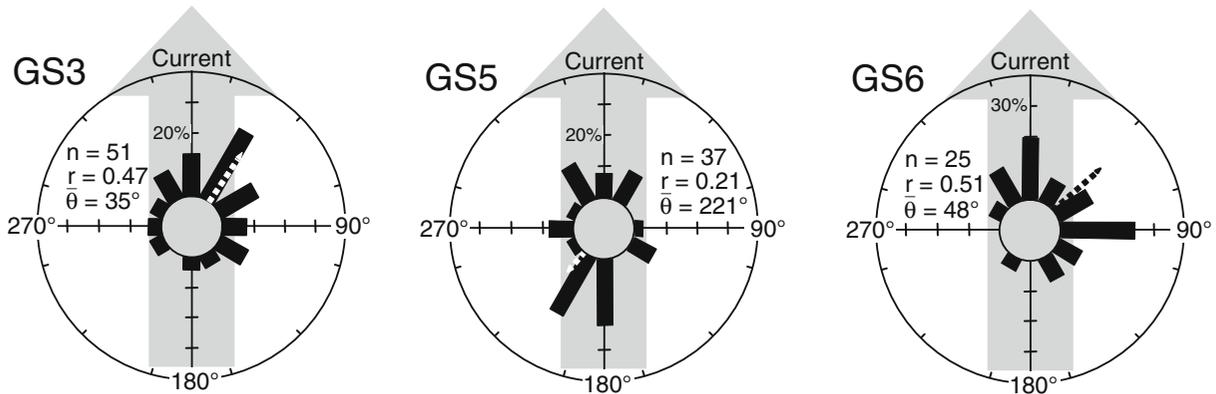
Benthic movements

Fig. 8 Circular histograms showing the angle of orientation of green sturgeon with respect to the current of each directional movement in the top half (surface) and bottom half (benthic) of the water column. Large *gray arrow* indicates current direction, small dotted arrow indicates mean angle to the current and *black bars* show distribution of the bearings. Bearings are grouped in bins of 30° (e.g. 346°–15°, 16°–45°, etc.)

concentrated around a mean angle (212°, $r=0.39$; 126°, $r=0.79$ respectively) which was significant by Rayleigh's test ($P<0.05$, Table 4). These movements were also significant by V Test assuming a predicted angle of 180° ($P<0.05$, Table 4) indicating that the sturgeon were moving into the current. The movements of GS2 were not concentrated around a mean angle according to Rayleigh's Test ($r=0.22$, $P=0.397$).

Discussion

Considerations for use of vector analysis

The vector analysis method uses the subtraction of two values, total movement and water current, to derive a third value reflecting the movement of the animal. While this approach permits researchers to examine additional aspects of swimming behavior and performance without the use of specialized telemetry, it also introduces potential sources of error. The two most significant concerns in an analysis of this kind are the accuracy of the measurements of current and the precision of the measurements of movement. For the former, it is clearly preferable to directly measure the movement vector of the water at the same location at which the fish is swimming. In cases where this is not possible, such as when an interest in the role of currents arises after field tracking is complete, it may be possible to use a hydrographic model to estimate the current vectors experienced by the fish.

Hydrographic tidal models vary in complexity. The most sophisticated are governed by the conservation

Table 4 Orientation of green sturgeon with respect to current heading during surface and benthic movements. Angle to current = mean heading of the fish relative to the current; R = Rayleigh's R coefficient of concentration of movement; p_R = result of Rayleigh's test for uniformity; V = V test for uniformity versus a specified mean angle (surface movements=0°, benthic movements=180°), p_V = result of V test

Fish ID	Angle to current	R	p_R	V	p_V
Surface movements					
GS3	35°	0.45[a]	<0.001	0.396[a]	0.001
GS5	221°	0.21	0.185	0.160	0.916
GS6	48°	0.51[a]	0.001	0.334[a]	0.009
Benthic movements					
GS2	219°	0.22	0.397	0.173	0.144
GS3	212°	0.39[a]	<0.001	0.317[a]	<0.001
GS6	126°	0.79[a]	<0.001	0.467[a]	0.030

[a] significant ($p<0.05$)

equations of mass and momentum and account for the effects of variables such as basin geomorphology, bottom friction, and salinity-based density changes (e.g. Cheng et al. 1993); however, these models, when available at all, are processor-intensive and are generally not well suited to calculating current conditions at specific locations and times. In many cases, simpler hydrographic models have been developed for commercial and recreational applications. These models are typically based on published tidal harmonic constants and include basin bounding functions and basic hydrographic modeling. In a well studied region such as San Francisco Bay, these simpler models can provide a reasonable approximation of the current vectors experienced by the fish, provided that the models are validated in order to verify the accuracy and degree of resolution. Based on our tests in this study, there was no significant difference detected in the direction of the current or the current speed measured in the field versus that predicted by the Force 2 model, although the model was less reliable when the currents were very slow, particularly around slack tide. Given these results, we felt it was reasonable to use the Force 2 model to derive estimates of current vector for use in our analyses, though we excluded those data where we were not confident of the model. To account for resolution of the data, heading histograms were summarized in 30° increments, greater than ±1 standard deviation of the measured error in the current model predictions.

The second source of possible error in this kind of analysis comes from the challenge of determining the position of the animal itself. In the method of active tracking employed in this study, the goal is for the tracking boat to mimic the movement of the fish. The success in accomplishing this is influenced by winds and currents, GPS error, boat handling skill, and the ability to precisely localize the signal from the tag. Low precision in determining the positioning of the fish will imply directional headings that are not accurate. The influence of this lack of precision will be more pronounced at lower travel speeds when the distance covered by the animal between positions is small. Much of this error can be minimized by a sufficiently experienced crew, and positional precision errors can be offset by smoothing the data as described by Klimley et al. (2005). By selecting an appropriate time interval between points, one reduces the amount of positioning error relative to the actual distance moved, minimizing inaccuracies yet retaining useful directional detail. Using a 5-min interval, at the mean rates of speed recorded in this study (surface: 0.9 m sec^{-1}, benthic: 0.6 m sec^{-1}), a tracking error of 20 m between positions, equivalent to three boat-lengths, would introduce less than 5° error into the heading calculation.

Green sturgeon and currents

While we acknowledge that the sample size in this study is small, the initial evidence suggests that green sturgeon movements in the San Francisco Bay Estuary are influenced and often aided by the cyclical currents in the region. For example, GS3 conducted an extensive long-distance movement from San Pablo Bay into Suisun Bay, covering 22.5 km in approximately 13 h. This movement was timed with the tidal current moving in the same direction, and the orientation of this fish was closely related to the flow of the water. Notably, the movement ceased when the tide changed and the currents reversed. The fish was subsequently relocated while it was moving non-directionally on two consecutive days, first 9 km then an additional 10 km farther into Suisun Bay. Given this stepwise movement, it is possible that this sturgeon employed a tactic akin to traditional STST to facilitate its movement, moving unidirectionally on repeated flood tides. Like GS3, GS6 was first observed making a rapid, current-oriented movement from San

Pablo Bay into the Carquinez Straits in the direction of Suisun Bay. It is not know if this fish entered Suisun Bay at all. If it did, GS6 did not remain for long as it was relocated 2 days later, 11 km to the west of the last detection, in the middle of San Pablo Bay.

The track of GS5 was in some ways the most dramatic and the results of the analysis the most puzzling of the movements observed in this study. The fish started moving almost immediately upon release, first slowly near the shore, then rapidly on an ebb tide through Raccoon Strait between the Tiburon Peninsula and Angel Island and eventually out of the Golden Gate headed towards the Pacific Ocean. We observed during the track that the fish was moving rapidly at all times, noticeably outpacing the outgoing current, as evinced by the need to continuously use the motor in the tracking boat in order to keep up. While the mean headings of the total movement and the current were very similar, vector analysis revealed that the distribution of the fish's movements was actually bimodal but still aligned with the axis of the current. This would seem to indicate that fish's movement was not unidirectional (Rayleigh's Test and V test $P>0.05$, Table 4), though it was linear along the current axis ($r=0.34$, $P=0.005$) when tested by doubling the angles in the manner described by Zar (1998). The results of this analysis suggest that the fish was swimming both with and against the flow at different times; however, this does not correlate with the field observations that the fish was consistently swimming faster than the current. Such a result may be due to error modeling the currents in the lee of Angel Island. It is known that even sophisticated hydrographic models fail to predict island wakes unless the grid is sufficiently fine-scale (Cheng et al. 1993). If the current vectors estimated for this track were faster than the total recorded movement of the fish, the vector calculations would imply that the fish was actually swimming opposite to the direction of the flow. This instance highlights both the difficulty of using a model retroactively rather than collecting measurements directly in the field and the importance of field testing a model in all locations in which it is to be used.

A notable feature of all of the movements aligned with the current is that all were conducted high in the water column, in the deeper regions of the estuary. In contrast, green sturgeon were also recorded swimming directionally while near or on the bottom in the shallower, low-current regions of the estuary. The mean current speeds in these areas were almost half the speeds found during surface swimming. These benthic movements were not aligned in the direction of the flow, and, in two out of three instances (GS3, GS6), were at headings opposed to the current (Fig. 8).

The green sturgeon that were observed moving near the bottom may have been taking advantage of the distinct properties of moving in fluids. Sturgeon are negatively buoyant, despite the presence of a non-respiratory swim bladder. As with similarly armored, benthic fishes, they offset the tendency to sink by generating lift over their body (Wilga and Lauder 1999). This tactic is most effective at higher swimming speeds, whereas at slower speeds, the fishes need to maintain a high angle of attack relative to the current in order to generate sufficient lift. For example, juvenile white sturgeon (~29 cm TL) swimming up in the water column maintained a mean angle of attack of 20° at speeds of 0.5 body lengths (BL) sec^{-1}, but this decreased sharply to 8° at 1 BL sec^{-1} and eventually dropped to 0° at 3 BL sec^{-1} (Wilga and Lauder 1999). However, objects moving near the fluid-substrate interface will benefit from decreased drag (Vogel 1981) and will gain additional lift from the hydrodynamic ground effect which can result in substantial energy savings. Blake (1979) described the phenomenon in fishes and reported that mandarin fish (*Synchropus picturatus*) realize a savings of 30–60% of the energetic cost of swimming when using the ground effect to hover near the substrate while in a current.

It is possible that the green sturgeon we observed engaged in directional movement near the substrate were gaining an energetic advantage in the form of increased lift and reduced drag. This has not been explored in sturgeon, but in another armored, benthic fish, the northern spearnose poacher (*Agonopsis vulsa*), swimming in the ground effect almost eliminated the angle of attack needed to maintain buoyancy (Nowroozi et al. 2009). Those authors reported that poacher (10.1–17.5 cm TL) swam at an angle of attack of 5°–30° when swimming greater than 1 cm off of the bottom but this was reduced to only 0.41° when within 1 cm of the bottom. The tendency to swim into currents while near the bottom that we observed in two of the three green sturgeon may be a tactic to move efficiently, even at slow swimming speeds.

It is doubtful that the currents anywhere in the estuary are fast enough to completely thwart the

movements of green sturgeon. The species is a long-distance migrant, making extensive and repeated movements from the northeastern Pacific Ocean to spawning locations hundreds of kilometers up swift-flowing coastal rivers (Erickson and Hightower 2007; Moyle 2002). The fish in our study were sometimes observed swimming as rapidly as 2.1 m sec^{-1}; however, for both surface and benthic swimming, the mean swimming speed was considerably slower, around 0.5–0.6 m sec^{-1}. This is slower than the maximum sustained swimming speed of 0.8 m sec^{-1} (for fish 1 m total length) reported for the species by Lankford et al. (2005). It is possible that the mean swimming speed we observed may reflect a preferred speed for green sturgeon, and that the fish exert similar effort (energy spent per unit time) during all long-distance movements, but increase the efficiency (distance traveled per unit energy) of their transport when possible by using the currents and possibly ground effects. It has been argued that a theoretical threshold current speed exists for each individual below which it costs more to wait for the right current than it does to simply swim and exert extra energy (Weihs 1978). Based on this assumption, it is not surprising to see current-assisted swimming utilized in the swiftest flowing areas of the bay, and benthic oriented swimming in the shallow, slower areas.

The results described here are the first report of an acipenserid fish closely aligning with the flow and employing current-assisted swimming akin to STST. Interestingly though, movement patterns similar to what we have described have been observed in tracking studies of other species of sturgeon. Species such as shortnose (*A. brevirostrum*, McCleave et al. 1977; Moser and Ross 1994), Atlantic (*A. oxyrhynchus oxyrhynchus*, Moser and Ross 1994) and Gulf sturgeon (*A. o. desotoi*, Sulak and Clugston 1999; Fox et al. 2002), have been reported to swim near the bottom in shallow water, but to also occasionally make lengthy, directional movements while swimming at the surface. The studies of Sulak and Clugston (1999) and Fox et al. (2002) did not examine the influence of current, but McCleave et al. (1977) and Moser and Ross (1994) observed that the total movements of the tagged fish were oriented to the axis of the current. Based on the recorded movements of the fish compared to the magnitude of the tidal current, Moser and Ross (1994) reported that Atlantic sturgeon in an estuary showed positive rheotaxis on all tides, while shortnose sturgeon oriented positively on ebb tides and had no preference on flood tides. The study did not record swimming depths or calculate the actual orientation of the fish relative to the current, rather the fish were assumed to be aligned parallel to the mean direction of flow. McCleave et al. (1977) also observed that the movements of shortnose sturgeon oriented along the axis of the tide, though there was no apparent relation to which direction they moved, with some fish moving bimodally and some unimodally, either with or against both ebb and flood tides. Unfortunately, only one fish in that study carried a depth-sensing transmitter so it is not known if the direction of movement was related to the position of the fish in the water column.

Conclusion

Most studies that have related the movements of fish to water currents have focused primarily on large-scale migrations, for instance plaice moving through the English Channel (e.g. Greer Walker et al. 1978); however, given the prevalence of water currents in the lives of fishes, it is reasonable to assume that fishes have evolved to factor these variables into their movements at other times too. When current has been considered in studies of small-scale daily movements, the animal has typically been treated as if it were perfectly aligned to the direction of flow. The fish vectors and the current vectors were assumed to be parallel and were consequently either summed or subtracted completely from the total movement during analysis (e.g. McCleave et al. 1977; Moser and Ross 1994); however, perfect alignment is rarely the case. Even when actively following the current, fish may also move within the water mass for myriad reasons including avoiding perceived threats, finding food, or detecting other navigational cues. These movements may briefly align the fish at oblique or even opposite angles to the net direction of flow. Simply assuming perfect orientation will have the effect of exaggerating the influence of the current, under-representing the movement of fish, and may potentially cause researchers to miss interesting elements of behavior.

These behaviors merit further attention, as does the question of what mechanisms animals might utilize to orient along with a water mass within which they are suspended, often in the absence of visual or tactile

cues (see Klimley et al. 2002; Metcalfe et al. 2006 for reviews). While lab studies are certainly warranted, as telemetry technology improves it becomes increasingly possible to consider these questions in free-swimming organisms as well. Vector analysis can be a useful tool in this pursuit, permitting researchers to parse out the specific orientation of the animal from the movements of the water mass. Further, the increasing availability and sophistication of hydrodynamic models may also permit these analyses when current data either cannot be or where not recorded during in the field.

To date, this method has been primarily used to date to examine basin-scale movements; however, with the use of higher resolution tracking and current data, this tool can be applied to smaller scale phenomena such as daily movements. The role of STST to maximize efficiency in migratory movements has been well established. Intuitively, we would expect similar behavior to be beneficial to fishes during daily movements too, yet there has been little research in this area to date. Given our observations of an acipenserid in California and Parker and McCleave's (1997) observations of current-related daily movements in American eels (*Anguilla rostrata*) in Maine, coupled with the abundance of observations of STST in a variety of species, we expect current-assisted movement may be widespread in fishes and likely in other taxa and we encourage researchers to direct their attention to these behaviors.

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