

SWIMMING AGAINST THE TIDE: ADAPTATIONS OF THREE SPECIES OF
FISH FOR LIFE IN THE INTERTIDAL ZONE

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ABSTRACT

Intertidal fish at Kaikoura do not swim against the tide, but instead are adapted so that they do not have to swim at all. Specialisations are major in the clingfish, less so in the tripterygiids and minor in the rockfish. This is reflected in the way that each species manages to remain within rockpools.

INTRODUCTION

The waters around the Kaikoura region have an interesting current pattern. Two oceanic currents meet at Kaikoura; warm water from the north meets cold water from the south and the combined current then heads out towards the Chatham Islands (Heath 1975). The consequence of this is that the Kaikoura region has a very diverse fauna, including over 200 species of fish, with both northern and southern forms represented (Francis 1979; Roberts & van Berkel 1983).

The intertidal region has a rich invertebrate (Marsden 1981) and fish fauna (Darby 1964). The rockfish (*Acanthoclinus fuscus*) is common throughout the whole of the intertidal zone and is commonly found completely out of water, sheltering under large stones. Triplefins (Tripterygiidae) are very common in rockpools up to about the mid-shore level. Several species of triplefins are present although there is much confusion regarding their nomenclature (see for example Ayling & Cox 1982; Darby 1964;

Thompson 1981). Hardy, of the National Museum, Wellington, is currently revising the whole family (pers. comm.). The variable triplefin (*Tripterygion varium*) and the common triplefin (*T. capito*) are both common inhabitants of the Kaikoura Peninsula. A third group of intertidal fishes, the clingfish (Gobiesocidae) can be found on the mid to low shore, clinging to the undersurfaces of rocks, using the sucker formed from modified pelvic and pectoral fins. Several other species of fish are often found on the low shore though they are probably not strictly intertidal fish, but shallow water animals which have been stranded by the receding tide.

While information is available regarding the ecology and life histories of these intertidal fish (Ayling & Cox 1982; Jillett 1968a; b) very little is known about their physiology, or how these animals are adapted for life in the harsh environment of the intertidal zone (Davison 1984). It is probable that they show similarities with intertidal and estuarine fish from Northern Hemisphere temperate waters (Davenport 1981; Gibson 1982; Laming *et al.* 1982) although this remains to be demonstrated, and the rockfish, at least, shows affinities with tropical fishes (Davison 1984).

The present work examines the morphological adaptations of the three main groups of intertidal fish which allow them to survive in their chosen habitat. In particular, attention is paid to those features which allow them to remain on the shore while being exposed to the actions of waves.

MATERIALS AND METHODS

Rockfish (*Acanthoclinus fuscus*), triple fins (*Tripterygion varium*) and clingfish (*Diplocrepis puniceus*) were collected from the shore at South Bay on the Kaikoura Peninsula. Rockfish ranged from 5-18cm total length with most of the work being carried out on 10-12cm fish. Triplefins ranged from 5-15cm with most work being carried out on individuals 8-10cm in length, while all clingfish were 4-6cm long. All fish were kept in seawater aquaria at the Edward Percival Field Station, and at the University of Canterbury until required.

HISTOCHEMISTRY

Fish were killed and blocks of muscle tissue were dissected from regions immediately posterior to the body cavity, from close to the caudal fin, and also from the pectoral fin (pectoral flexor muscle). The tissue was quickly frozen in liquid nitrogen and then sections were cut at 8µm at -25°C in a cryostat.

Sections were air dried at -25°C and then stained within 24 hrs for lipid (Sudan black) succinic dehydrogenase (SDH) and alkaline stable adenosine triphosphatase (ATPase). Sections for the ATPase reaction were preincubated at pH 10.2 for time periods ranging from 5-10 min and then incubated in the presence of ATP for 20 min at pH 9.4 (Davison & Macdonald 1985; Guth & Samaha 1970; Johnston *et al.* 1974). As this is an artefact staining technique, relying on the differing stabilities of the different muscle fibre types at high pH, preincubation over the time span used allowed differentiation of these fibre types.

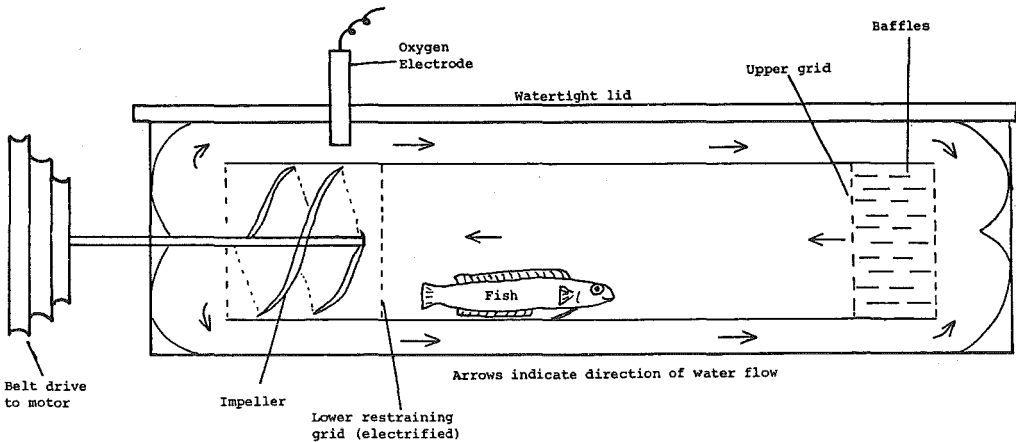


Fig. 1. Diagram of the swimming respirometer. Water is drawn through the central tube at a known speed, using the impeller, and returned along the outer tube. The fish is kept within the two restraining grids and swims against the water flow.

SWIMMING EXPERIMENTS

Swimming experiments were carried out using a small Blazka-type tunnel respirometer (Fig. 1) (Blazka *et al.* 1960). Each fish was placed in the respirometer and left for several hours, with the water flow at a slow speed of less than 0.5 body lengths per second (bl s^{-1}) in order to allow them to become accustomed to the machine. The water speed was then increased by increments of approximately 0.5 bl s^{-1} and the behaviour of the fish was observed.

The oxygen consumption of rockfish and triplefin was determined at 15°C using closed box respirometry (Davison 1984)

in still water, in slow moving (1 bl s^{-1}) and also in fast moving (2.5 bl s^{-1}) water.

RESULTS

Diagrams of the structure of the myotomal musculature of each fish species can be seen in Fig 2, together with information describing the size and numbers of fibre types. Little difference was seen between the two sampling sites from the myotomes of each species (see for example Love 1970; Davison & Macdonald 1985) and so the data has been pooled. For each species the muscle was composed of three fibre types; small diameter fibres (SDF), oxidative fibres and white fibres. The SDF were characterised by having a small uniform diameter, and an almost total lack of staining for any of the techniques used. The oxidative fibres had a large mean diameter and stained for all of the methods used. Dense staining of fibres at long preincubation times for the ATPase reaction, and the moderate staining for lipid and SDH indicated that these fibres were intermediate (also called pink) muscle fibres (Johnston *et al.* 1977). White fibres had a very large diameter, showed little staining for SDH and lipid, but were stable at short preincubation times for ATPase.

Triplefins and clingfish had small numbers of SDF and pink fibres, so that virtually the whole of the myotome was composed of white muscle (Fig 2). The size of these fibres was very small in the clingfish, but of a 'normal' size in the triplefin myotome. The rockfish possessed large numbers of SDF and quite high numbers of pink fibres. Within the rockfish there was a distinct gradation of staining for SDH and lipid within the pink fibres. Those cells next to the SDF showed high levels of staining, with a gradual decrease in staining intensity with proximity to the white muscle. This pattern is common in teleost fish (Davison & Goldspink 1984; Patterson *et al.* 1975).

Red muscle was not found in the myotome of any species. Red muscle was found, however, in the muscle tissue of the pectoral fin. In both the rockfish and the triplefins the pectoral flexor muscle was a mixed muscle, a mosaic of at least three fibre types, a structure expected from bottom living fish using labriform locomotion (Davison & Macdonald 1985). Red muscle fibres were intermediate in size between SDF and intermediate fibres, stained heavily for SDH but were completely unstable at high pH for the ATPase stain. Pectoral fin muscle was not sampled for the clingfish.

A common feature for all three species when placed into the respirometer was that they did not swim. Different methods were,

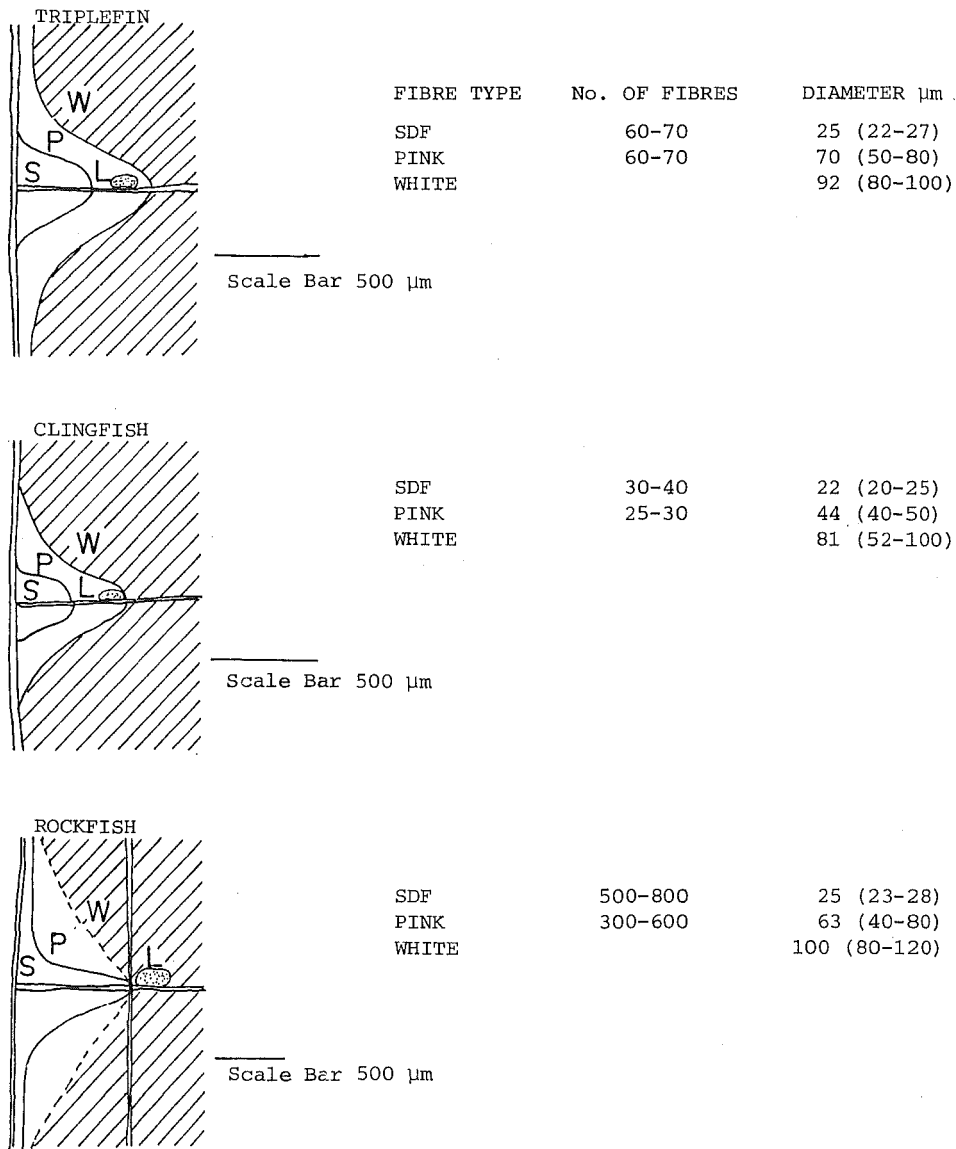


FIG 2. Diagrams of cross sections of the myotomal muscles of triplefins, clingfish and rockfish, showing the location of small diameter fibres (S), pink fibres (P) and white muscle (W). Only part of the white muscle mass is shown. The position of the lateral line (L) is indicated. The rockfish diagram is drawn on a different scale to the other two drawings as indicated by the scale bars. The data to the right of the drawings indicate pooled data from five fish for each species, giving the number of fibres as a range, and fibre-diameter as the mean, and also the range.

however, employed to effect this.

The clingfish was found on the shore clinging to rock surfaces. In the aquarium they were found either firmly attached to rocks or onto the side of the tank. This was achieved by using the ventral sucker formed from the modified fins. In still water these fish remained motionless for most of the time, swimming only in short bursts of high speed activity. Within the swimming tunnel, these fish clung to the sides of the swimming chamber and remained motionless over the whole of the speed range of the machine. This was equivalent to about six body lengths per second. When dislodged, the fish swam rapidly until they could reattach themselves to the perspex walls.

The triplefins typically were found motionless on the bottom of the aquarium tank, often hidden beneath stones. In still water they moved using a rowing action of their large pectoral fins (labriform locomotion) with the head usually held much higher than the tail (indicating a fish heavier than water) and with the body held rigid. Within the swimming tunnel, the fish remained on the bottom, with the pectoral fins spread wide and angled such that they formed a wedge (together with the head) which served to push the animals down onto the substrate due to the force of the running water. This allowed the larger individuals to remain motionless over the speed range of the machine. Smaller animals were able to remain on the bottom for up to approximately 2.5 bl s^{-1} . Above this speed the animals could not stay in the same place on the smooth perspex and slid backwards until they hit the lower restraining grid. At this point they swam upstream using a sprint and glide action with little contribution from the pectoral fins. The fish would swim for only a few minutes, after which they fell back on to the lower restraining grid.

In the still water of the aquarium tank, the rockfish behaved in a similar manner to the triplefins in that they were mainly hidden under stones and moved slowly (usually at feeding times) using labriform locomotion. These fish did not fare well within the swimming tunnel, essentially because they were the least well adapted to withstand flowing water. At low speeds the fish were able to remain on the bottom of the tunnel by throwing their bodies into a series of sine waves, allowing them to grip on to the bottom of the machine. This was not very effective, and at speeds above 1 bl s^{-1} they were swept off the bottom of the tunnel and carried downstream to the lower restraining grid. Although this grid was electrified, these fish made no attempt to swim away from it (i.e. into the water current). If the fish were physically removed from the grid and pushed into the current they swam in a very erratic manner, using both the myotome and the pectoral fins, moving rapidly up and down the swimming tunnel and making no attempt to orientate themselves into the current. This 'panic escape' type of swimming was maintained only for a

few seconds after which the fish returned to the lower grid, occasionally making attempts to go with the current rather than swim against it.

Oxygen consumption was low in both still, and in slow moving water, as long as the fish were not swimming (Table 1), and were similar to values found in an earlier study on rockfish (Davison 1984). The oxygen consumption of the fish in slow moving water was higher than those in still water, but this was not significantly different (T test). In fast moving water, oxygen consumption was high (Table 1) although as both fish species did not swim for long periods, and as much of the swimming was high speed sprinting, it is probable that the metabolic rate was actually much higher, due to the anaerobic nature of the exercise.

TABLE 1. OXYGEN CONSUMPTION ($\text{mg O}_2 \text{ g}^{-1} \text{ h}^{-1}$) \pm SE OF TRIPLEFIN AND ROCKFISH AT REST AND AT TWO WATER SPEEDS.

	Rest	Water speed	
		1 bl s^{-1}	2.5 bl s^{-1}
Triplefin	0.09 \pm 0.02 (N=10)	0.10 \pm 0.03 (N=10)	0.38 (N=3)
Rockfish	0.08 \pm 0.02 (N=10)	0.10 \pm 0.04 (N=10)	0.48 (N=2)

DISCUSSION

It is generally accepted that there are four major types of muscle in fish, with possibly several minor types (Davison 1983; Davison & Macdonald 1985; Johnston 1981). Red muscle is used for slow speed swimming, while the large bulk of white muscle is used for high speed sprinting, using glucose anaerobically. Pink muscle has not been thoroughly investigated but it is thought to be an 'intermediate' type of muscle, with a speed of contraction somewhere between the red and white (Johnston *et al.* 1977). Small diameter fibres are virtually unstudied, though it is possible that they are a type of tonic muscle used in postural control (Davison 1983; Davison & Macdonald 1985). These four muscle fibre types were present in all three species of fish used in this study, although the distribution of the fibres differed and this can be related to the anatomy of the fish and the environment in which these fish live.

The major point to emerge from this work is that all three species are adapted for life in their intertidal habitat not by their ability to swim against the tide, but by their ability to avoid having to swim at all. Obviously, a fish only a few cm long would be unable to maintain its position against the full force of a wave and so these fish avoid the direct action of the wave by hiding in crevices and under stones, and then being modified so that they do not have to swim against the residual water movement. This has two advantages; it allows each fish to remain within a particular rockpool (these fish are probably territorial, Jillett 1968a; b) and also it drastically reduces the energy expenditure required for staying in that rockpool, an important factor for a fish which has a limited feeding time.

Each species is modified for this intertidal habitat in a different way, though each method appears to be successful, as all three groups are common on the shore. The clingfish is highly specialised with its powerful sucking disc. As this fish is literally stuck to the rock surface it has no need for slow cruising muscle or for postural muscles within the myotome. This is shown in Fig 2, where it can be seen that there are very low numbers of SDF and pink fibres and that these fibres are very small, indicating possibly that they are not extensively used. There was no red muscle in the myotome. There may be fibres of this type in the pectoral muscle but this was not demonstrated here, and as this fish was never observed to swim slowly, or use its pectoral fins for swimming, it is unlikely that red muscle within the pectoral fins would have much importance. The major locomotory muscle in this fish is the white myotome, used to push the fish along at high speed.

The triplefins show a type of specialisation found also in several freshwater fish from New Zealand adapted for life in fast flowing rivers. The large wedge shaped head and pectoral fins can be seen in the bullies (Eleotridae) and in the torrentfish (Cheimarrichthyidae) (McDowall 1978). No work has been carried out on torrentfish, but the anatomy of the common bully (*Gobiomorphus cotidianus*) has been fully described (Davison 1983). None of these fish use the myotomal muscle for slow speed swimming but instead use the red muscle of the pectoral fins. Red muscle has been completely lost from the myotome, and the trunk muscle is composed of almost only white muscle fibres (for sprinting) with a few SDF and pink fibres. The tripplefin has more (and larger) pink and SDF than the clingfish, reflecting the different methods used to resist the water flow. The clingfish is stuck to the rock surface, allowing water to simply flow over it, without much need for postural control. The triplefin, however, must orientate itself into the water current, and then ensure that the myotome is held in the correct position, thus needing the small diameter fibres.

The rockfish had the least modified body for withstanding water flow through a water tunnel. This was perhaps an 'unfair' test for this animal as it has been reported that this animal avoids wave surge by wedging itself into cracks and crevices using its body and dorsal and ventral fins (Ayling & Cox 1982; Jillet 1968a). Presumably, it does not swim against the current, but instead allows itself to be swept along with the water until it is carried into a crevice small enough to allow it to become wedged. This method of avoiding the need to swim is reflected in the structure of the myotome. As with the triplefins, the labriform type of slow speed swimming has resulted in well developed pectoral fins powered by red muscle and a loss of red fibres from the myotome. In contrast to the triplefins, however, the rockfish possesses large numbers of both pink muscle fibres and SDF. Assuming that the SDF are tonic fibres, then this large number of muscle cells is required to allow the fish to throw its body into folds to wedge itself into its crevice, and then to hold the body in this static position. The reason for the large number of pink fibres is unclear. While it is possible that these fibres are involved in the tonic control of the myotome, the structure of the fibres, and the contraction characteristics make it unlikely that this is so (Johnston *et al.* 1977). Thompson (1981) states that rockfish move "with eel-like undulations" although this was not observed in the present study, and the pink muscle could play a role here.

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