

Impact of Foraging Blacksmiths on Constituents in the Water Column: Implications on School Behavior and Structure

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Abstract. Blacksmiths, *Chromis punctipinnis*, which are obligatory planktivores, often form large relatively stationary schools in currents within and adjacent to giant kelp forests in southern California. The individual school members forage on zooplankton carried by the currents. Several attributes of these schools were examined to assess what impact they might have on the water that passes through each school. Measures of oxygen tension, ammonium concentration, and zooplankton abundances were obtained immediately upstream and downstream of several schools. Feeding rates of blacksmiths in the front and rear of schools were also measured. In addition, spiking experiments by introducing various concentrations of ammonium and additional zooplankton immediately upstream of schools were utilized to determine how they might affect school behavior(s). The measures demonstrate that oxygen tension and plankton densities were significantly reduced and ammonium concentrations increased behind large schools of *Chromis* relative to levels measured in the front of the schools. Internal structural changes observed within the schools appear to relate with declines in oxygen and zooplankton abundance, but no correlation could be associated with increases in ammonium concentrations.

Keywords: Metabolic effect; oxygen; ammonium; fish school behavior; *Chromis punctipinnis*; blacksmith; Catalina Island.

Introduction

Medium to large schools of fishes can alter the chemistry and nutrients of the water that they occupy: specifically lower oxygen and increase carbon dioxide (McFarland and Moss 1967), increase ammonium levels (Oviatt et al. 1972; Meyer et al. 1983; Bray et al. 1986), and dramatically decrease planktonic organisms from ingestion (Bray 1980; Koslow 1981; Hamner et al. 1988). Most investigations of schooling fish do not relate these

alterations in water constituents to possible changes in school behavior (for examples see McFarland and Moss 1967; Moss and McFarland 1970).

The hypothesis that changes in respiratory gases from school metabolism affect school behavior, as presented by the above authors, can be extended to include the excretion of nitrogenous wastes by the school (primarily ammonium). Accordingly, if these products of group metabolism approach deleterious levels, movements within a fish school should be modified by school members to minimize the potentially adverse effects from inhabiting densely populated volumes of water. Simply stated, individual fish may respond to minimize their exposure to the less favorable conditions created from group metabolism, including the reduction in available food. Such individual behavioral modifications would result in a regular changing school structure.

This paper explores aspects of the metabolic and foraging impact of young adult blacksmiths, *Chromis punctipinnis*, in order to relate dynamic attributes of school structure to the described hypothesis. Blacksmiths are obligate planktivores that often form large foraging schools in and adjacent to the giant kelp beds along the coast of southern California and surrounding the Channel Islands (Hobson et al. 1981). These foraging groups are readily observed using scuba. Because the schools often maintain stationary positions relative to reefs and kelp, their impact on the water that passes through them can be measured.

Materials and Methods

Observations and measurements were made during November and December 1991 near Big Fisherman Cove within the Catalina Marine Life Refuge. Observations of blacksmith schools were made from approximately 12 to 15 m depth on the edge of a rocky prominence that dropped off seaward to deeper water. This area was char-

acterized by greater current flow than the shallower areas inshore, and it was here that large schools of *Chromis* were encountered.

School size and density

Abundance and density of fish in the schools encountered were determined by counting fish in a given location of each school by 2 divers. Dimensions of the location were then measured with a meter tape, and later the volume calculated and used to estimate fish density. When counts from the 2 observers varied greatly, they were discarded. When fish density within a school was not constant, which was usual in large schools, counts and measures were repeated for the locations of different densities. In addition, the overall dimensions of each school were measured and used to calculate total numbers of fish, as well as, the average fish density in a school.

Current measures

Current flow through each school was determined by the rate of travel of fluorescein dye injected into the water at the front of each school. The measuring unit consisted of a syringe attached to one end of a 1-m pole. Several cc's of dye were injected, and the time required for the dye to travel the length of the pole recorded.

Oxygen measures

Oxygen concentrations of the water were measured by filling groups of 4, 60-cc syringes with seawater from immediately in front of and behind schools. The samples were returned to a support skiff and oxygen determined with a YSI Model 58 oxygen meter. To assess variations in oxygen that may have occurred immediately upstream from schools, the probe of the oxygen meter was lowered at varied locations to the depth of the school where no blacksmiths were observed.

Ammonium measurements

Concentration. Ammonium concentrations were measured upstream and downstream to determine the amount released by each fish school. Two 250-cc plastic vials were filled with water from immediately upstream, 2 vials filled from immediately downstream and, to serve as controls, 2 were filled from each side of the schools not occupied by fish. Vials were returned within 1 hr to the laboratory at Wrigley Marine Science Center and ammonium concentrations determined according to Liddicoat et al (1975), except that dark incubation in a refrigerator for 1 hour replaced ultraviolet incubation.

Field experiments. To determine the effects of increased ammonium concentrations on school behavior, ammonium chloride concentrations of 0.4, 1.0, 2.0, 20

and 125 $\mu\text{m}\cdot\text{l}^{-1}$ were injected from 60-cc syringes into the current in front of the schools at 5-min intervals.

Measures of foraging

Plankton samples. The type and amount of zooplankton ingested by blacksmiths were determined by suspending 2 plankton nets (0.15 m dia, mesh size 0.3 mm) immediately preceding and behind schools with the higher densities. Both nets were set simultaneously and suspended for 30 min. Eight collections were executed.

Plankton release manipulations. To determine the effects of increased zooplankton on school behavior, additional plankton were released in front of foraging schools. Plankton were collected with a 0.5-m diameter 0.5-mm mesh net towed from a skiff at about 1 knot. Plankton were placed in a large plastic bag containing seawater and fluorescein dye, the latter serving to highlight the areas of increased plankton density following release. Dye from bags that did not contain plankton were also ejected into the foraging schools to serve as controls. Observations were made from the side of each school. Four such release manipulations were carried out.

Feeding rate experiments. It has been suggested (R. N. Bray, pers. comm. 1990) that the rate of pecking at plankton by blacksmiths could serve to index feeding success (i.e., those fish pecking at a higher rate are more successful in capturing prey). To determine the relative feeding success for fish in front of a school versus those in the rear, an analysis of peck frequency was performed. This involved counting the number of pecks per 30 sec made by 5 fish selected at random in front and 5 fish in the rear of a school. The mean rate of pecking was calculated for each group of 5 fish.

Results

Observations on schooling

Blacksmith schools were always oriented essentially into the current when feeding. Small scale movements of individual fish or small groups of fish (2–10) were observed within larger schools. These movements involved occasional increased rates of swimming relative to neighbor fish, decreasing their distance from the front of the school. At the same time individual fish were seen to stop swimming and drift toward the rear of the school. Frequently in the very large schools (> 12,000 fish) the entire rear portion of the school would break into several small schools (400–500 fish) and swim off perpendicular to the current. These small schools would often rejoin the large school after a few minutes, reminiscent of the behavior observed in striped mullet schools (McFarland and Moss 1967).

Table 1. Relationship between the number of blacksmiths, current velocity, oxygen reduction and ammonium increases through each school. Oxygen concentrations upstream of the schools were 7.80 ± 0.015 (1SD) $\text{mg}\cdot\text{liter}^{-1}$, $n = 11$; ammonium concentrations were 0.018 ± 0.009 (1SD) $\mu\text{moles}\cdot\text{liter}^{-1}$, $n = 10$.

Number of fish	Density fish·m ⁻³	Current cm·sec ⁻¹	Oxygen decrease mg·l ⁻¹ (1SD, n = 4)	Ammonium increase $\mu\text{m}\cdot\text{l}^{-1}$ (1SD, n = 3)
35	1.3	0.28	7.73 (0.048)	0.009 (0.005)
40	1.4	0.28	7.78 (0.014)	0.010 (0.003)
45	1.5	1.38	7.74 (0.014)	0.028 (0.017)
50	1.9	0.28	7.76 (0.018)	— —
2,300	11.6	14.2	7.24 (0.053)*	0.228 (0.010)
2,450	11.8	6.7	7.40 (0.075)*	0.235 (0.010)
3,200	12.0	11.4	7.24 (0.041)*	0.201 (0.010)
4,900	11.0	14.2	7.22 (0.050)*	0.203 (0.018)
6,800	12.0	13.9	7.23 (0.041)*	0.204 (0.006)
> 12,000	16.7	17.0	7.20 (0.045)*	0.225 (0.009)
> 20,000	> 14	22.2	6.97 (0.082)*	0.335 (0.017)

* = $p \leq 0.005$, t-test.

Foraging schools did not form in the observation location below current velocities of approximately 4–5 $\text{cm}\cdot\text{sec}^{-1}$. Instead blacksmiths were observed congregating near the reef bottom, either as individuals or in small groups. As current levels increased during a day's observations (measured by dye travel), blacksmiths were observed moving to deeper water areas outside the kelp cover, where they formed large schools. The reverse was observed as current decreased, small groups breaking off from the main school and retreating to the more shallow areas within the kelp beds.

In the largest schools, fish density varied being highest near the front of the school and lowest toward the rear of a school. In general the largest number of fish in a school and the highest fish densities were observed at the highest current flows (Table 1). Currents often exceed 1 $\text{m}\cdot\text{sec}^{-1}$ in this area, a flow much greater than the 22 $\text{cm}\cdot\text{sec}^{-1}$ observed for the largest school encountered. We did not determine the highest current flow at which blacksmiths stop foraging.

Foraging

In all schools, observed feeding occurred as defined by a rapid extension and contraction of the jaws of individual fish. The rate of pecking was not observed to exceed 1 flick per second. In the 5 feeding schools where pecking was counted, the rate declined toward the rear of

each school (Table 2). Correlated with this diminishment in feeding rate was the removal of significant amounts of zooplankton from the water column as it passed through the school (Table 3).

In the 4 plankton release experiments, a movement of blacksmiths into the area of increased zooplankton density (marked by the dye) was obvious. This behavior occurred along the schools, but subsided as the current swept the plankton/dye mixture downstream toward the rear of the schools. The increase in fish density was not quantified. Similar movements of blacksmiths into, or evasion of, the dye alone were not observed.

Measures of oxygen and ammonium

The mean concentrations of dissolved oxygen and ammonium in the study location not occupied by blacksmith schools were $7.80 \text{ mg}\cdot\text{l}^{-1}$ and $0.018 \mu\text{moles}\cdot\text{l}^{-1}$ (Table 1). Significant reductions in oxygen and increases in ammonium occurred in all of the large schools examined, but were not detectable in the smallest schools (Table 1). Results from the ammonium spiking experiments were consistent: no response was observed until the $125\text{-}\mu\text{mole}^{-1}$ solution of ammonium chloride was released. At this concentration the fish were observed to form a vacuole around the area of ammonium/dye solution and swim aside. Again no obvious avoidance of fluorescein dye released alone was observed.

Table 2. Comparison of the mean rates of feeding at the front and rear of foraging schools of blacksmith. Means are number of mouth flicks by five individual fish per 30 sec (1SD). Significance was determined by t-test within each days data set for front versus the rear of school means.

Number flicks	19 Nov	21 Nov	24 Nov	25 Nov	26 Nov
Front of school	20.0* (1.6)	19.6* (3.8)	18.0* (3.5)	21.0 ns (5.8)	20.4* (3.5)
Rear of school	12.8 (3.6)	11.0 (2.2)	11.5 (2.8)	13.0 (4.7)	10.8 (2.5)

* = $p \leq 0.05$, t-test.

Table 3. Reduction in abundances of major groups of zooplankton collected in front of and behind foraging schools of blacksmith. Groups are listed in order of decreasing abundance. For each collection ($n = 8$) differences in abundance between the front and rear of schools were tested with a Mann-Whitney U-test.

Group	Cumulative abundance front of schools	Cumulative abundance behind schools
Copepods	253	47*
Pteropods	87	21*
Chaetognaths	54	13*
Larvaceans	17	11
Fish eggs	16	8
Ostracods	14	3*
Amphipods	7	0*
Siphonophores	2	1
Paracarids	0	1

* = $p \leq 0.05$, Mann-Whitney U-test.

Discussion

The results in general fit the hypothesis that the metabolic impact of fish schools on constituents of the water that they occupy can be sufficient to modify school behavior(s), at least when schools achieve large size and high densities (McFarland and Moss 1967). The same can be said for the impact of large numbers of planktivorous fishes on the availability of zooplankton as currents sweep and/or fish schools swim through water containing concentrations of plankton. The net result is that individual fish at the rear of large schools are exposed to potential physiological constraints and, in planktivorous species, to a reduction in the availability of food. In either instance, or as for blacksmiths in both circumstances, the behavioral response(s) predicted for members of a fish school would be a movement away from the constraining condition(s) and into regions of the school where conditions are more favorable. The small internal movements observed within blacksmith schools fit these predictions. They also agree with the avoidance responses to lowered oxygen and increased carbon dioxide concentrations, as experimentally demonstrated for small schools of northern anchovy, *Engraulis mordax* (Moss and McFarland 1970). For example, anchovies avoided, they momentarily increased their swimming speeds and their nearest neighbor orientation to reductions of oxygen of $0.55 \text{ mg}\cdot\text{l}^{-1}$. The average reduction in oxygen for blacksmith schools was $0.59 \text{ mg}\cdot\text{l}^{-1} \pm 0.14$ (1SD). In these schools the internal shifts in position of members would lead over time to an averaging of each member's exposure to the various oxygen levels produced within the school. Reductions in oxygen greater than 5% (Table 1) may physiologically drive internal structural turnover in many fish schools, because the individuals literally sense and avoid the change.

Why do members at the front of a fish school exchange their more favorable position with members in less favorable conditions? Although the exchange may well be driven by a physiological mechanism, the answer likely lies in the protection from predators offered by a school's integrity (Hobson 1968, 1979; Radakov 1973; Pitcher and Wyche 1983; Morgan and Godin 1985; Pitcher 1986; Magurran and Pitcher 1987). If dominance prevailed and a spatial hierarchy developed, rear members would suffer the physiological consequences of chronic exposure to lowered oxygen (and increased dissolved carbon dioxide). Continued exposure to unfavorable conditions is known to lower the capacity of a great many species to maintain a constant swimming speed (Fry and Hart 1948; Fry 1957; Basu 1959). Thus members at the rear of large schools, who could not exchange position because of a dominance hierarchy based on feeding, would be subject to an intensification of predation. Amortized over time the number of fish could be reduced to levels that would be insufficient to provide adequate protection from predators. And, if so, dominant fish would ultimately pay their dues.

The field data provide little correlation between increased ammonium concentrations associated with blacksmith schools and modifications in behavior. The largest increase in ammonium level recorded downstream from a school was $0.35 \mu\text{moles}\cdot\text{l}^{-1}$, and agrees with earlier values obtained from behind blacksmith schools (Bray et al. 1986). In fact a behavioral avoidance was not achieved until ammonium concentrations of $125 \mu\text{moles}\cdot\text{l}^{-1}$ were introduced upstream; concentrations some 300 times larger than those normally produced by schools. Thus, we conclude that metabolically produced ammonium concentrations, as measured behind schools in this study, have no affect on school behaviors. This conclusion seems reasonable in light of the chemical properties of ammonia in water; ammonia, which is the prime nitrogenous waste in teleosts, rapidly forms ammonium ions, which are highly diffusible and sequestered rapidly by plants such as phytoplankton and kelp (Bray et al., 1986).

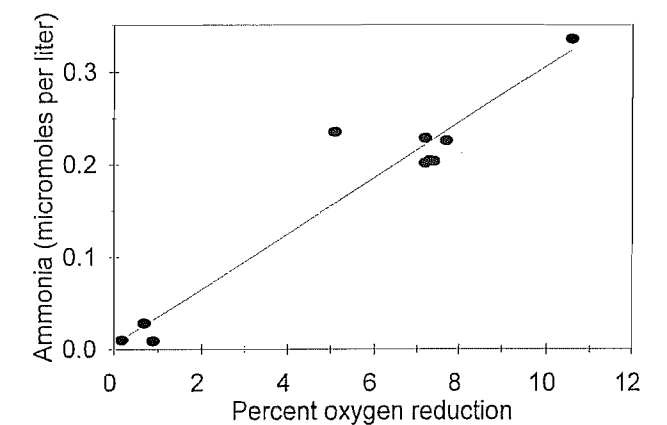


Figure 1. Comparison of the increase in ammonium concentrations with reductions in oxygen produced by schools of foraging blacksmith. The linear equation $\text{NH}_4^+ = 0.005 + 0.03 \times (\% \text{O}_2 \text{ reduction})$ yields $r^2 = 0.93$. Data are plotted from values in Table 1. In general, as oxygen reduction and ammonium increase, school size increases.

Is the source of ammonium downstream from large blacksmith schools a product of the members metabolism? Because ammonium concentrations were virtually similar wherever blacksmiths did not occur (mean = $0.018 \mu\text{moles}\cdot\text{l}^{-1} \pm 0.009$ [1SD]), the increases resulted primarily from blacksmith metabolism, with little contribution from zooplankton. If so, the ammonium increase should be a linear function of oxygen reduction (Fig. 1).

Although there appears to be a relation between current velocity, the number of blacksmiths in a school and fish densities within a school (Table 1), we are reluctant to fit the data to an equation. There are several reasons. The visual counting method, although useful for this study, lacked the precision required to carefully relate

these variables. It is obvious that for the very largest schools numbers could only be roughly approximated (Table 1). Even with school numbers of 2,000–6,000 and the fact that 2 divers were in reasonable agreement, the results still lack the rigor required. Also we could not obtain measures from schools of intermediate sizes (i.e., from 100–1,500 individuals) because we did not encounter them, except as they migrated from and back to the shallows. This likely would require data during periods of the month(s) when currents tend to be sustained around 5 to 10 cm-sec⁻¹. What we can conclude, however, is that blacksmith densities (ca. 10–15 fish/m³) do not achieve the densities observed in migrating striped mullet of similar individual size (ca. 100 fish/m³) where the individuals of each species are similar in size as compared, for example, with anchovies. This makes sense for planktivorous fish that ingest significant numbers of macrozooplankton (for blacksmiths as much as 70–80 % of their primary food, Table 3).

We conclude that the social structure and behaviors of blacksmith schools when foraging represent a complex blend of responses to several variables, the most important of which include current velocity, macrozooplankton concentrations, and the metabolic impact of the school on itself.

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Biogeographic and Ecological Implications of Kelp Rafting as a Dispersal Vector for Marine Invertebrates

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Abstract. Islands represent discontinuous habitat for terrestrial taxa, yet it is less obvious that they are also “biological islands” for certain marine species as well. Intertidal and subtidal marine invertebrates, especially those that lack a meroplanktonic larval stage, may face significant difficulty in crossing biogeographic barriers such as the San Pedro Channel. Taxa that are asexual, brood their young, or have “crawl away” juveniles may have significantly lower inherent dispersal ability, yet are often well-represented and exhibit relatively low rates of endemism on islands. Kelp such as *Macrocystis* and *Pelagophycus* provide habitat for numerous marine species. Upon detachment from the substrate, kelp plants drift with the wind and currents, dispersing large numbers of individuals from many taxa over relatively long distances. This mechanism may assist in maintaining these species’ geographic ranges as well as increasing genetic exchange between isolated populations. Marine species so dispersed have a high potential for reproductive establishment upon arrival due to the numbers transported, age structure, reproductive status and genetic diversity of the propagules. Of ecological interest is the potential simultaneous introduction of commensals, symbionts, parasites, and predators. Colder ocean temperatures following the last glacial period in addition to historic reductions of kelp due to sea otter hunting, kelp harvesting and other anthropogenic activity suggest kelp may have had an even more significant role in the past.

Keywords: *Macrocystis*; *Pelagophycus*; *Nereocystis*; Phaeophyta; Channel Islands; Santa Catalina Island; brooding.

Introduction

The Channel Islands off southern California offer an excellent opportunity for the investigation of dispersal phenomena in benthic marine invertebrates. The intertidal and subtidal habitats of these islands offer examples of “biological islands.” Although the substrate and medium are continuous with those of similar mainland habitats, the depth of the intervening channels creates significant biogeographic barriers.

Three mechanisms are often posited to account for the present-day distributions of benthic marine taxa: vicariance events linked to continental drift, pelagic larval dispersal, and rafting or “epiplanktonic dispersal” (Edgar 1987). The Channel Islands formed in regional tectonic events initiating in the Miocene when local folding and faulting began. The islands represent exposed portions of topographic highs along submarine ridges and most likely had no mainland connections. Therefore, vicariance events are unlikely mechanisms for explaining the distributions observed. It is assumed the current biota colonized island intertidal and subtidal habitats through cross-channel pelagic dispersal, either by a dispersal stage or rafting.

Dispersal in marine invertebrates is often linked to reproductive mode and life histories (Grant 1990). Most sexually reproducing taxa offer a wide range of dispersal options. Some produce free-swimming meroplanktonic larvae, either planktotrophic or lecithotrophic, that may disperse with ocean currents. Other species brood, either ovoviviparously to a larval stage or viviparously to a benthic subadult. Non-swimming, “crawl away” juveniles are not likely to disperse readily (Highsmith 1985). Taxa that reproduce strictly asexually or through autotomy may possess no free-swimming dispersal stage.

Several authors (Fell 1962; Dell 1972; Highsmith 1985) have suggested the often regionally cosmopolitan distributions of species with limited inherent dispersal capabilities may be explained by rafting on drift material including wood and kelps such as *Macrocystis*. The scarcity of macroalgae in the tropics makes rafting a less likely dispersal mode there than in the temperate zone (Highsmith 1985).

The Southern California Bight, with its historically extensive kelp forests, offers an opportunity to test the hypothesis that “kelp rafting” may help explain the distribution of some marine invertebrates and the low rates of endemism in the region. Our research asked 2 fundamental questions: (1) given local oceanographic conditions, is drift kelp capable of transporting invertebrates over the distances and drift paths required for mainland-to-island or inter-island dispersal; and (2) are marine invertebrates without pelagic larval stages, such as brooders, actually found on drift kelp?