

Use of substratum ripples for flow refuging by Atlantic cod, *Gadus morhua*

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Synopsis

The ability to maintain position in a current without actively swimming (station-holding) was measured on substratum ripples for Atlantic cod, *Gadus morhua*, a benthopelagic fusiform species. The current velocities tested ranged from 0–111 cm sec⁻¹. Ripples were sinusoidal, with twelve combinations of ripple wavelength (10, 25, 50, 125 cm) and ripple amplitude (1.0, 2.5, 5.0 cm). Ripple wavelengths were chosen to approximate 0.5, 1.0, 2.0 and 5.0 times fish total length. The potential of ripples to locally retard current and thereby provide a refuge from the flow was measured as a velocity ratio, $u_{\text{trough}}/u_{\text{free-stream}}$, where u_{trough} is the flow velocity measured at a height of 0.5 cm from the bottom of a trough and $u_{\text{free-stream}}$ the flow velocity measured at a height of 10 cm above ripple crests. Cod usually swam steadily above substratum ripple crests in the free-stream flow. They used substratum ripples to hold station on only 3 of the 12 ripples tested by refuging from the flow in the ripple troughs (flow refuging). These ripples had wavelengths approaching twice the body length, with ripple amplitudes that produced velocity ratios of 0.44–0.65, thus providing at least a 35% flow reduction in the troughs. In addition, these ripples were only used at intermediate velocities starting at 49–78 cm sec⁻¹ and ending at 81–109 cm sec⁻¹ depending on the ripple morphology, suggesting there may be costs involved in flow refuging, probably in stability control. Flow refuging on substratum ripples could dramatically impact the physiology and ecology of cod in high current velocities by providing areas of retreat for energetic savings, but also offering opportunities for enhanced feeding and migration.

Introduction

Currents are a common feature of aquatic habitats, including tidally-swept shores and sea floors, rivers and streams. Numerous studies have demonstrated the importance of habitat structure in freshwater communities (see Diana 1995), where currents create numerous crevices among boulders, logs or root wads etc, providing regions of reduced flow. These regions are used by the fusiform benthopelagic fish that dominate these communities to hold station

(Fausch 1984, Probst et al. 1984, Rankin 1986, Facey & Grossman 1990), thus reducing energetic expenditure, where station-holding is defined as the ability to maintain position in a current without actively swimming (Arnold & Weihs 1978, Webb 1989).

However, less attention has been directed towards tidally-swept situations (Lough et al. 1989, Gerstner & Webb 1998), where benthopelagic fish, such as Atlantic cod, *Gadus morhua*, are common. While these areas contain patches of boulders and pebbles, much of the substrata is composed of sand

which forms substratum ripples in currents. On the Scotian Shelf, cod are most highly concentrated in areas with sand-gravel bottom types (Scott 1982) and on Georges Bank, 0-group cod have been observed resting in the troughs of small sand ripples (R.G. Lough personal communication to Arnold et al. 1994). Therefore, substratum ripples could provide areas of reduced flow for station-holding by cod.

Ripple wavelength and amplitude vary depending on the current velocity, and the particle size and density of the substrata. However, accurate prediction of ripple morphology is often difficult because of unstable turbulent flows (Dyer 1986). In areas of the North Sea, ripple wavelengths vary from 10–20 cm with amplitudes of 1–3 cm (Cook 1985). These smaller ripples are often superimposed on sand waves which can reach amplitudes of 2–3 m in areas of the North Sea (Arnold et al. 1994) and 2–8 m on Georges Bank (Lough et al. 1989). In the North Sea, flow velocities of 38–55 cm sec⁻¹ have been found at 100 cm above the substratum (Cook 1985), while peak spring tidal current velocities near the bottom range from 60–220 cm sec⁻¹, depending on the location (Arnold et al. 1994). Similarly, maximum tidal current velocities up to 40 cm sec⁻¹ have been found near the bottom on Georges Bank, with storm current velocities exceeding 1000 cm sec⁻¹ (Lough et al. 1989).

In this study, I tested combinations of ripple wavelengths, ripple amplitudes and flow velocities to span combinations found in current-swept habitats. Thus the purpose of this study was to determine the physical characteristics of a simple structure found in cod habitat, sinusoidal substratum ripples, used to promote station-holding. I define the ability to station-hold by using areas of reduced current velocity as flow refuging.

Methods

Fish

Atlantic cod were caught near Lowestoft, England using a beam trawl and held in the laboratory for 4–6 weeks before the start of the experiments. Fish

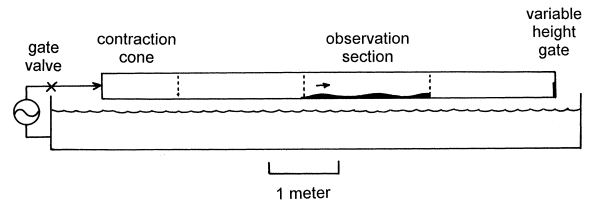


Figure 1. Diagram of the flume used in the experiments. Ripple profiles were placed in the observation section. Gate height and pipe valves on the water input were used to regulate free-stream current velocity while maintaining a relatively constant water depth. Dashed lines indicate grid barriers. Flow direction is from left to right.

were held in 1200 l tanks, continuously aerated and flushed with filtered sea water. All fish were fed twice a week on chopped lugworm and sand eels. Fish were starved for at least 12 hours prior to the start of all experiments, while acclimating in the flume. Eight cod were tagged with small pieces of thread on the dorsal fin, and six of eight fish were used for each ripple profile. Cod averaged 33.0 ± 0.4 cm total length (mean \pm 95% confidence interval) and 330.8 ± 12.5 g.

Apparatus

Station-holding performance was measured using increasing velocity tests. Experiments were performed in a flume described in detail by Arnold (1969) (Figure 1). Briefly, water entered a 600 cm long flume with a 30 cm square cross section, via a contraction cone. This design ensured a rectilinear flow profile throughout the flume, except as modified by test substrata. Free-stream current velocities ($u_{\text{free-stream}}$) were measured at a height of 10 cm above ripple crests using a Kent type 265 miniflow miniature propeller current meter (diameter = 1.0 cm). Measurements of flow profiles showed free-stream values were reached at this height.

Sinusoidal substratum ripples were constructed from 0.02 cm thick, foam-backed vinyl flooring sheeting attached to a balsa wood frame, weighted with a 0.95 cm thick Plexiglass sheet. Ripples extended over at least 125 cm of the flume floor, the wavelength of the largest ripple. The observation section started with a ripple rise from trough to

crest. All combinations of four ripple wavelengths ($\lambda = 10, 25, 50$ and 125 cm) and three ripple amplitudes ($h = 1.0, 2.5,$ and 5.0 cm) were examined, with one exception. A reference (control) planar surface was used instead of a $\lambda = 125$ cm, $h = 1.0$ cm ripple. Ripple wavelengths were chosen to approximate 0.5, 1.0, 2.0 and 5.0 times fish total length.

Experimental procedure

Pairs of cod were acclimated to the flume for at least 12 hours overnight, at a free-stream velocity of 5–10 cm sec⁻¹. Pairs were used because individuals of this schooling species appeared stressed when alone. Following the acclimation period, the free-stream velocity was increased 5–10 cm sec⁻¹ at two minute intervals following the same sequence for all fish. Minimum refuge velocity, $u_{\text{refuge-min}}$, is defined as the free-stream current velocity at which a fish first moved towards the substratum to utilize flow refuges to avoid swimming. Maximum refuge velocity, $u_{\text{refuge-max}}$, is defined as the free-stream current velocity at which a fish moved away from the substratum and resumed swimming. Minimum and maximum refuge velocities and station-holding behaviors were recorded for each fish at each velocity interval. Fish were considered holding station if they were able to maintain position for any part of the interval, although fish that held for part of the interval generally held for the whole interval. The experiment was terminated when a fish started burst swimming, often soon after maximum refuge velocity. Thus, the length of the experiments ranged from 12–26 minutes. The maximum velocity tested on any ripple was 111 cm sec⁻¹. At the end of all experiments, the fish were weighed and measured.

Flow patterns

Flow profiles were determined by measuring flow velocity at 1 cm intervals from the substratum to the water surface over ripple crests and troughs, at a free-stream velocity intermediate between minimum and maximum refuge velocity (45–65 cm sec⁻¹). Flow patterns are described in detail else-

where (Gerstner & Webb 1998). Data from the flow profiles were used to calculate a velocity ratio, $u_{\text{trough}}/u_{\text{free-stream}}$, where u_{trough} is the flow velocity measured at a height of 0.5 cm from the bottom of a trough. The relationship between velocity and height above the substratum is generally logarithmic until free-stream velocities are reached, so that cod body depth did not experience a single constant current velocity. The same applies along the body length. Thus the velocity at 0.5 cm is a reference, comparable to the use of focal-point water velocity at a fish's head to estimate microhabitat use for other species, such as salmonids (Fausch 1984). The actual shape of the flow profile can be calculated from this height and the height at which the free-stream velocity is reached (Arnold & Weihs 1978). Thus, velocity ratio is a measure of the *potential* of ripples to locally retard current and thereby provide a refuge from the flow.

Results

Behavior

Cod swam several centimeters above the ripple crests to maintain position in the current at most velocities. I measured exceptions at intermediate velocities of 49 to 78 cm sec⁻¹ ($u_{\text{refuge-min}}$) on some ripples with large λ and h , when cod moved into the ripple trough to flow refuge. In some cases cod held station without swimming, by first placing the pectoral fins in the 'parr position' (Arnold et al. 1991) and then pressing them to the substratum at higher velocities. Most cod positioned themselves in the lee of the crest without actively swimming, stabilizing themselves with fin movements. As flow velocities increased to 81 to 109 cm sec⁻¹ ($u_{\text{refuge-max}}$) cod were displaced from the ripple troughs and began swimming again. At these velocities, cod used burst and coast behaviors (Weihs 1974, Videler & Weihs 1982) above all substratum ripples tested.

For the ripples used to flow refuge, $u_{\text{refuge-min}}$ values were 63.9 ± 9.0 cm sec⁻¹ (mean \pm 95% CI) for the ripple with $\lambda = 50$ cm and $h = 2.5$ cm, 48.8 cm sec⁻¹ for the ripple with $\lambda = 50$ cm and $h = 5$ cm and 78.1 ± 14.8 cm sec⁻¹ for the ripple with =

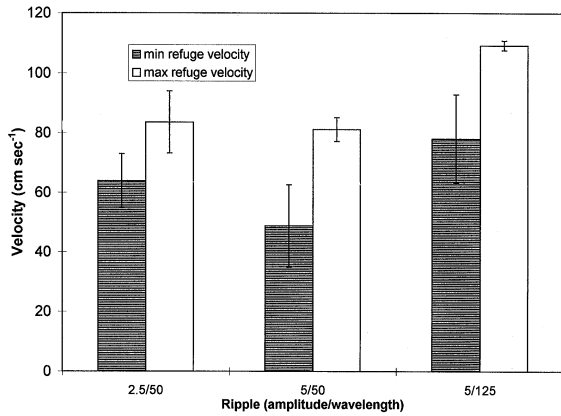


Figure 2. Minimum and maximum refuge velocity which cod used for flow refuging on three substratum ripples. Data are means \pm 95% confidence intervals.

125 cm and $h = 5$ cm (Figure 2). The velocity at which swimming was resumed ($u_{\text{refuge-max}}$) was 83.6 ± 10.7 cm sec⁻¹ for the ripple with $\lambda = 50$ cm and $h = 2.5$ cm, 81.2 ± 4.0 cm sec⁻¹ for $\lambda = 50$ cm and $h = 5$ cm, and 109.3 ± 1.6 cm sec⁻¹ for $\lambda = 125$ cm and $h = 5$ cm.

Flow patterns

The flow reduction in the troughs of substratum ripples ranged from a velocity ratio of 0.82 on the pla-

Table 1. Summary of results of flow visualization over rippled substrata with various wavelengths and amplitudes. Ripples retard flow in the troughs, which is shown as the velocity ratio (trough flow velocity/free-stream current velocity).

Ripple wavelength (cm)	Ripple amplitude (cm)	Velocity ratio	Used for flow refuging?
10	5.0	-0.19	no
	2.5	-0.14	no
	1.0	0.60	no
25	5.0	-0.17	no
	2.5	0.10	no
	1.0	0.69	no
50	5.0	0.44	yes
	2.5	0.62	yes
	1.0	0.74	no
125	5.0	0.65	yes
	2.5	0.80	no
Planar		0.82	no

nar surface to -0.19 (backflow) on the ripple with $\lambda = 10$ cm and $h = 5.0$ cm (Table 1). Velocity ratios were 0.44 ($\lambda = 50$ cm, $h = 5$ cm), 0.62 ($\lambda = 50$ cm, $h = 2.5$) and 0.65 ($\lambda = 125$ cm, $h = 5$ cm) for the three ripple profiles used by cod to flow refuge.

Discussion

Cod used flow refuges to hold station only at intermediate current velocities, and only on three ripple profiles tested, with wavelengths of 50 cm and 125 cm, and amplitudes of 2.5 cm and 5 cm. They appeared unable to take advantage of the larger reductions in flow velocity found on shorter ripples, since they could not contour their bodies to the ripple troughs. Cod used in these experiments averaged 33 cm total length. Thus, the smallest ripple used to flow refuge was a minimum of two body lengths. These findings are similar to those found for plaice, *Pleuronectes platessa*, that maximize station-holding performance on substratum ripples approximating two body lengths (Gerstner & Webb 1998).

However, cod did not use all ripples with λ approximating two body lengths to flow refuge, only those with amplitudes of 2.5 cm and 5.0 cm, but not 1.0 cm. The large amplitude ripples provided flow reduction of at least 35% in the troughs, while the velocities in the troughs on small amplitude ripples was similar to free-stream flows, and therefore appeared to provide insufficient flow reduction to be useful to cod for flow refuging.

Finally, cod only used ripples to flow refuge at intermediate velocities of 49–109 cm sec⁻¹. At higher velocities, they were unable to remain in the trough flow refuges. At low velocities, even though they appeared able to use refuges, they chose to swim steadily. It might be thought that cod were progressively fatigued in the increasing velocity test, using trough refuges to recover. However, even though the same time-velocity sequence was used for all fish on all ripples, mean $u_{\text{refuge-min}}$ values differed on each of the ripple profiles used for flow refuging. In addition, burst swimming behavior, which precedes exhaustion was the same irrespective of the use of ripples as refuges. Thus, the most parsimonious ex-

planation for cod flow refuging at intermediate intervals is velocity and not time. Swimming at low velocities, even when flow refuging appears feasible is consistent with observations on Georges Bank, where juvenile cod swim above the substratum in currents of 3–23 cm sec⁻¹ (Lough et al. 1989).

However, it would seem energetically desirable to avoid swimming at all current velocities. The use of troughs to avoid swimming only at intermediate velocities suggests that flow refuging may be associated with energetic costs as well as benefits. Flow is often turbulent near ripples, and this may incur costs for posture and stability control. Shtaf et al. (1983) found critical swimming velocities were reduced by even low levels of turbulence. I suggest that flow refuging becomes more economical at intermediate current velocities, whereas steady swimming is less costly overall at low velocities.

The use of flow refuges to hold station over a narrow range of substratum ripples and only at intermediate velocities contrasts with plaice, which use the whole range of ripple profiles at all velocities, until they are displaced and begin to swim (Gerstner & Webb 1998). This may be associated with differences in body morphology between the dorso-ventrally compressed plaice form and the fusiform cod. Plaice-like forms, lying on their sides are much more dorso-ventrally flexible in the plane of the substratum, enabling these fish to contour the body to ripples. Cod, with a vertical orientation, are in the plane of the substratum, and cannot match the body to steep, short ripples, even when flow velocities are greatly reduced in the troughs.

Although cod flow refuged only at intermediate velocities and used a limited range of substratum ripples, the physiological and ecological benefits of this behavior could be extensive. Swimming is energetically costly for most fishes (Brett & Groves 1979). The ability to use substratum ripples as flow refuges and avoid swimming will reduce energetic expenditures. This energetic savings is likely to have substantial impact on cod energy budgets, allowing them to devote more energy into other components of the budget, such as feeding or reproduction. Use of substratum ripples as flow refuges may also allow cod to live near high velocity habitats or stay in these areas for longer periods of time, there-

by expanding the fish's niche breadth. These high velocity habitats are often areas of abundant food resources, and from a refuge, fish can enter the higher free-stream flow only to feed as needed (Fausch 1984, Lough et al. 1989). Higher flows can also provide transport for cod migration (Arnold et al. 1994). Thus, flow refuging on substratum ripples can provide areas of retreat from high current velocities for energetic savings, but also offer opportunities for enhanced feeding and migration.

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References cited

- Arnold, G.P. 1969. A flume for behaviour studies of marine fish. *J. exp. Biol.* 51: 671–679.
- Arnold, G. P. & D. Weihs. 1978. The hydrodynamics of rheotaxis in the plaice (*Pleuronectes platessa*). *J. exp. Biol.* 75: 147–169.
- Arnold, G.P., P.W. Webb & B.H. Holford. 1991. The role of pectoral fins in station-holding of Atlantic salmon parr (*Salmo salar* L.). *J. exp. Biol.* 156: 625–629.
- Arnold, G.P., M. Greer Walker, L.S. Emerson & B.H. Holford. 1994. Movements of cod (*Gadus morhua* L.) in relation to the tidal streams in the southern North Sea. *ICES J. mar. Sci.* 51: 207–232.
- Brett, J.R. & T.D.D. Groves. 1979. Physiological energetics. pp. 279–352. *In:* W.S. Hoar, D.J. Randall & J.R. Brett (ed.) *Fish Physiology*, Volume 8, Academic Press, New York.
- Cook, P. H. 1985. The behavior of the plaice (*Pleuronectes platessa* L.) in relation to bottom currents and sediment type. Ph.D. Thesis, University of East Anglia, Norwich. 165 pp.
- Diana, J. S. 1995. Biology and ecology of fishes. Cooper Publ. Corp., Carmel. 441 pp.

- Dyer, K. R. 1986. Coastal and estuarine sediment dynamics. John Wiley and Sons, Chichester. 342 pp.
- Facey, D.E. & G.D. Grossman. 1990. The metabolic cost of maintaining position for four North American stream fishes: effects of season and velocity. *Physiological Zoology* 63: 757-776.
- Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Can. J. Zool.* 62: 441-451.
- Gerstner, C.L. & P.W. Webb. 1998. The station-holding performance of plaice, *Pleuronectes platessa*, on artificial substratum ripples. *Can. J. Zool.* (in press).
- Lough, R.G., P.C. Valentine, D.C. Potter, P.J. Auditore, G.R. Bolz, J.D. Neilson & R.I. Perry. 1989. Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. *Mar. Ecol. Prog. Ser.* 56: 1-12.
- Probst, W.E., C.F. Rabeni, W.G. Covington & R.E. Marteney. 1984. Resource use by stream-dwelling rock bass and smallmouth bass. *Trans. Amer. Fish. Soc.* 112: 283-294.
- Rankin, E.T. 1986. Habitat selection by smallmouth bass in response to physical characteristics in a natural stream. *Trans. Amer. Fish. Soc.* 115: 322-334.
- Scott, J.S. 1982. Selection of bottom type by groundfishes of the Scotian Shelf. *Can. J. Fish. Aquat. Sci.* 39: 943-947.
- Shtaf, L.G., D.S. Pavlov, M.A. Skorobogatov & A.S. Baryekian. 1983. Fish behavior as affected by the degree of flow turbulence. *Voprosy ikhtiologii* 3: 314-321. (in Russian).
- Videler, J.J. & D. Weihs. 1982. Energetic advantages of burst-and-coast swimming of fish at high speed. *J. exp. Biol.* 97: 169-178.
- Webb, P.W. 1989. Station-holding by three species of benthic fishes. *J. exp. Biol.* 145: 303-320.
- Weihs, D. 1974. The energetic advantages of burst swimming. *J. theor. Biol.* 49: 215-229.