Chapter 9

Conclusion

In this thesis insight into the ecological significances of *Aipysurus laevis* venom in predator-prey interactions was provided by the following contributions:

1. demonstration of the presence of myotoxic venom components in addition to the previously known neurotoxins.
2. different levels of resistance to the venom exhibited by the various prey species.
3. presentation of an evolutionary model of predator-prey interaction.

9.1 Myotoxic components

Ventilation, behavioural and ultrastructural studies treated in this thesis suggest that there are minor venom components affecting prey as well as the previously known major ones. The major toxic components act quickly and are neurotoxic; they are known to be responsible for ventilatory cessation (Section 1.1.3). The minor toxic components appear to be myotoxic. Evidence supporting this hypothesis is discussed in the following subsections.

9.1.1 Open and extended mouths

Fish in advanced stages of envenomation had open and extended mouths, resulting from sustained contraction of the sternohyoideus muscle. This response is not likely to be a reaction to repetitive neural stimulation of the muscle, as in a tetnus-like effect, because neurotoxins would block neuromuscular transmission (Spence and Mason, 1987). Rather, it is hypercontraction associated with muscle damage, and breakdown of calcium regulation by the sarcoplasmic reticulum (Harris *et al.*, 1980).

Venom fraction 6, which is said to be neurotoxic, did not elicit the open and extended mouth response during envenomation. Venom fraction 4, however, did cause this response to a high degree, suggesting it is a strong myotoxin.

9.1.2 Incomplete mouth closure

During the later stages of envenomation those fish surviving the neurotoxic effect maintained significantly higher ventilation rates than those of the controls. This was thought to be caused by the inability of the envenomated fish to close their mouth during ventilation, because of hypercontraction (Section 9.1.1). Water reflux back out of the mouth reduces the positive differential pressure gradient across the gills, thereby induces hypoxia (Section 1.8). Compensation for hypoxia is responsible for the elevated ventilation rates (Moyle and Cech, 1982), and because this occurred during later stages of envenomation, myotoxic rather than neurotoxic components were probably responsible. Those fish that survived envenomation with venom fraction 6, a suspected neurotoxin, never exhibited this condition. Fraction 4, which was thought to be myotoxic, did cause incomplete mouth closure.

9.1.3 Bottom rubbing

Rubbing the chin (sternohyoideus muscle) on the bottom of the aquarium, as if to eliminate some irritant (Appendix F), was observed periodically during later stages of envenomation. This was possibly a response to sensation emanating from muscle damaged by envenomation.

9.1.4 Ultrastructural change

The strongest evidence supporting the hypothesis of myotoxic components affecting the prey species came from ultrastructural examinations. Evidence of muscle necrosis was observed in muscle of fish envenomated with *A. laevis* whole venom, and venom fractions. Neurotoxins were not thought to be responsible, since muscle necrosis is not known to be related to neural activity of the muscle (Harris *et al.*, 1980), and neurotoxins have not been shown to produce muscle lesions (Mebs, 1978).

The results presented in this thesis indicate the presence of myotoxic components in the venom of *A. laevis*, but they also show what fractions of *A. laevis* venom (fractions 2, 3 and 4) are responsible for those effects. Venom fraction 4 was shown to contain the major myotoxic factor.

9.2 Fish resistance to venom

The manner in which different species of fish responded to *A. laevis* venom was shown by ventilation and behavioural studies to be similar, with the only major differences being resistance to the venom.

Venom resistance is defined as the ability of the fish to withstand the venom's effects. This was determined by comparisons of the speed with which fish responded to the different doses, and by the doses required to kill them.

Inter- and intraspecific differences in resistance to venom were observed.

Intraspecific variability (Appendix B) indicated the presence of resistance among individuals, which could allow for possible resistance in the future for that species if those traits were selected for.

Interspecific comparisons from LD50 studies for the marine prey species showed *Dascyllus aruanus* as having the highest overall resistance to *A. laevis* venom, with *Chromis atripectoralis* having the least. Comparisons of mean times to death revealed the *Istiblennius* species as having the greatest resistance at the higher doses, but with the pomacentrids being most resistant at the lower ones.

Morphological and/or physiological adaptations differed among the species of fish in this study. The presence of cutaneous respiration in the *Istiblennius* species

(Graham, 1976), and low oxygen requirements due to their secretive manners (Fry, 1957; Moyle and Cech, 1982), allowed for high resistance of these fish to high venom doses; they possessed the ability to sustain metabolism long after the shutdown of the ventilatory mechanism. The pomacentrids, which did not possess these attributes, succumbed to the high dose of venom much quicker. The opposite effect occurred at low venom doses, to which the pomacentrids demonstrated more resistance. This was possibly due to differences of the groups' metabolisms.

More information regarding the different levels of response of marine fish to envenomation by *A. laevis* venom is found in Berman (1981).

9.3 Evolutionary model of predator-prey interaction

When examining the ecological significance of snake venom, both components of the predator-prey relationship should be considered.

Prey restrainment, through envenomation, has allowed venomous snakes to become highly evolved (Russell, 1980; Savitzky, 1980), with prey immoblization decreasing snake injury and chances of prey escaping (Gans, 1978; Sutherland, 1983; Heatwole, 1987). This permits a larger variety of prey and larger prey size to be incorporated into the snake's diet.

Being mostly fish eaters (piscivorus) hydrophiids would especially benefit from efficient restraintment since their prey have many avenues of escape in an aquatic environment. Personal observations have revealed *A. laevis* as having extreme difficulties rediscovering lost prey items even when they are in close proximinity (unpublished observations). An increase in effectiveness of the venom would therefore increase efficency through lowering the chances of prey escaping and requiring less handling time.

With marine fish possessing different resistances to venom (Section 9.2), hydrophiid species could either selectively prey on those species that are less resistant or

make adjustments in venom chemistry that overcome resistances. Generalized feeders, i.e. *A. laevis*, could possess an array of toxic components to cover a wide range of resistance types. Heavy predation on one species may select for greater resistance in the prey. Once this develops the predator may shift to a less resistant group. The resistant fish would then be freed from predation and in time, because of reduced predation, selection for resistance would be relaxed and the cycle could start again. Thus, there may, over a long period of time, be an evolutionary scanning of potential prey species with concentration on the least resistant one at the moment.

More specialized feeders, i.e. *Laticauda* and *Hydrophis* species that feed primarily on eels (Heatwole, 1987), occur among the hydrophiids. Morphological adaptations, such as a small head and long thin neck in some of the *Hydrophis* species, would allow for the specialists to successfully pursue and capture their prey. Likewise, the venom may be specifically adapted for those prey.

Unlike generalized feeders, the specialized feeders probably lack the ability to change prey type once resistance to their venom increased. They are limited by their morphological specialization and/or prey avaliability to what they can eat. Any resistance demonstrated by the prey must be counteracted by a change in chemistry of the venom that would increase its potency. With time these venoms would become more and more potent.

9.4 Final remarks

Through more work on the effects of snake venom on prey species, a better understanding of evolutionary and functional significance of the venom would be obtained.

Today's increase in human activities in the natural habitat for sea snakes, requires a better understanding of the behaviours and venom potentials of the hydrophiids in order to decrease the risk and dangers of envenomations. By examining individual species separately over-generalization, which has occurred in the past regarding aggressiveness (Zimmerman, 1988) and venom potency, can be replaced by more accurate and specific information.

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Appendix A

LD values for marine fish species

LD values at different doses of *Aipysurus laevis* venom for five marine fish species.

LD values using probit analysis for five marine prey species envenomated with *Aipysurus laevis* venom. Doses and fiducial limits (FD) are shown for each LD level. (ALL DOSES IN mg / Kg)

LD's	*Chromis nitida*		*Chromis atripectoralis*		*Dascyllus aruanus*	
(% survival)	Dose	F.D. Limits	Dose	F.D. Limits	Dose	F.D. Limits
10	0.3597	0.7546 – 0.2690	0.1004	0.1245 – 0.0929	0.4700	0.9035 – 0.3559
15	0.3175	0.5991 – 0.2454	0.0972	0.1167 – 0.0907	0.4214	0.7473 – 0.3279
20	0.2875	0.4997 – 0.2277	0.0946	0.1109 – 0.0890	0.3863	0.6435 – 0.3068
25	0.2641	0.4286 – 0.2130	0.0925	0.1063 – 0.0875	0.3586	0.5668 – 0.2894
30	0.2446	0.3742 – 0.2003	0.0907	0.1023 – 0.0861	0.3354	0.5064 – 0.2742
35	0.2280	0.3310 – 0.1886	0.0890	0.0988 – 0.0848	0.3153	0.4570 – 0.2605
40	0.2132	0.2955 – 0.1775	0.0875	0.0957 – 0.0835	0.2973	0.4153 – 0.2477
45	0.1998	0.2660 – 0.1668	0.0860	0.0930 – 0.0821	0.2808	0.3795 – 0.2353
50	0.1875	0.2441 – 0.1560	0.0846	0.0904 – 0.0800	0.2656	0.3842 – 0.2232
55	0.1759	0.2199 – 0.1451	0.0831	0.0881 – 0.0792	0.2512	0.3205 – 0.2111
60	0.1648	0.2017 – 0.1337	0.0817	0.0861 – 0.0774	0.2373	0.2957 – 0.1986
65	0.1542	0.1860 – 0.1219	0.0803	0.0842 – 0.0755	0.2238	0.2735 – 0.1855
70	0.1436	0.1722 – 0.1097	0.0788	0.0825 – 0.0733	0.2103	0.2533 – 0.1717
75	0.1331	0.1596 – 0.0971	0.0772	0.0809 – 0.0708	0.1967	0.2347 – 0.1569
80	0.1222	0.1478 – 0.0842	0.0755	0.0793 – 0.0681	0.1826	0.2171 – 0.1409
85	0.1107	0.1359 – 0.0708	0.0736	0.0776 – 0.0648	0.1674	0.1999 – 0.1233
90	0.0977	0.1232 – 0.0566	0.0712	0.0757 – 0.0609	0.1501	0.1816 – 0.1034
95	0.0812	0.1072 – 0.0403	0.0678	0.0730 – 0.0554	0.1276	0.1593 – 0.0788
99	0.5740	0.0836 – 0.0211	0.0619	0.0685 – 0.0462	0.0942	0.1266 – 0.0466

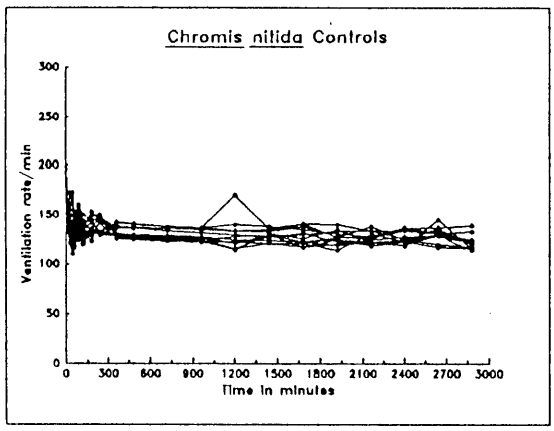
LD's	*Istiblennius meleagris*		*Istiblennius edentulus*	
(% survival)	Dose	F.D. Limits	Dose	F.D. Limits
10	0.1202	0.3497 – 0.0960	0.3302	0.4525 – 0.2930
15	0.1128	0.2890 – 0.0921	0.3124	0.4064 – 0.2810
20	0.1072	0.2485 – 0.0892	0.2989	0.3737 – 0.2714
25	0.1027	0.2184 – 0.0866	0.2877	0.3484 – 0.2630
30	0.0987	0.1946 – 0.0844	0.2781	0.3277 – 0.2551
35	0.0952	0.1750 – 0.0823	0.2695	0.3104 – 0.2455
40	0.0920	0.1584 – 0.0803	0.2615	0.2957 – 0.2398
45	0.0890	0.1439 – 0.0784	0.2541	0.2830 – 0.2319
50	0.0862	0.1312 – 0.0764	0.2469	0.2721 – 0.2235
55	0.0834	0.1198 – 0.0744	0.2400	0.2625 – 0.2146
60	0.0807	0.1095 – 0.0721	0.2332	0.2540 – 0.2052
65	0.0779	0.1002 – 0.0696	0.2263	0.2464 – 0.1953
70	0.0752	0.0919 – 0.0666	0.2193	0.2392 – 0.1848
75	0.0723	0.0847 – 0.0627	0.2119	0.2322 – 0.1738
80	0.0692	0.0787 – 0.0576	0.2040	0.2250 – 0.1619
85	0.0658	0.0737 – 0.0512	0.1952	0.2174 – 0.1488
90	0.0617	0.0692 – 0.0433	0.1847	0.2086 – 0.1337
95	0.0562	0.0692 – 0.0331	0.1700	0.1965 – 0.1137
99	0.0470	0.0569 – 0.0197	0.1457	0.1764 – 0.0837

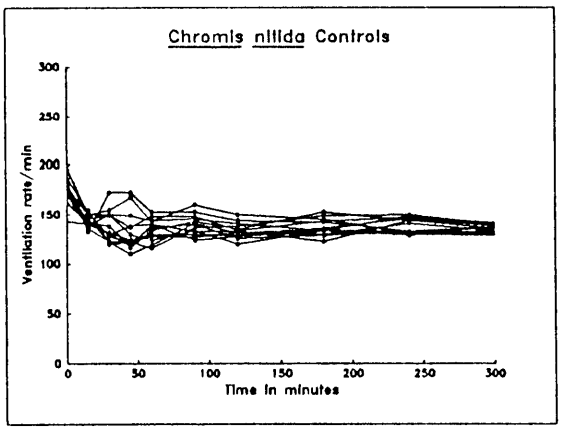
Appendix B

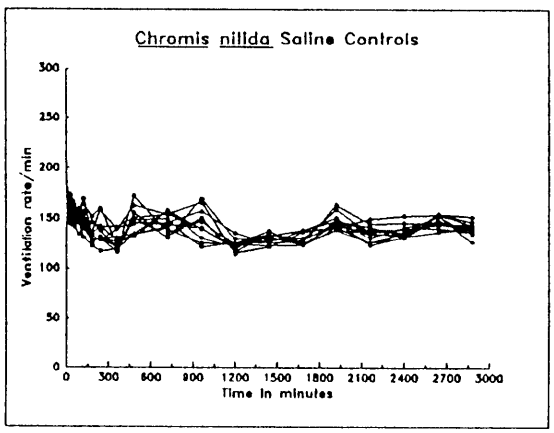
Profiles of variability (whole venom)

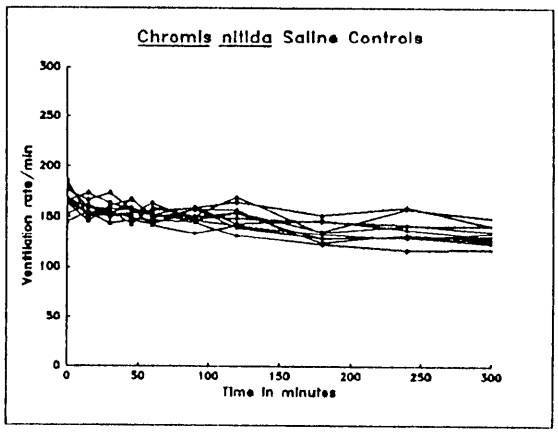
Profiles of variability in ventilation rates for *Chromis nitida*, *Dascyllus aruanus* and *Istiblennius meleagris* for control and envenomated groups.

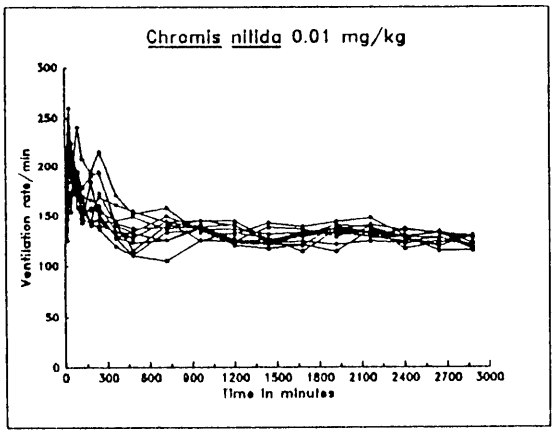
Profiles of *Chromis nitida* ventilation rates / min., illustrating variability between fish for the different experimental sets. The left column represents the entire experiment (2880 minutes), with the right showing the first 300 to 400 minutes at an enlarged scale.

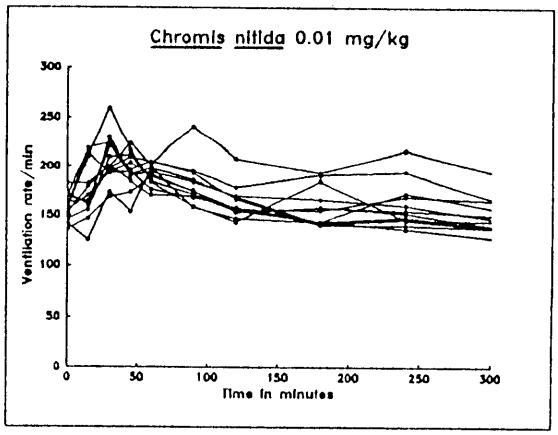




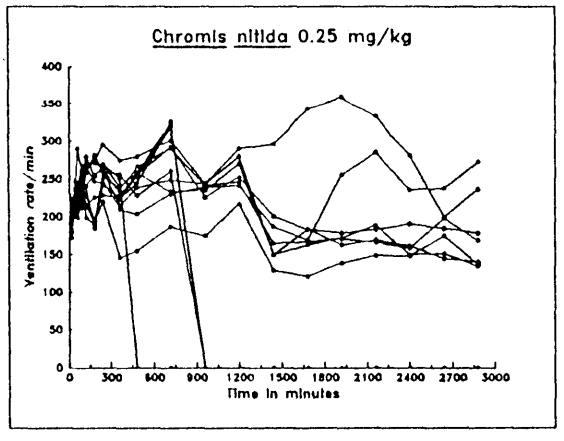


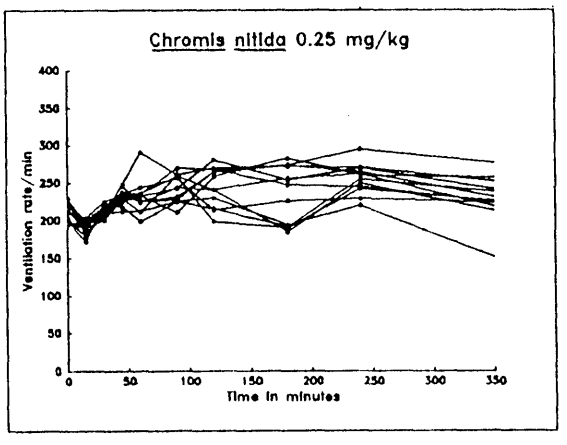


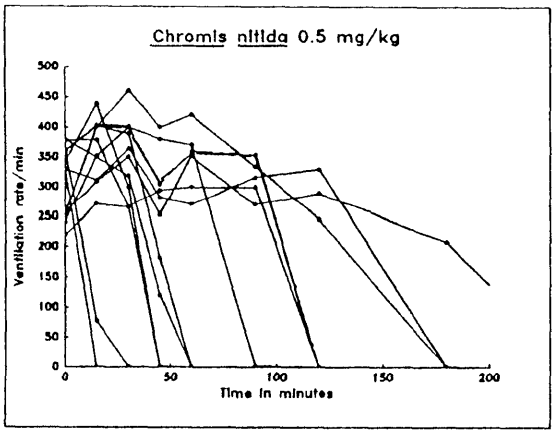




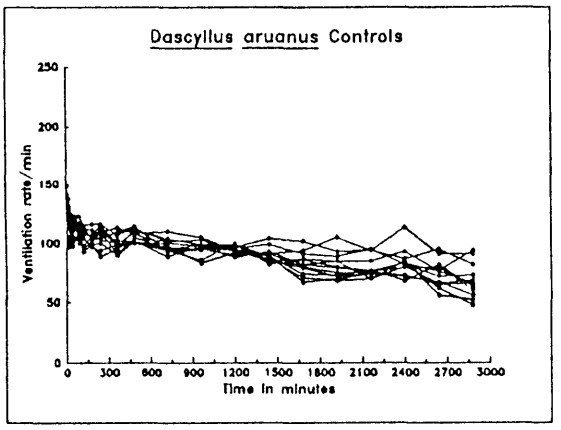
Profiles of *Chromis nitida* ventilation rates continued.

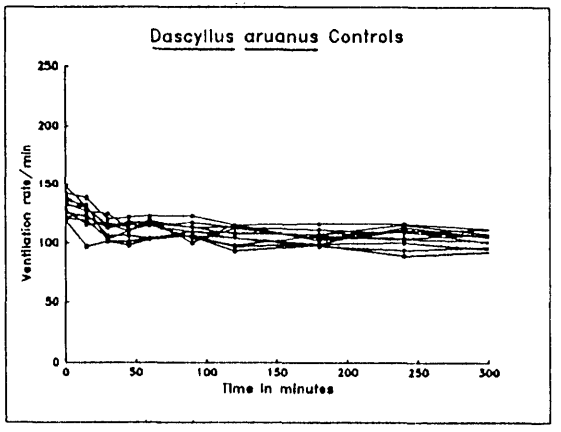


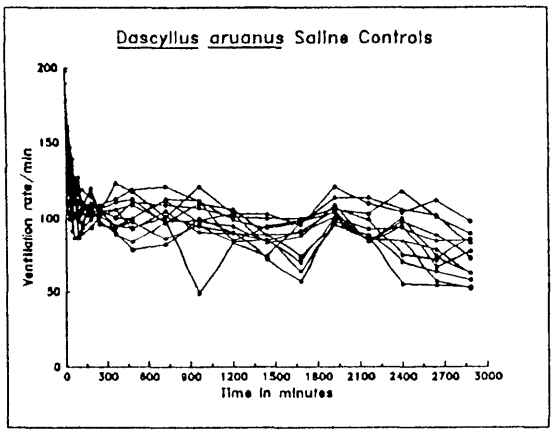


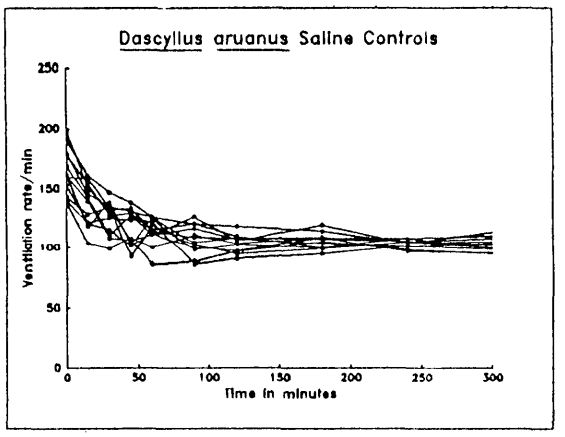


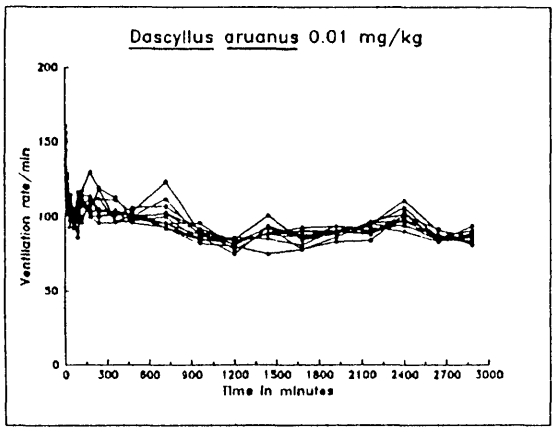
Profiles of *Dascyllus aruanus* ventilation rates / min., illustrating variability between fish for the different experimental sets. The left column represents the entire experiment (2880 minutes), with the right showing the first 300 to 400 minutes at an enlarged scale.

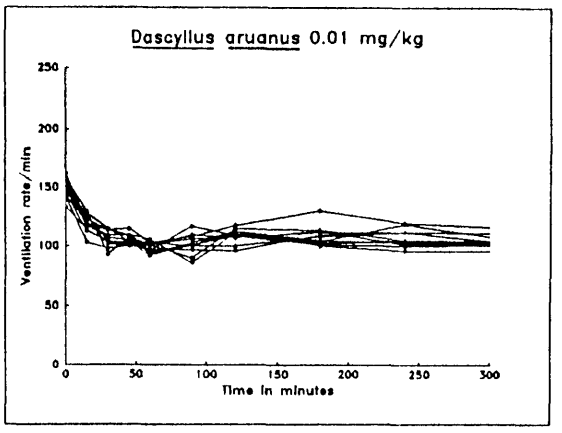




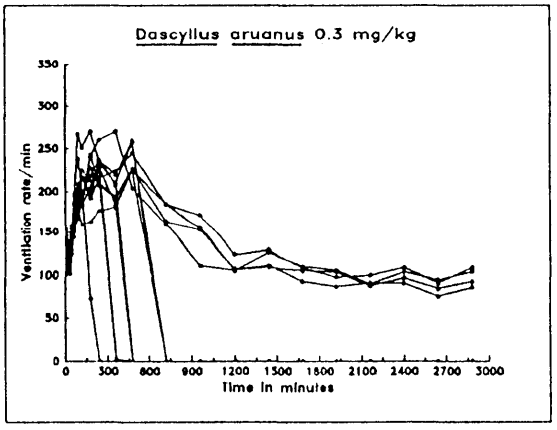


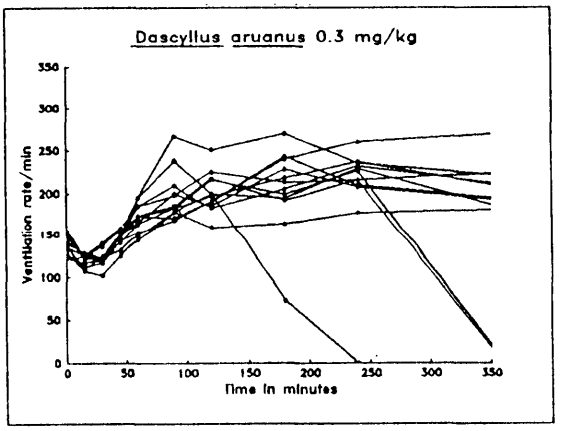


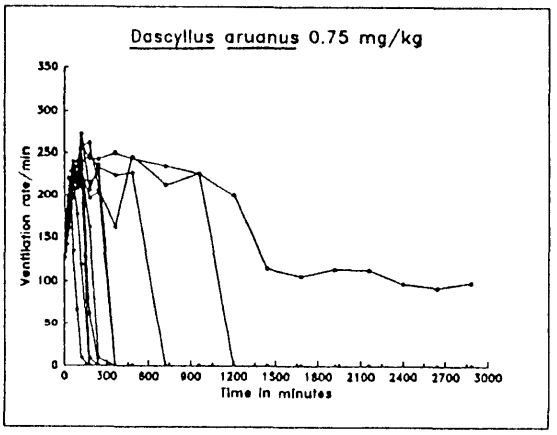


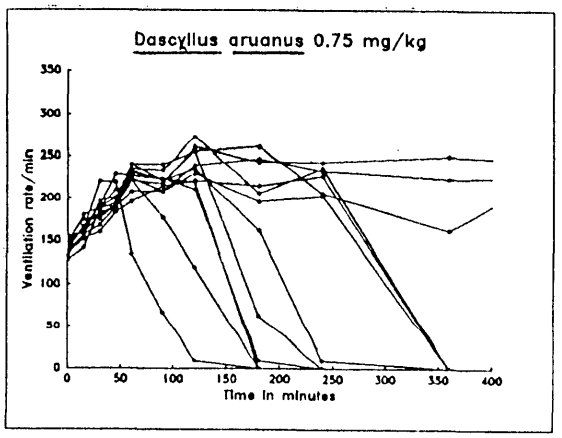


Profiles of *Dascyllus aruanus* ventilation rates continued.

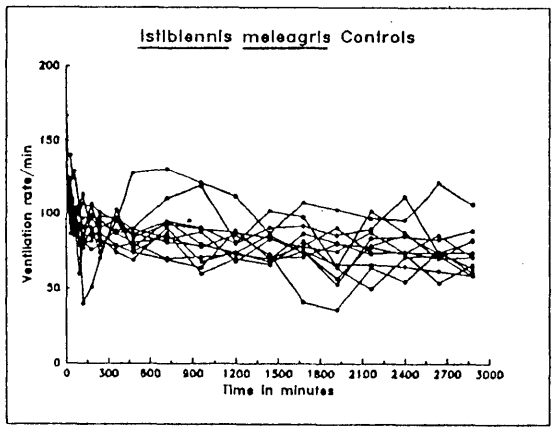


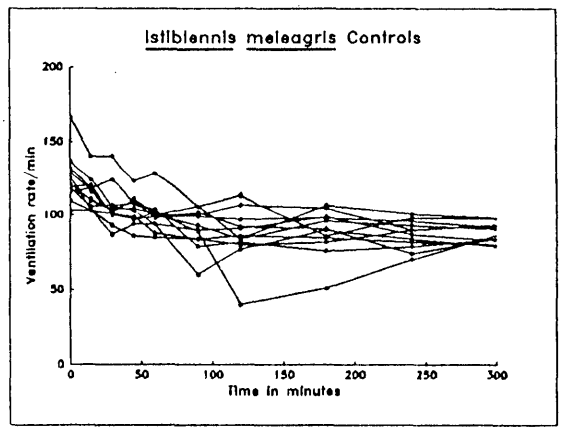


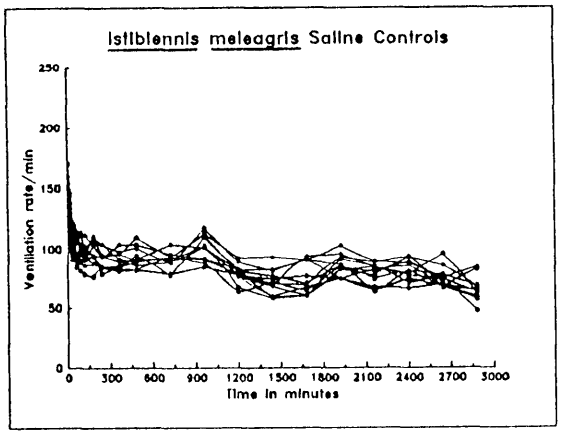


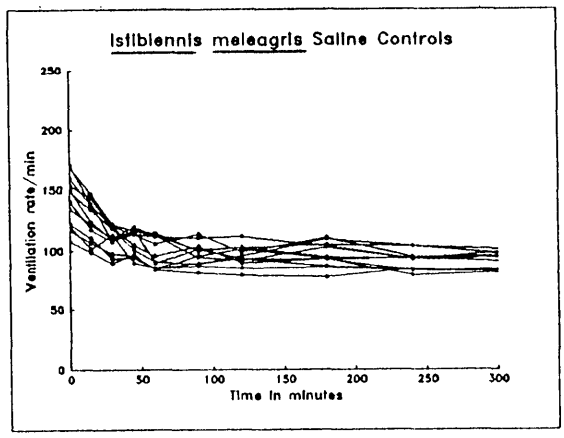


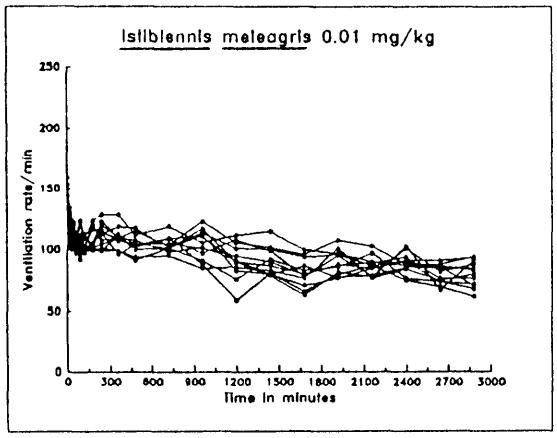
Profiles of *Istiblennius meleagris* ventilation rates / min., illustating variability between fish of the different experimental sets. The left column represents the entire experiment (2880 minutes), with the right showing the first 300 to 400 minutes at an enlarged scale.

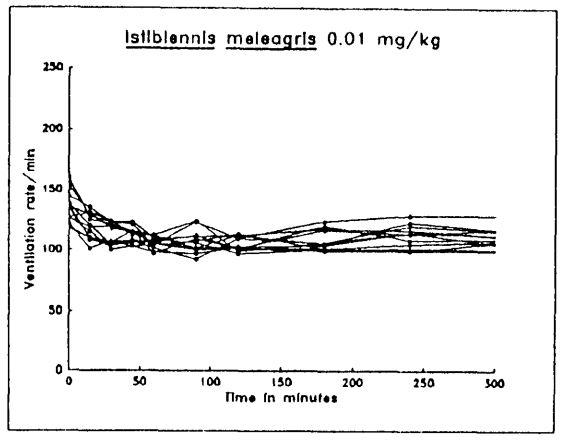




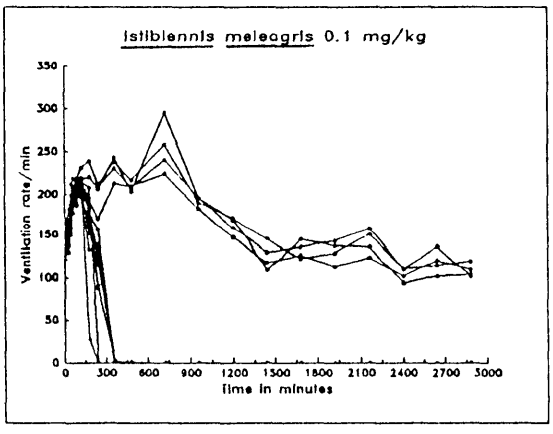


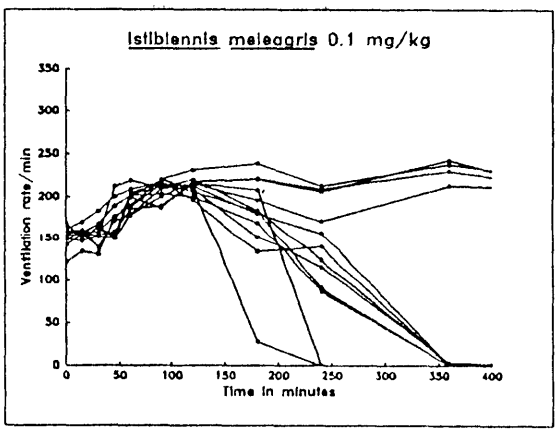


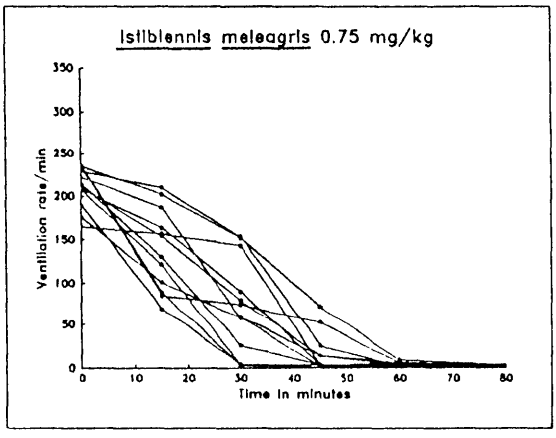




Profiles of *Istiblennius meleagris* ventilation rates continued.







Appendix C

Probability values (whole venom)

Probability values from ventilation studies for *Chromis nitida*, *Dascyllus aruanus* and *Istiblennius meleagris*.

Probability values obtained with one-way analysis of variance from ventilation rate studies of *Chromis nitida*, comparing different experimental groups, C1 to C21 are experimental times (Table 5.2), 1 – control group, 2 – saline-injected control group, 3 – low venom dose group, 4 – medium venom dose group, 5 – high venom dose group and dashes indicating all fish dead.

	1–2	1–3	1–4	1–5	2–3	2–4	2–5	3–4	3–5	4–5
C1	0.299	0.011	0.000	0.000	0.128	0.000	0.000	0.000	0.000	0.000
C2	0.279	0.058	0.003	0.000	0.412	0.058	0.000	0.272	0.001	0.011
C3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.368	0.000	0.000
C4	0.946	0.887	0.848	0.079	0.942	0.904	0.074	0.962	0.064	0.058
C5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
C6	0.976	0.926	0.860	0.019	0.951	0.887	0.019	0.935	0.017	0.014
C7	0.001	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.067
C8	0.364	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.022	0.460
C9	0.379	0.000	0.000	—	0.000	0.000	—	0.000	—	—
C10	0.103	0.267	0.000	—	0.009	0.000	—	0.000	—	—
C11	0.006	0.640	0.000	—	0.002	0.000	—	0.000	—	—
C12	0.002	0.206	0.000	—	0.059	0.000	—	0.000	—	—
C13	0.001	0.066	0.000	—	0.107	0.000	—	0.000	—	—
C14	0.129	0.440	0.000	—	0.028	0.000	—	0.000	—	—
C15	0.953	0.469	0.000	—	0.513	0.000	—	0.000	—	—
C16	0.965	0.963	0.000	—	0.998	0.000	—	0.000	—	—
C17	0.000	0.207	0.000	—	0.012	0.000	—	0.000	—	—
C18	0.083	0.156	0.000	—	0.746	0.000	—	0.000	—	—
C19	0.013	0.753	0.000	—	0.031	0.000	—	0.000	—	—
C20	0.000	0.415	0.000	—	0.000	0.000	—	0.000	—	—
C21	0.001	0.819	0.000	—	0.002	0.000	—	0.000	—	—

Probability values for *Dascyllus aruanus* as previously described.

	1–2	1–3	1–4	1–5	2–3	2–4	2–5	3–4	3–5	4–5
C1	0.000	0.000	0.218	0.005	0.009	0.000	0.000	0.004	0.198	0.098
C2	0.013	0.331	0.463	0.000	0.001	0.002	0.000	0.810	0.000	0.000
C3	0.001	0.124	0.004	0.000	0.000	0.603	0.000	0.000	0.000	0.000
C4	0.261	0.067	0.000	0.000	0.004	0.000	0.000	0.000	0.000	0.000
C5	0.994	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
C6	0.725	0.279	0.000	0.000	0.462	0.000	0.000	0.000	0.000	0.617
C7	0.451	0.491	0.000	0.000	0.152	0.000	0.000	0.000	0.000	0.198
C8	0.833	0.658	0.000	0.000	0.816	0.000	0.001	0.000	0.001	0.507
C9	0.559	0.533	0.000	0.000	0.230	0.000	0.000	0.000	0.000	0.849
C10	0.655	0.481	0.000	0.000	0.796	0.000	0.000	0.000	0.000	0.944
C11	0.104	0.180	0.000	0.000	0.767	0.000	0.000	0.000	0.000	0.880
C12	0.453	0.488	0.000	0.000	0.954	0.000	0.000	0.000	0.000	0.089
C13	0.821	0.213	0.002	0.000	0.306	0.012	0.000	0.000	0.000	0.128
C14	0.509	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000
C15	0.320	0.889	0.000	0.020	0.391	0.000	0.008	0.000	0.017	0.813
C16	0.883	0.469	0.112	0.119	0.563	0.015	0.132	0.040	0.198	0.906
C17	0.000	0.002	0.000	0.001	0.001	0.293	0.446	0.108	0.029	0.212
C18	0.000	0.000	0.006	0.001	0.923	0.999	0.073	0.945	0.067	0.094
C19	0.362	0.004	0.037	0.277	0.042	0.138	0.463	0.981	0.931	0.926
C20	0.531	0.015	0.080	0.173	0.061	0.183	0.261	0.990	0.704	0.719
C21	0.339	0.001	0.001	0.054	0.012	0.009	0.115	0.372	0.568	0.945

Probability values for *Istiblennius meleagris* as previously described.

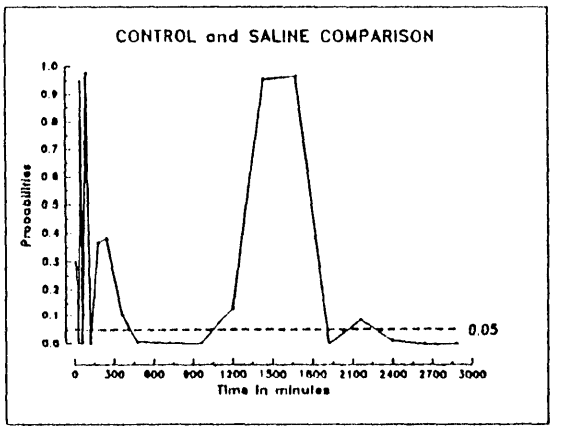
	1–2	1–3	1–4	1–5	2–3	2–4	2–5	3–4	3–5	4–5
C1	0.020	0.136	0.000	0.000	0.381	0.097	0.000	0.013	0.000	0.000
C2	0.315	0.590	0.000	0.012	0.638	0.003	0.118	0.001	0.044	0.122
C3	0.729	0.526	0.000	0.003	0.774	0.000	0.001	0.000	0.001	0.000
C4	0.578	0.183	0.000	0.000	0.435	0.000	0.000	0.000	0.000	0.000
C5	0.680	0.152	0.000	0.000	0.067	0.000	0.000	0.000	0.000	0.000
C6	0.147	0.001	0.000	0.000	0.028	0.000	0.000	0.000	0.000	0.000
C7	0.509	0.000	0.000	—	0.051	0.000	—	0.000	—	—
C8	0.317	0.013	0.000	—	0.121	0.000	—	0.000	—	—
C9	0.705	0.014	0.000	—	0.034	0.000	—	0.000	—	—
C10	0.985	0.285	0.005	—	0.277	0.005	—	0.043	—	—
C11	0.592	0.143	0.000	—	0.345	0.000	—	0.001	—	—
C12	0.930	0.020	0.000	—	0.016	0.000	—	0.000	—	—
C13	0.008	0.001	0.000	—	0.052	0.000	—	0.000	—	—
C14	0.620	0.032	0.000	—	0.010	0.000	—	0.000	—	—
C15	0.123	0.018	0.000	—	0.000	0.000	—	0.000	—	—
C16	0.349	0.811	0.000	—	0.242	0.000	—	0.000	—	—
C17	0.016	0.002	0.000	—	0.390	0.000	—	0.000	—	—
C18	0.844	0.109	0.000	—	0.073	0.000	—	0.000	—	—
C19	0.723	0.042	0.000	—	0.089	0.001	—	0.019	—	—
C20	0.742	0.468	0.000	—	0.294	0.000	—	0.000	—	—
C21	0.070	0.174	0.000	—	0.003	0.000	—	0.000	—	—

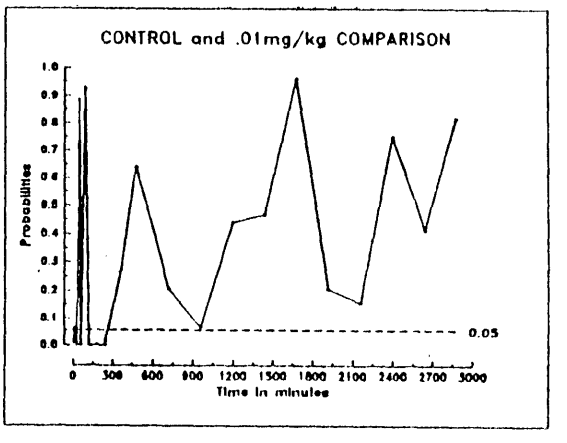
Appendix D

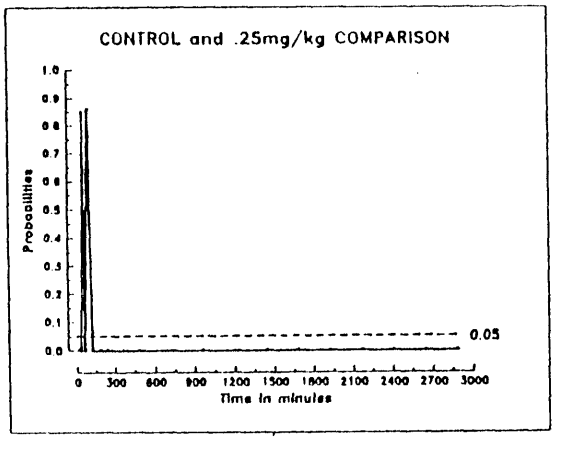
Profiles of probability (whole venom)

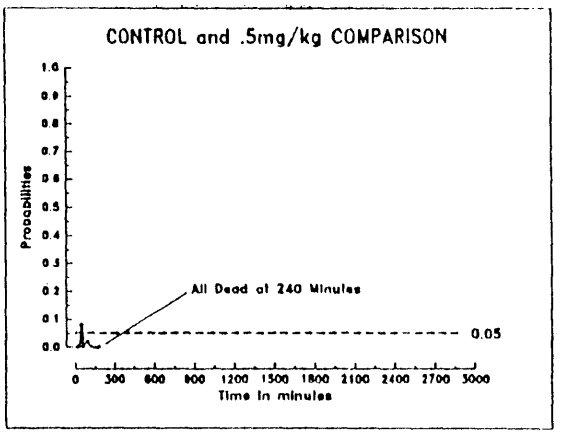
Profiles for comparisons of probabilities from ventilation studies of *Chromis nitida*, *Dascyllus aruanus* and *Istiblennius meleagris*.

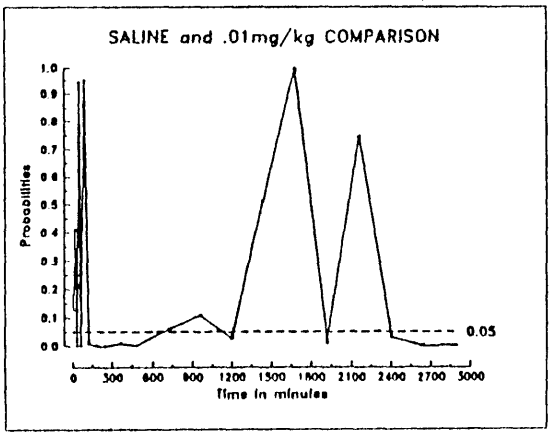
Profiles of the probability comparisons (Appendix C) from the ventilation rate studies of *Chromis nitida* for the different experimental groups, examining significance at the 0.05 level.

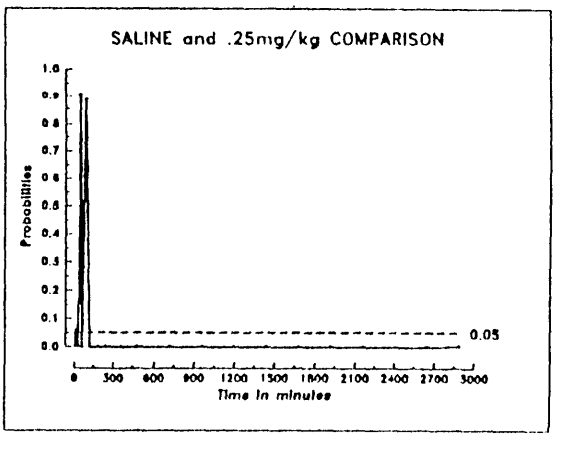




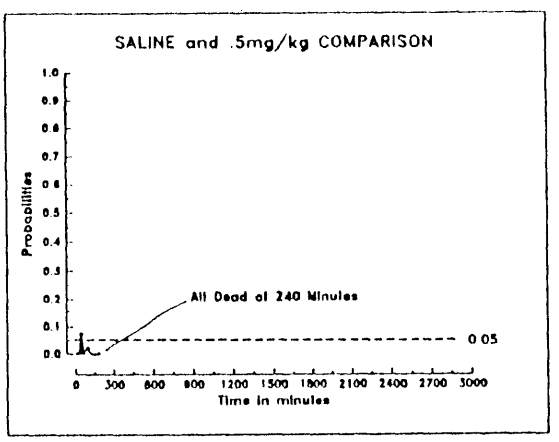


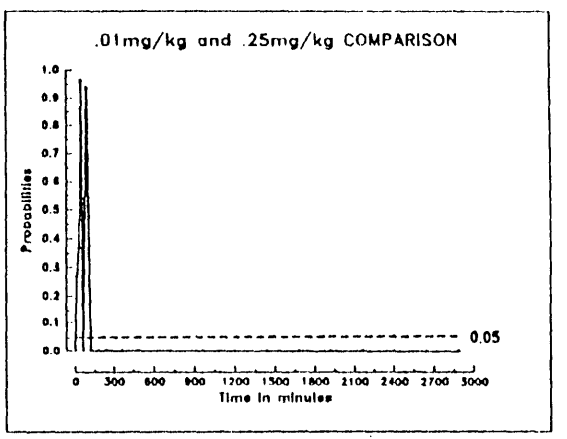


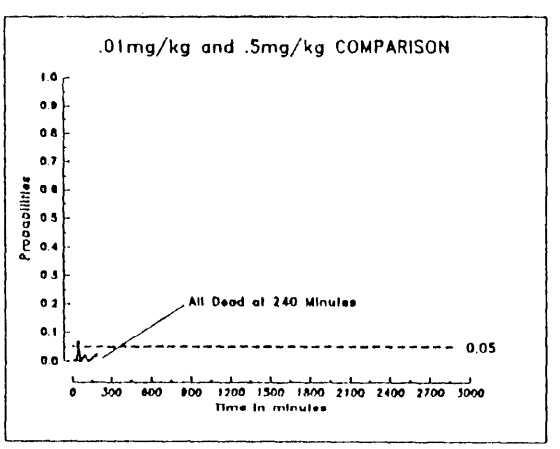


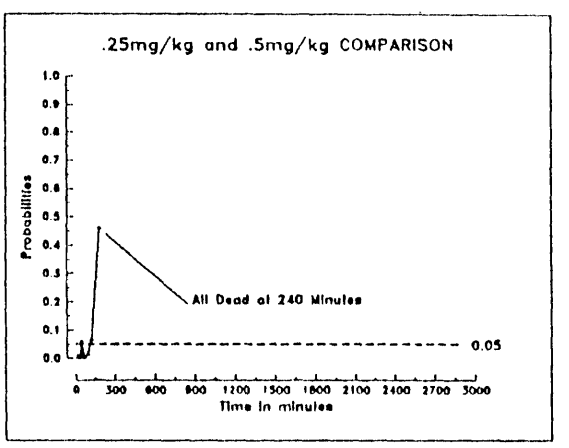


Profiles of probability comparisons for *Chromis nitida* continued.

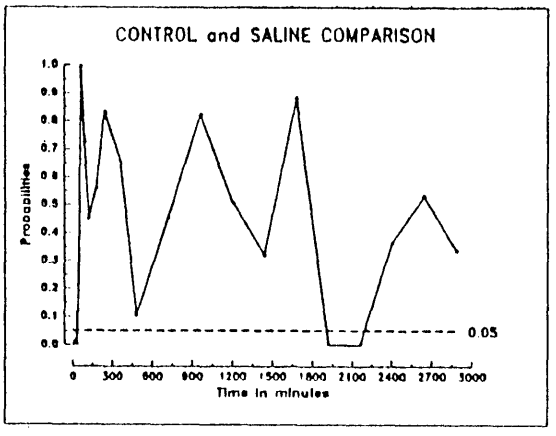


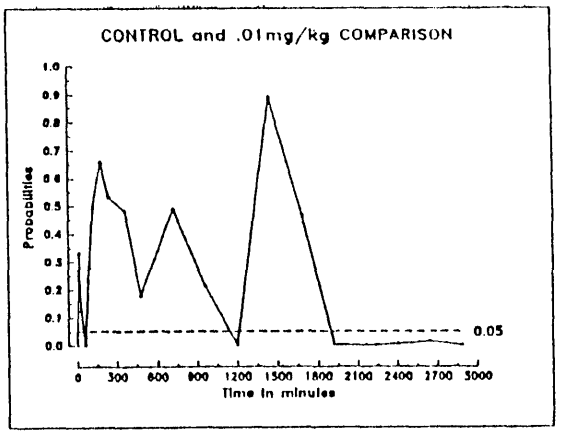


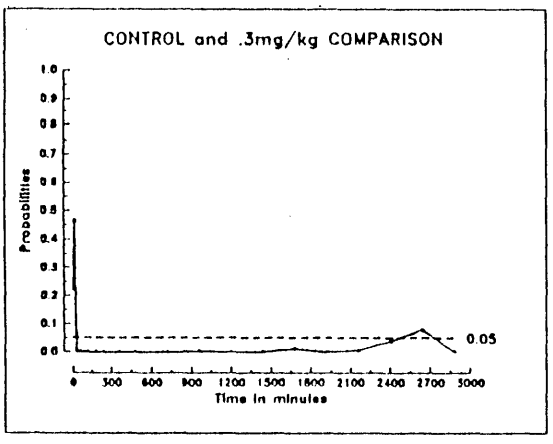


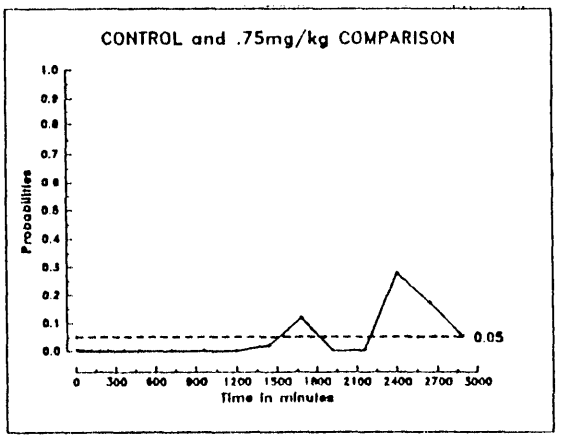


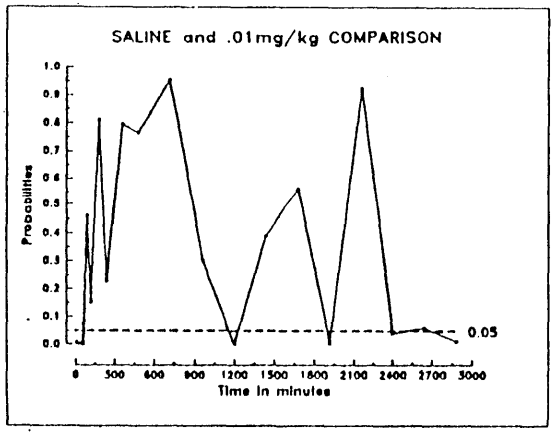
Profiles of the probability comparisons (Appendix C) from the ventilation rate studies of *Dascyllus aruanus* for the different experimental groups, examining significance at the 0.05 level.

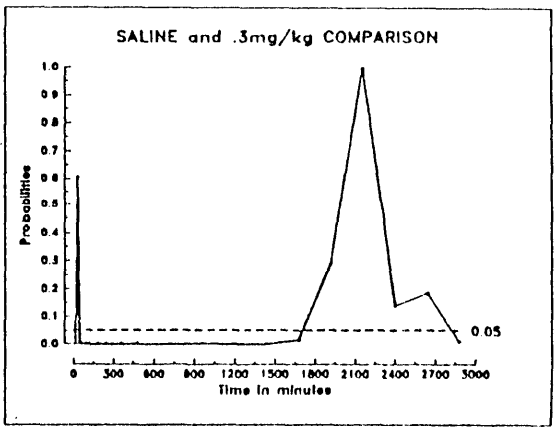




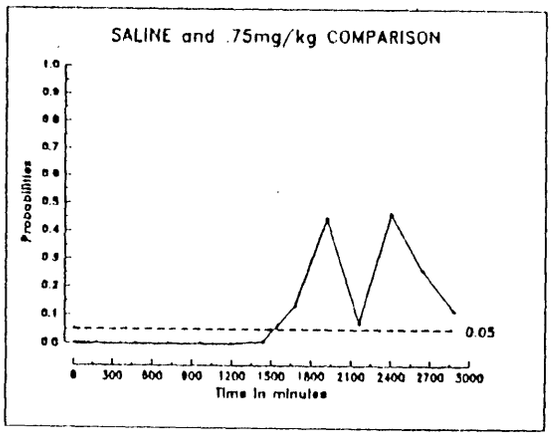


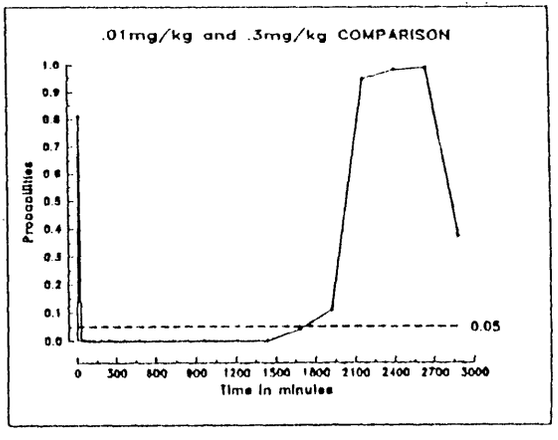


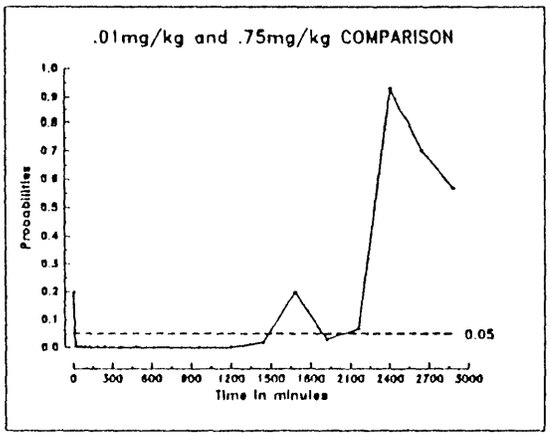


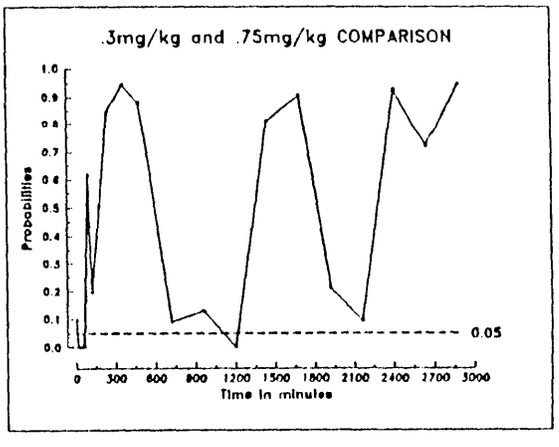


Profiles of probability comparisons for *Dascyllus aruanus* continued.

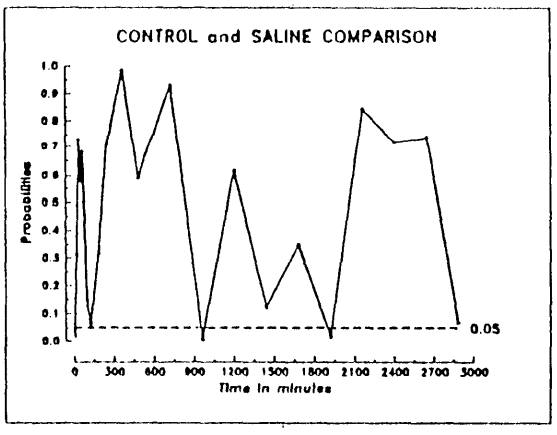


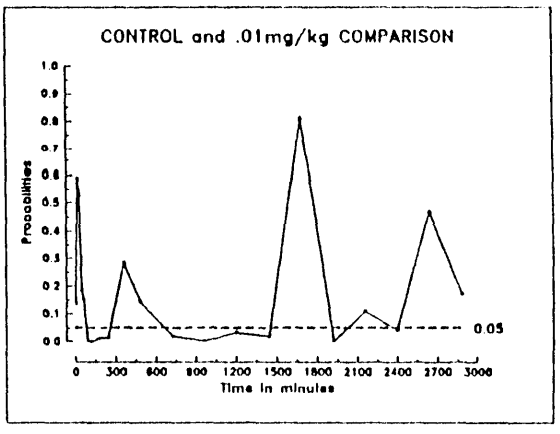


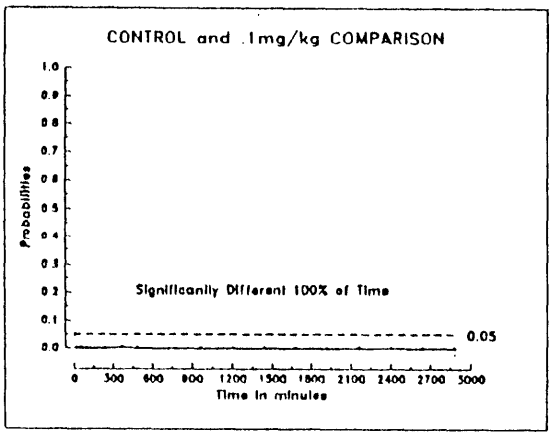


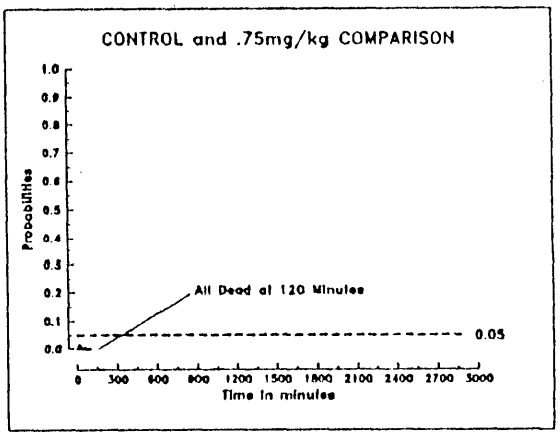


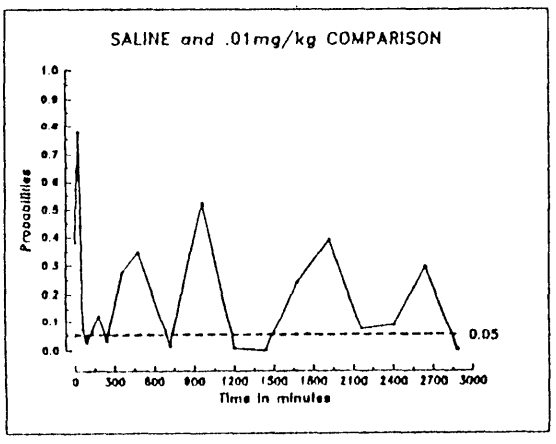
Profiles of the probability comparisons (Appendix C) from the ventilation rate studies of *Istiblennius meleagris* for the different experimental groups, examining significance at the 0.05 level.

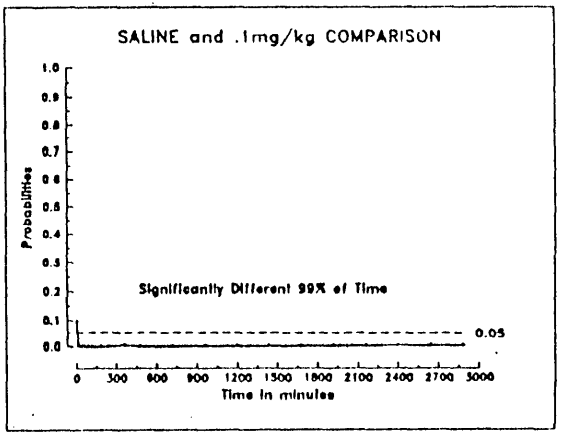




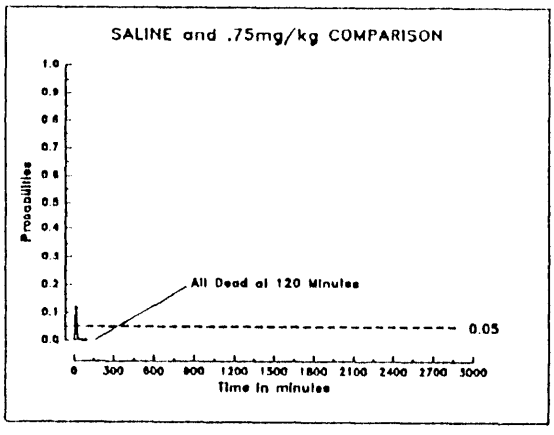


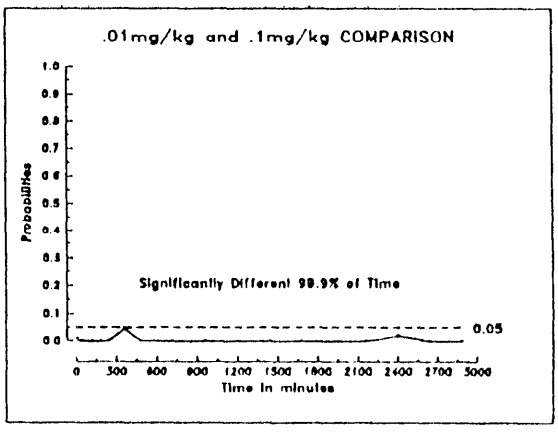


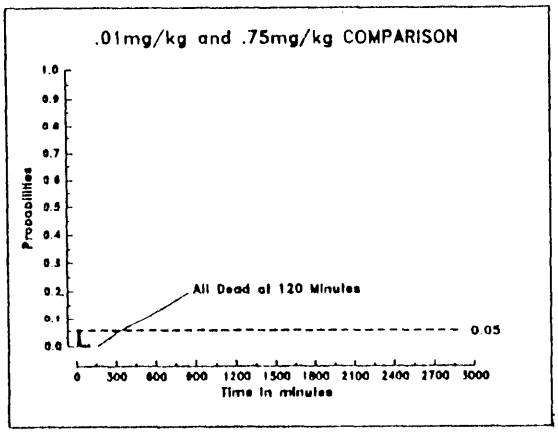


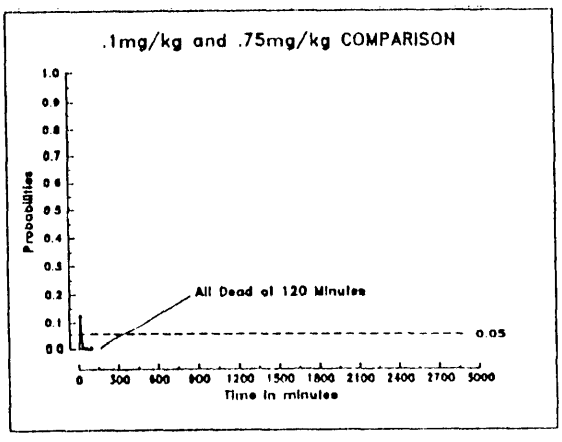


Profiles of probability comparisons for *Istiblennius meleagris* continued.









Appendix E

Standard error of the means (whole venom)

Standard error of the means for ventilation studies of *Chromis nitida*, *Dascyllus aruanus* and *Istiblennius meleagris*.

Standard error of the means obtained from the one-way analysis of variance for the ventilation studies of *Chromis nitida* for the experimental groups, C1 to C21 are experimental times (Table 5.2).

Columns	Control*	Saline	Low Dose	Medium Dose	High Dose
C1	24.8	26.9	26.9	26.9	26.9
C2	141.0	152.8	152.8	152.8	166.7
C3	25.5	27.6	27.6	27.6	33.1
C4	60.1	65.1	65.1	65.1	97.7
C5	15.0	16.3	16.3	16.3	32.6
C6	14.6	15.8	15.8	15.8	63.0
C7	15.3	16.5	16.5	16.5	39.7
C8	18.3	19.9	19.9	19.9	238.4
C9	17.7	19.2	19.2	19.2	-
C10	14.3	15.5	15.5	15.5	-
C11	17.6	19.0	19.0	20.7	-
C12	15.8	17.1	17.1	18.6	-
C13	9.4	10.2	10.2	17.4	-
C14	8.7	9.5	9.5	16.2	-
C15	10.3	11.2	11.2	19.2	-
C16	13.6	14.8	14.8	25.3	-
C17	15.0	16.3	16.3	27.9	-
C18	12.0	12.9	12.9	22.2	-
C19	9.3	10.1	10.1	17.4	-
C20	7.3	7.9	7.9	13.6	-
C21	11.4	12.4	12.4	21.2	-

\- All fish dead

* N = 13 all others N=12

Standard error of the means for *Dascyllus aruanus*, as previously described.

Columns	Control	Saline	Low Dose	Medium Dose	High Dose
C1	9.8	9.8	9.8	9.8	9.8
C2	11.6	11.6	11.6	11.6	11.6
C3	9.5	9.5	9.5	9.5	9.5
C4	10.0	10.0	10.0	10.0	10.0
C5	13.5	13.5	13.5	13.5	13.5
C6	51.9	51.9	519	51.9	51.9
C7	16.5	16.5	16.5	16.5	17.9
C8	76.7	76.7	76.7	76.7	115.0
C9	7.1	7.1	7.1	7.7	14.1
C10	8.0	8.0	8.0	10.7	32.1
C11	9.5	9.5	9.5	16.3	38.0
C12	7.8	7.8	7.8	23.4	46.9
C13	27.2	27.2	27.2	81.5	163.1
C14	2.8	2.8	2.8	8.4	33.8
C15	5.4	5.4	5.4	16.3	65.0
C16	12.4	12.4	12.4	37.0	148.2
C17	5.8	5.8	5.8	17.3	69.4
C18	5.0	5.0	5.0	15.1	60.4
C19	16.7	16.7	16.7	50.1	200.4
C20	14.2	14.2	14.2	42.6	170.4
C21	16.4	16.4	16.4	49.2	196.7

Standard error of the means for *Istiblennius meleagris*, as previously described.

Columns	Control	Saline	Low Dose	Medium Dose	High Dose
C1	26.4	26.4	26.4	26.4	26.4
C2	47.0	47.0	47.0	47.0	47.0
C3	63.1	63.1	63.1	63.1	63.1
C4	19.5	19.5	19.5	19.5	19.5
C5	8.1	8.1	8.1	8.1	9.7
C6	9.2	9.2	9.2	9.2	18.4
C7	11.0	11.0	11.0	11.0	–
C8	28.0	28.0	28.0	33.6	–
C9	46.2	46.2	46.2	55.4	–
C10	159.1	159.1	159.1	318.2	–
C11	87.7	87.7	87.7	210.6	–
C12	16.1	16.1	16.1	48.4	–
C13	16.7	16.7	16.7	50.0	–
C14	11.7	11.7	11.7	35.0	–
C15	10.8	10.8	10.8	32.4	–
C16	15.3	15.3	15.3	45.9	–
C17	14.4	14.4	14.4	43.1	–
C18	10.6	10.6	10.6	31.9	–
C19	9.8	9.8	9.8	29.4	–
C20	11.4	11.4	11.4	34.2	–
C21	11.0	11.0	11.0	32.9	–

– All fish dead

Appendix F

Behavioural descriptions

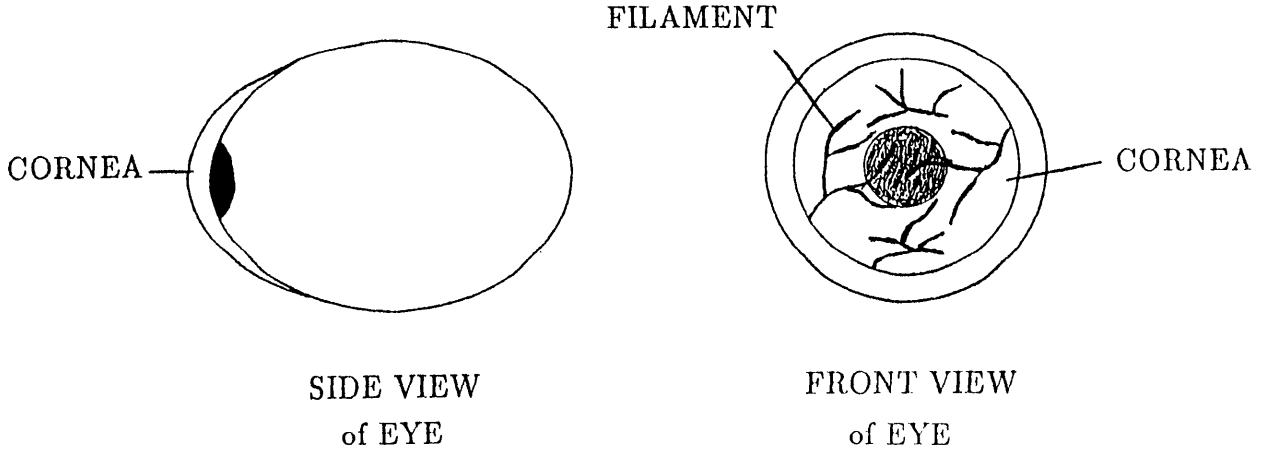
Behavioural descriptions for chapters 3, 6 and 8.

Behavioural descriptions for behaviours observed in chapters 3, 6 and section 8.3.3 of chapter 8. They represent the results of envenomation with both the whole and fractional components of *Aipysurus laevis* venom.

Bottom Rubbing: Fish rubbed their chin areas (sometimes sides) on the bottom of the aquarium, with quick and repeated movements, as if trying to remove something from that area. This was commonly observed in fish attempting to remove external parasites (Rohde, 1982), and may indicate an awareness of the envenomated fish to a change in that area; the area is in proximity of the sternohyoideus muscle, which is the major muscle in fish ventilation.

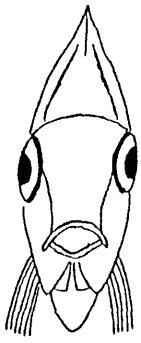
White Feces: This is the production of clear to white (mostly white) feces in envenomated fish, which was usually elongated and sticky in appearance. Normally the feces was red, short and dry in appearance. This condition was possibly due to the venom affecting the nerves servicing the digestive system, causing food to move more quickly through, thus not allowing for complete digestion to occur before fecal elimination.

White Eye: White filamentous-like structures found on the inner layer of the cornea of the eye. Its presence is possibly due to dilated blood vessels servicing the cornea, as the result of envenomation. The digrams below illustrate this condition.



Behavioural descriptions continued.

Eye Swelling: In some of the envenomated fish the eyes appeared to be protruding from their sockets, possibly due to an increase in internal eye pressure and / or the contraction of the ocular muscles forcing the eye outward. The digrams below illustrate both a normal and swollen condition.

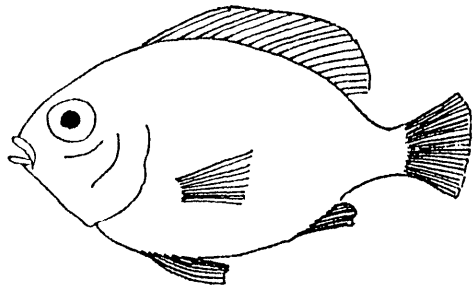


NORMAL EYE

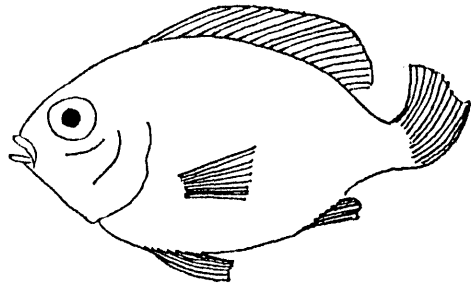
SWOLLEN EYE

Tail Position Change: The position of the tail is altered to either an upwards (top digrams) or sidewards (bottom digrams) position. This is a change from the normal tail positioning, with the tail not involved in swimming activities. The digrams below illustrate both the upwards and sidewards position changes.

SIDE VIEW

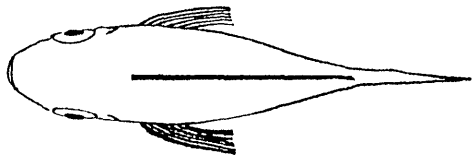


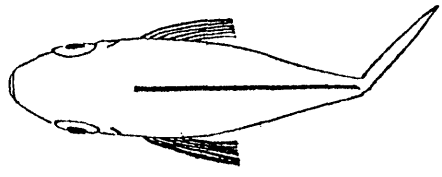
NORMAL



AFFECTED

TOP VIEW





Behavioural description continued.

Skip Breathing: A condition where there was a break in the regular rhythm of ventilatory movements, seen by a pause in part movements, followed by a rapid increase in rates and then a subsequent decrease. The length of the pauses varied according to severity of envenomation, but a pattern of movements was evident in all cases.

Stutter Breathing: A condition where there was a break in the regular rhythm of ventilatory movements, with irregular sporadic movements of the ventilatory parts, that appeared uncontrolable. No patterns were noticed in movements of the parts or frequency of occurrence of the response.

Appendix G

Behavioural stage times

Examinations of time to reach and duration of each behavioural stage.

Inter- and intraspecific comparisons between experimental groups, examining the time to reach each behavioural stage. Probability values were obtained from one-way analysis of variance, C – *Chromis nitida*, D – *Dascyllus aruanus*, I – *Istiblennius meleagris*, L – low venom dose, M – medium venom dose, H – high venom dose.

Low, medium and high venom dose examination for stage 1.

	CL	CM	CH	DL	DM	DH	IL	IM	IH
CL		–	√	√	√	–	√	–	√
CM			√	√	√	–	√	–	√
CH				√	√	√	√	√	–
DL					√	√	√	√	√
DM						–	√	√	√
DH							√	–	√
IL								√	√
IM									√
IH									

√ sig. at 0.01 × sig. at 0.05 – not sig.

Medium and high dose examinations for stages 1 to 6.

	CM Stages						CH Stages						DM Stages						DH Stages						IM Stages						IH Stages					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
CM							√	√	√	√	√	√	√	–	√	√	√	√	√	√	√	√	√	√	–	√	√	√	√	√	√	√	√	√	√	√
CH													√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	–	√	√	√	√	√
DM																			–	√	√	√	√	√	√	–	–	√	×	–	√	√	√	√	√	√
DH																									√	√	√	×	×	√	√	√	√	√	√	√
IM																															√	√	√	√	√	√
IH																																				

√ sig. at 0.01 × sig. at 0.05 – not sig.

Inter- and intraspecific comparisons for stage duration, as previously described.

Low, medium and high venom dose examination for stage 1.

	CL	CM	CH	DL	DM	DH	IL	IM	IH
CL		–	√	√	×	√	√	–	√
CM			√	–	–	√	√	–	√
CH				√	√	–	√	√	√
DL					–	√	×	√	√
DM						√	√	–	√
DH							√	√	√
IL								√	√
IM									√
IH									

√ sig. at 0.01 × sig. at 0.05 – not sig.

Medium and high venom dose examination for stages 1 to 5.

	CM Stages					CH Stages					DM Stages					DH Stages					IM Stages					IH Stages				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
CM						√	√	√	×	–	–	√	–	–	√	√	–	–	–	√	–	√	–	–	√	√	√	√	–	√
CH											√	–	√	–	√	–	√	√	√	√	√	–	√	√	√	√	√	–	×	√
DM																√	×	–	–	–	–	–	–	–	×	√	√	√	–	√
DH																					√	–	–	–	√	√	√	√	–	√
IM																										√	√	√	–	–
IH																														

√ sig. at 0.01 × sig. at 0.05 – not sig.

Medium and high venom dose intraspecific stage comparisons.

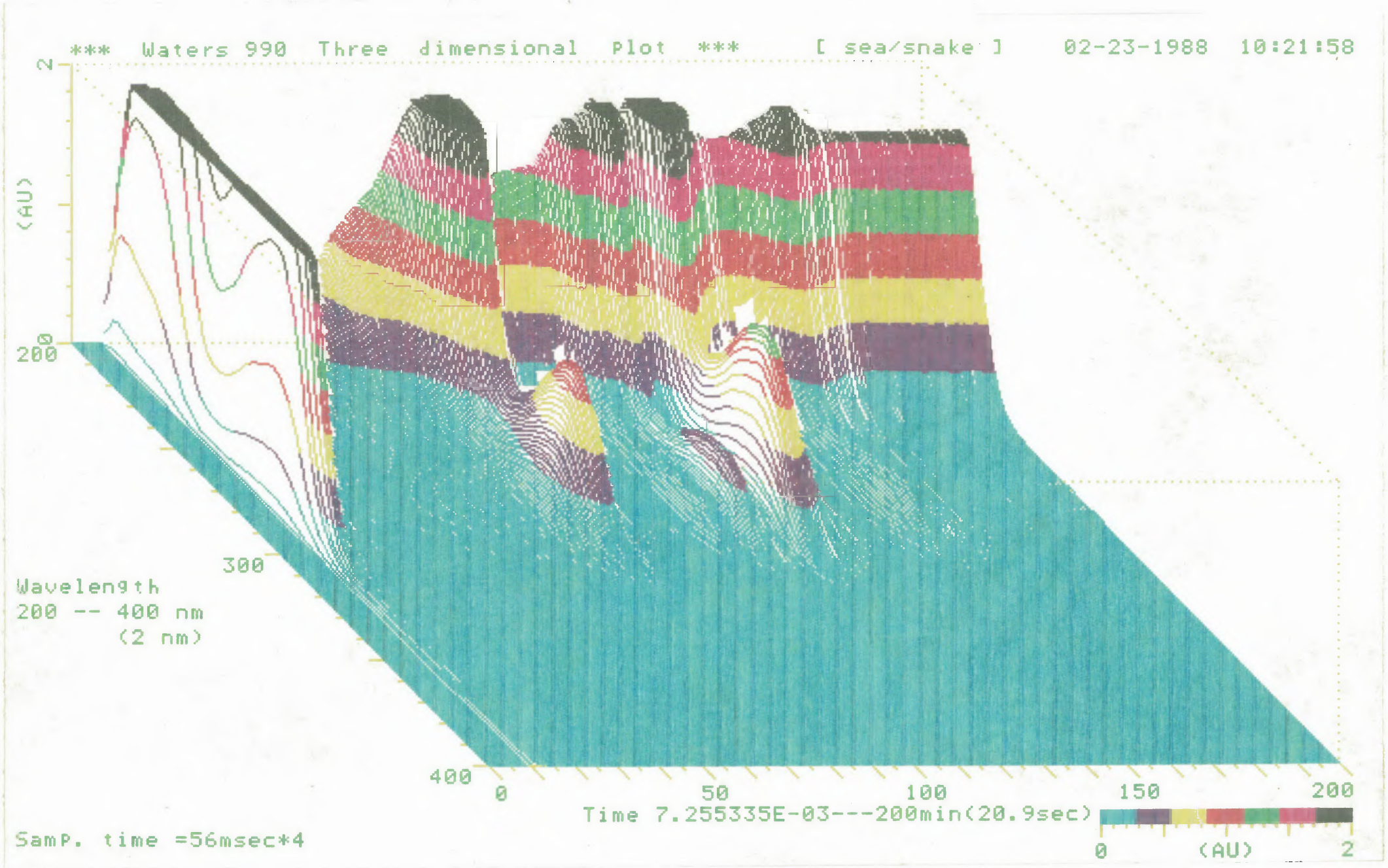
	1-2	1-3	1-4	1-5	2-3	2-4	2-5	3-4	3-5	4-5
CM	–	√	√	√	√	√	√	–	√	×
CH	–	√	√	√	√	√	√	–	–	–
DM	√	√	√	√	–	×	–	√	–	×
DH	–	–	√	×	–	√	√	√	√	–
IM	√	√	√	–	–	–	–	–	×	√
IH	–	–	×	√	–	–	√	–	√	√

√ sig. at 0.01 × sig. at 0.05 – not sig.

Appendix H

Three-dimensional chromatograph from venom fractionation

Three-dimensional chromatograph obtained from the fractionation of *Aipysurus laevis* venom.


*** Waters 990 Three dimensional Plot *** [sea/snake] 02-23-1988 10:21:58
2
(AU)
0
200
300
400
Wavelength
200 -- 400 nm
(2 nm)
0
50
100
150
200
Time 7.255335E-03---200min(20.9sec)
0
(AU)
2
Samp. time =56msec*4

Appendix I

Probability values (venom fractions)

Probability values from ventilation studies of venom fractions from *Aipysurus laevis* venom.

Probability values obtained with one-way analysis of variance from ventilation rate studies of *Dascyllus aruanus* comparing the different venom fraction groups, C1 to C21 are experimental times (Fig. 8.1), C - control, 1 - venom fraction 1, 2 - venom fraction 2, 3 - venom fraction 3, 4 - venom fraction 4, 5 - venom fraction 5, 6 - venom fraction 6, 7 - venom fraction 7, R - venom recombination group.

	C–1	C–2	C–3	C–4	C–5	C–6	C–7	C–R	1–2
C1	0.050	0.060	0.710	0.040	0.010	0.000	0.000	0.140	0.140
C2	0.310	0.000	0.120	0.980	0.030	0.030	0.000	0.040	0.000
C3	0.820	0.000	0.006	0.000	0.030	0.830	0.000	0.090	0.000
C4	0.020	0.000	0.009	0.000	0.000	0.170	0.000	0.004	0.000
C5	0.008	0.000	0.015	0.000	0.000	0.240	0.000	0.000	0.000
C6	0.220	0.000	0.009	0.000	0.000	0.000	0.740	0.000	0.000
C7	0.001	0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.000
C8	0.000	0.000	0.001	0.000	0.470	0.000	0.002	0.000	0.000
C9	0.000	0.030	0.140	0.005	0.050	0.000	0.390	0.000	0.000
C10	0.000	0.000	0.000	0.000	0.000	0.010	0.010	0.000	0.000
C11	0.010	0.000	0.070	0.000	0.000	0.000	0.780	0.000	0.420
C12	0.000	0.000	0.000	0.000	0.000	0.000	0.440	0.000	0.000
C13	0.001	0.000	0.000	0.000	0.000	0.000	0.350	0.000	0.000
C14	0.070	0.000	0.300	0.000	0.000	0.000	0.240	0.000	0.000
C15	0.660	0.003	0.040	0.000	0.270	0.000	0.950	0.010	0.001
C16	0.000	0.120	0.380	0.270	0.040	0.000	0.000	0.020	0.000
C17	0.000	0.640	0.810	0.990	0.000	0.000	0.000	0.020	0.000
C18	0.000	0.030	0.008	0.590	0.000	0.000	0.000	0.000	0.000
C19	0.000	0.250	0.300	0.910	0.003	0.000	0.000	0.000	0.000
C20	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000
C21	0.000	0.050	0.000	0.007	0.000	0.005	0.000	0.000	0.000

Probability values for venom fraction studies continued.

	1–3	1–4	1–5	1–6	1–7	1–R	2–3	2–4	2–5
C1	0.020	0.920	0.580	0.150	0.000	0.001	0.370	0.110	0.040
C2	0.010	0.300	0.002	0.260	0.000	0.002	0.000	0.000	0.000
C3	0.010	0.000	0.040	0.660	0.000	0.060	0.000	0.160	0.000
C4	0.000	0.000	0.070	0.350	0.000	0.000	0.000	0.250	0.000
C5	0.000	0.000	0.004	0.030	0.560	0.000	0.000	0.470	0.000
C6	0.150	0.000	0.000	0.010	0.380	0.000	0.000	0.050	0.005
C7	0.560	0.000	0.000	0.000	0.670	0.000	0.000	0.020	0.080
C8	0.240	0.000	0.000	0.001	0.210	0.006	0.000	0.000	0.000
C9	0.010	0.000	0.050	0.000	0.002	0.180	0.000	0.550	0.000
C10	0.240	0.000	0.200	0.000	0.001	0.000	0.000	0.820	0.000
C11	0.000	0.000	0.000	0.000	0.004	0.000	0.000	0.420	0.000
C12	0.310	0.000	0.240	0.000	0.000	0.000	0.000	0.970	0.000
C13	0.610	0.000	0.270	0.000	0.000	0.000	0.000	0.860	0.000
C14	0.440	0.000	0.000	0.000	0.004	0.000	0.000	0.610	0.000
C15	0.010	0.000	0.510	0.000	0.610	0.030	0.360	0.340	0.000
C16	0.000	0.000	0.000	0.610	0.320	0.020	0.020	0.650	0.001
C17	0.000	0.000	0.120	0.450	0.270	0.050	0.480	0.630	0.000
C18	0.000	0.000	0.000	0.620	0.630	0.440	0.560	0.110	0.000
C19	0.000	0.000	0.003	0.450	0.490	0.600	0.900	0.290	0.060
C20	0.000	0.000	0.410	0.030	0.570	0.670	0.310	0.230	0.000
C21	0.000	0.000	0.090	0.000	0.030	0.020	0.007	0.440	0.000

Probability values for venom fraction studies continued.

	2–6	2–7	2–R	3–4	3–5	3–6	3–7	3–R	4–5
C1	0.004	0.000	0.050	0.010	0.004	0.000	0.001	0.280	0.650
C2	0.000	0.180	0.000	0.130	0.520	0.000	0.001	0.590	0.030
C3	0.000	0.170	0.000	0.005	0.570	0.003	0.004	0.000	0.001
C4	0.000	0.410	0.000	0.000	0.000	0.000	0.000	0.780	0.008
C5	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.003
C6	0.000	0.000	0.000	0.000	0.000	0.290	0.020	0.000	0.000
C7	0.000	0.000	0.000	0.000	0.000	0.000	0.310	0.000	0.000
C8	0.000	0.000	0.000	0.000	0.010	0.000	0.950	0.000	0.000
C9	0.000	0.002	0.000	0.000	0.600	0.000	0.550	0.000	0.000
C10	0.000	0.000	0.000	0.000	0.020	0.000	0.030	0.000	0.000
C11	0.000	0.000	0.000	0.000	0.000	0.000	0.040	0.000	0.000
C12	0.000	0.000	0.000	0.000	0.870	0.000	0.000	0.000	0.000
C13	0.000	0.000	0.000	0.000	0.560	0.000	0.000	0.000	0.000
C14	0.000	0.002	0.000	0.000	0.000	0.000	0.030	0.000	0.000
C15	0.000	0.004	0.000	0.060	0.002	0.000	0.050	0.000	0.000
C16	0.000	0.000	0.000	0.050	0.230	0.000	0.001	0.120	0.002
C17	0.000	0.000	0.000	0.820	0.000	0.000	0.000	0.000	0.000
C18	0.000	0.000	0.000	0.030	0.000	0.000	0.000	0.000	0.000
C19	0.001	0.000	0.000	0.350	0.050	0.000	0.000	0.000	0.004
C20	0.020	0.000	0.000	0.850	0.000	0.120	0.000	0.001	0.000
C21	0.240	0.000	0.003	0.050	0.050	0.240	0.160	0.490	0.000

Probability values for venom fraction studies continued.

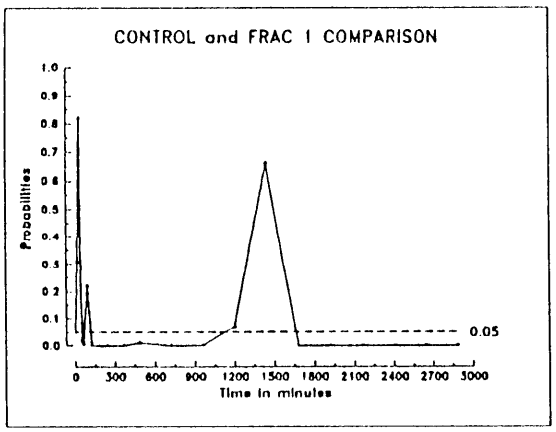
	4–6	4–7	4–R	5–6	5–7	5–R	6–7	6–R	7–R
C1	0.180	0.000	0.001	0.370	0.000	0.000	0.000	0.000	0.020
C2	0.030	0.000	0.040	0.000	0.006	0.920	0.000	0.000	0.005
C3	0.000	0.980	0.000	0.020	0.001	0.000	0.000	0.140	0.000
C4	0.000	0.730	0.000	0.007	0.003	0.000	0.000	0.000	0.000
C5	0.000	0.000	0.000	0.000	0.020	0.000	0.050	0.000	0.000
C6	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.004	0.000
C7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.890	0.000
C8	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.580	0.000
C9	0.000	0.000	0.000	0.000	0.260	0.002	0.000	0.000	0.000
C10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.550	0.000
C11	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.440	0.000
C12	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.110	0.000
C13	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.010	0.000
C14	0.000	0.008	0.000	0.000	0.000	0.080	0.000	0.020	0.000
C15	0.000	0.000	0.000	0.000	0.250	0.100	0.000	0.000	0.009
C16	0.000	0.000	0.002	0.001	0.020	0.600	0.180	0.010	0.140
C17	0.000	0.000	0.000	0.550	0.640	0.530	0.850	0.280	0.300
C18	0.000	0.000	0.000	0.000	0.000	0.009	0.930	0.260	0.240
C19	0.000	0.000	0.000	0.060	0.080	0.040	0.880	0.840	0.940
C20	0.170	0.000	0.002	0.004	0.800	0.250	0.008	0.120	0.360
C21	0.610	0.001	0.020	0.005	0.580	0.320	0.020	0.100	0.600

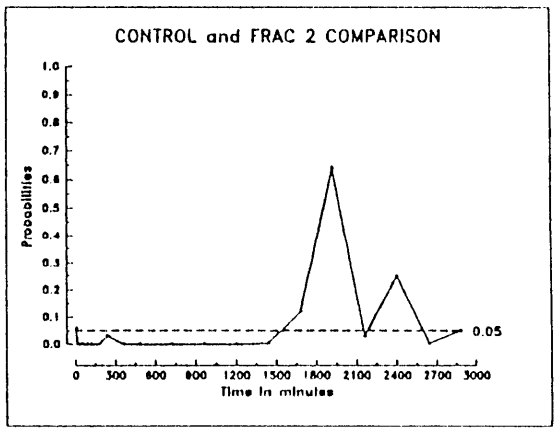
Appendix J

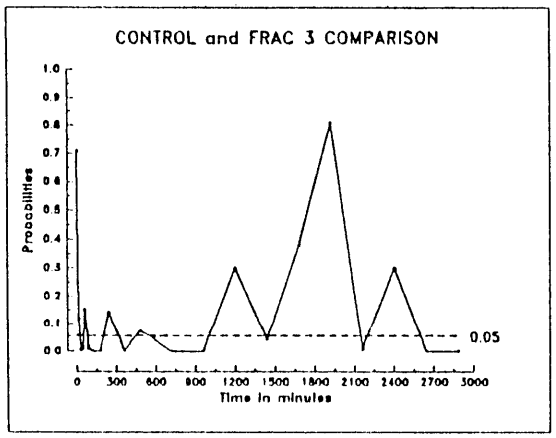
Profiles of probability (venom fractions)

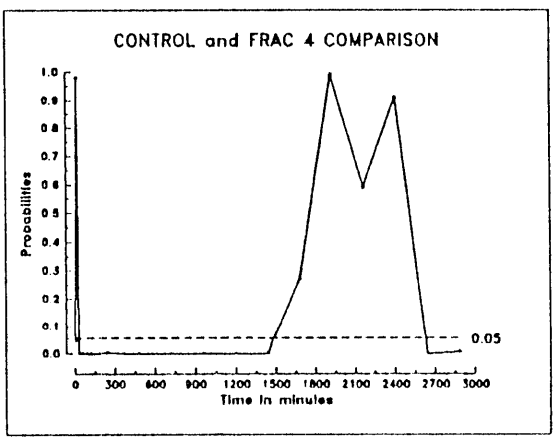
Profiles for comparisons of probabilities from studies of venom fractions from *Aipysurus laevis* venom.

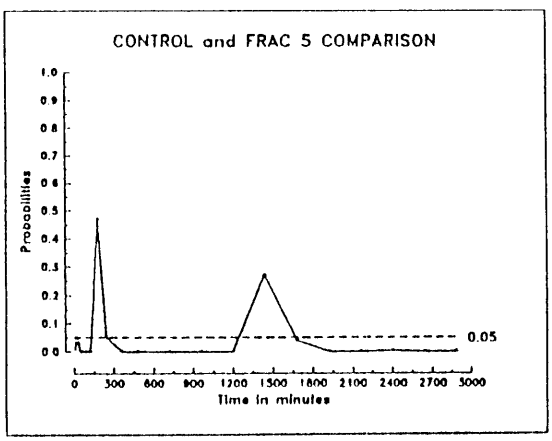
Profiles of the probability comparisons (Appendix I) from the ventilation studies of *Dascyllus aruanus* for the different venom fractions and the control groups, examining significance at the 0.05 level.

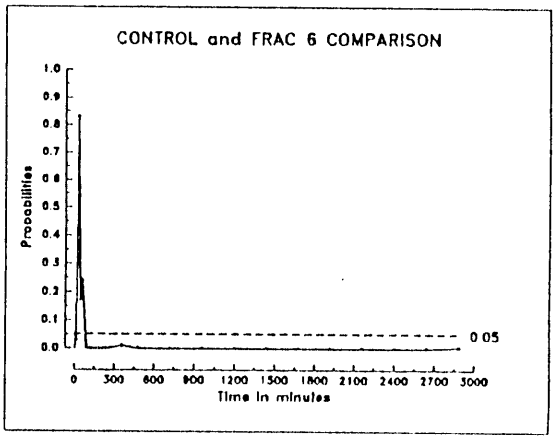




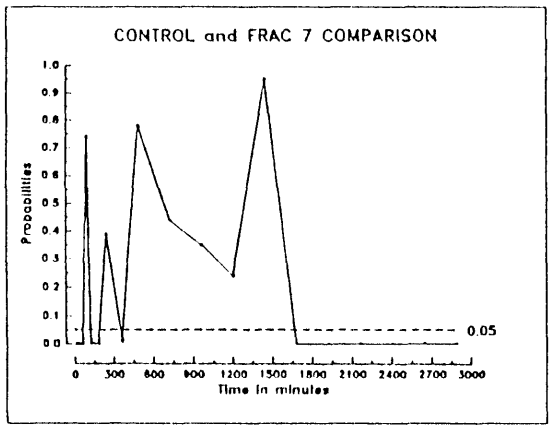


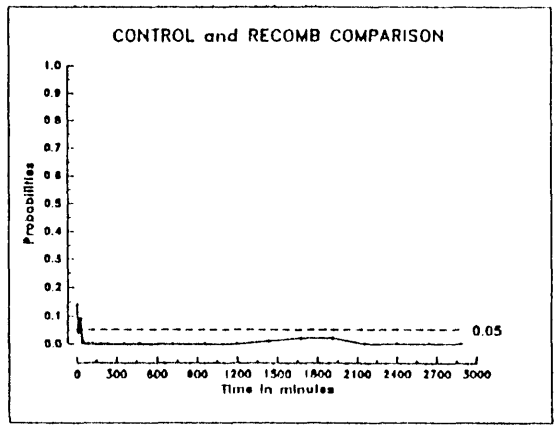


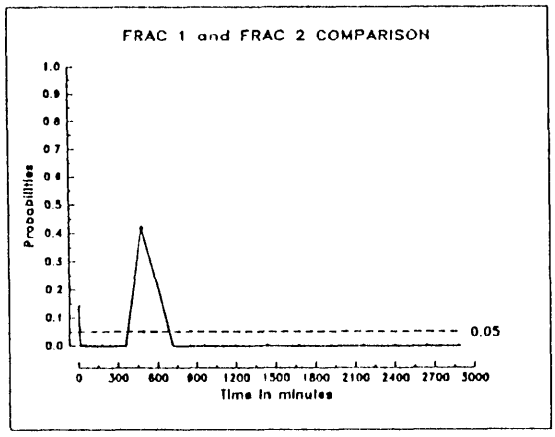


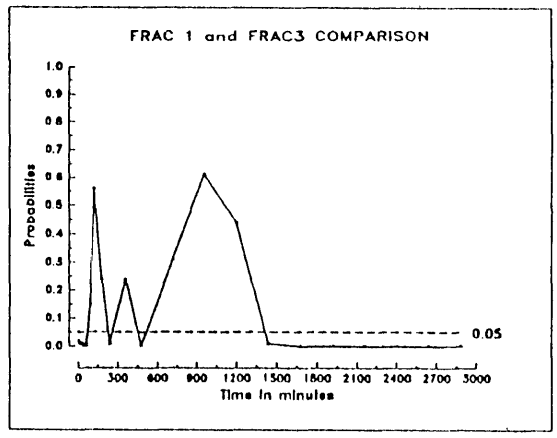


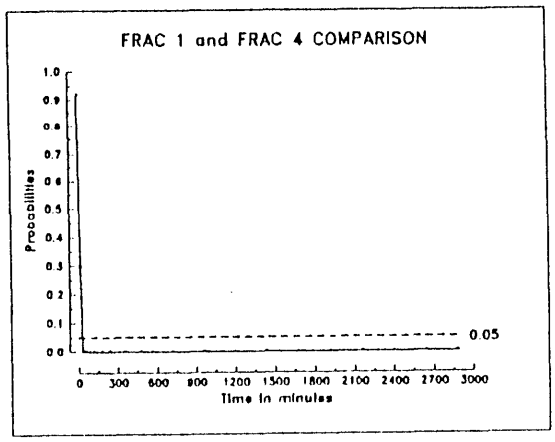
Profiles of probability comparisons for the venom fractions continued.

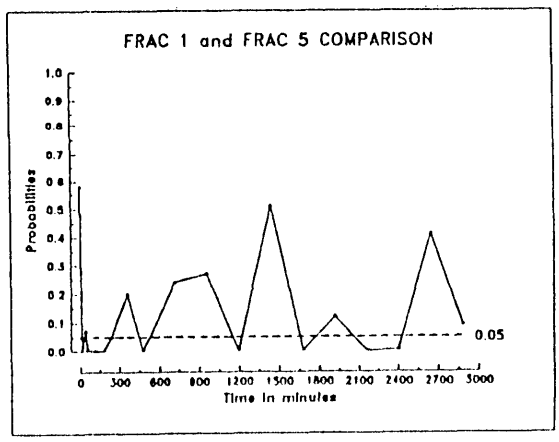




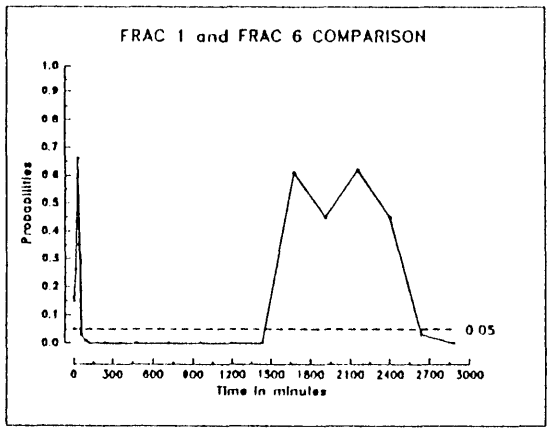


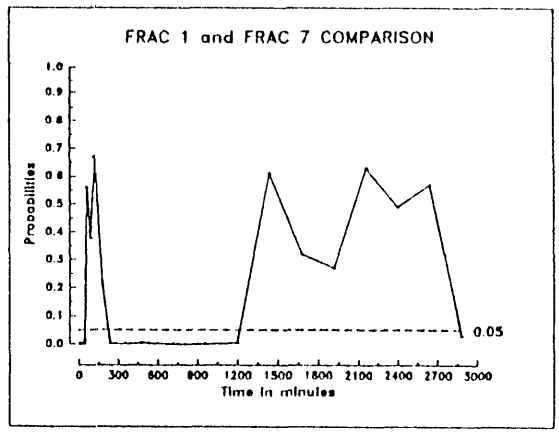


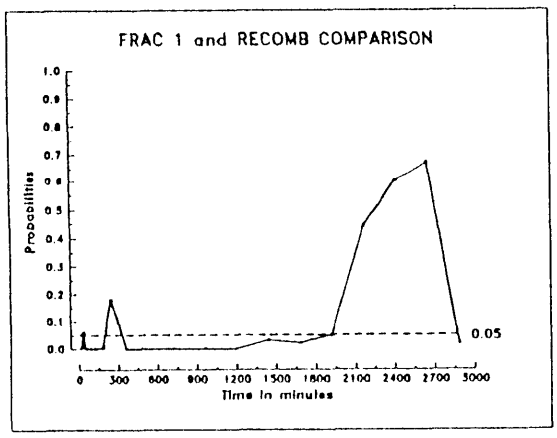


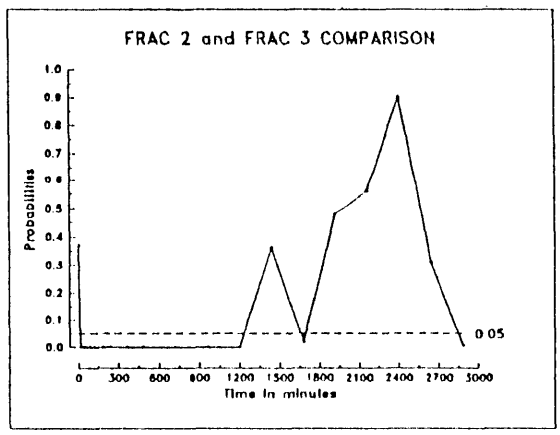


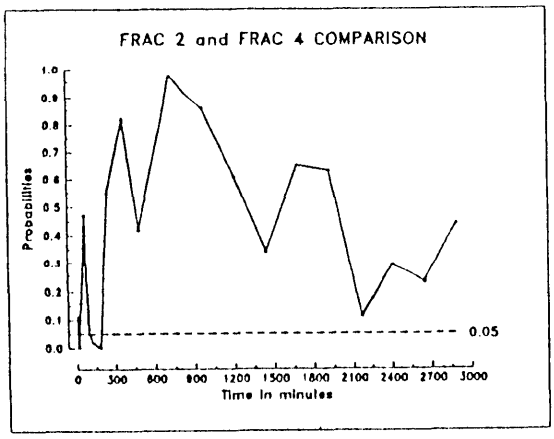
Profiles of probability comparisons for the venom fractions continued.

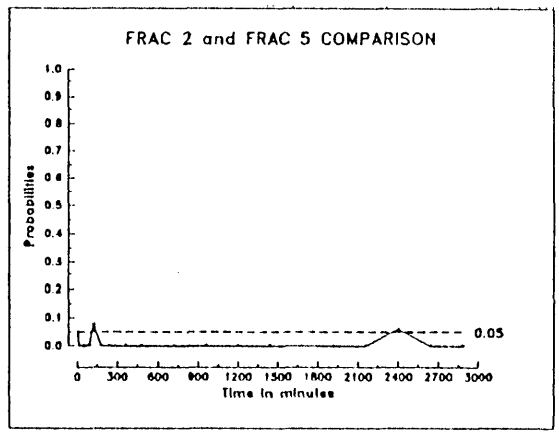




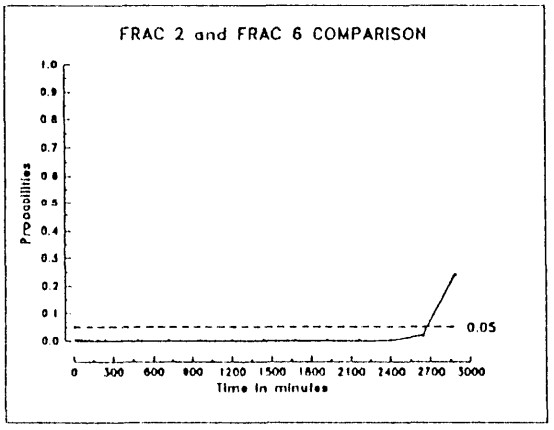


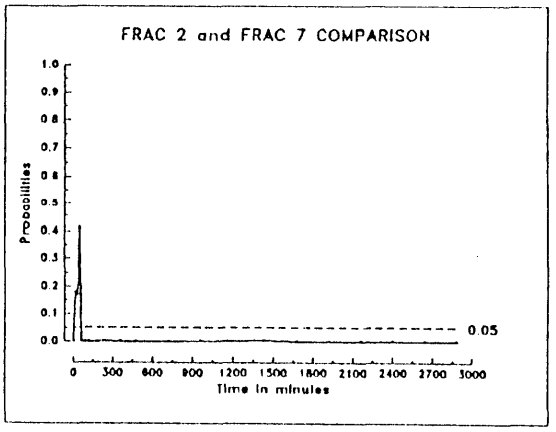


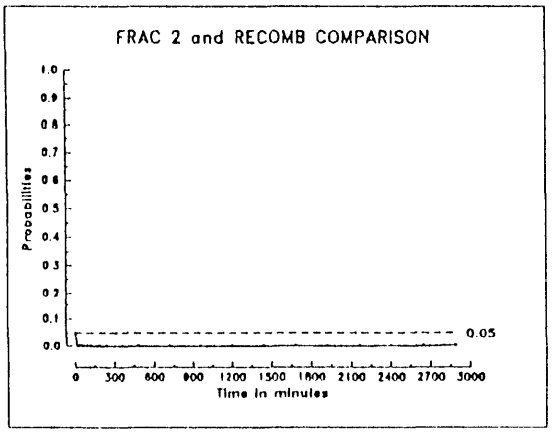


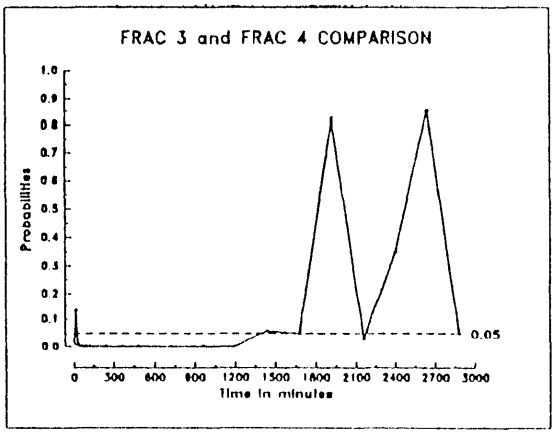


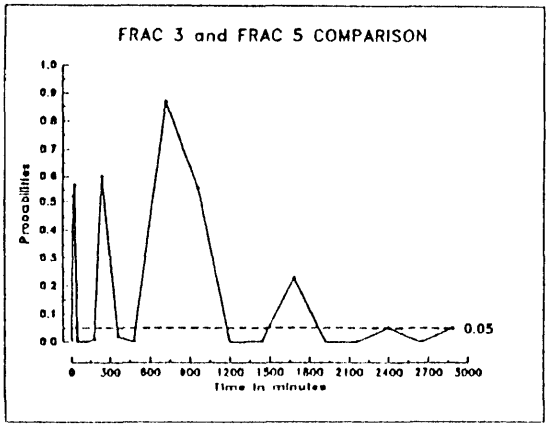
Profiles of probability comparisons for the venom fractions continued.

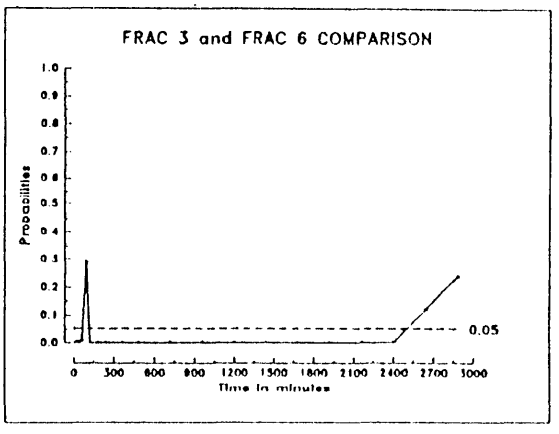




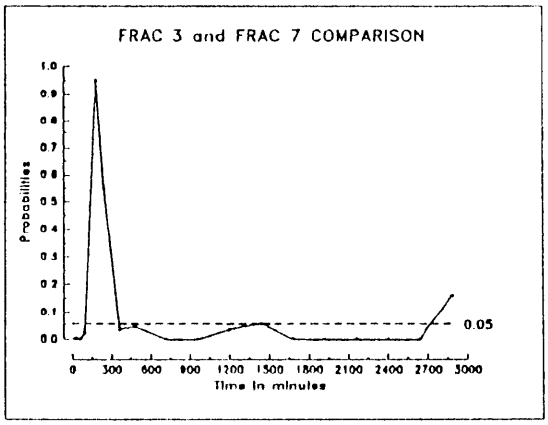


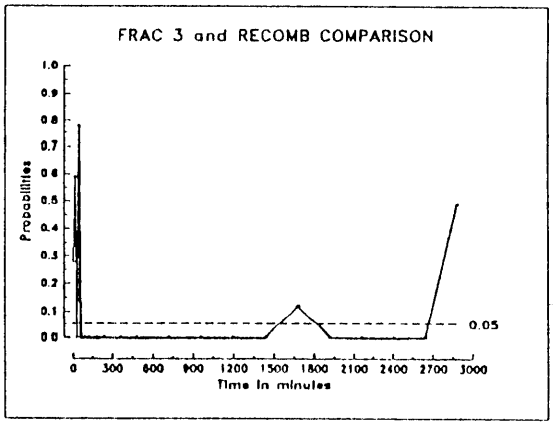


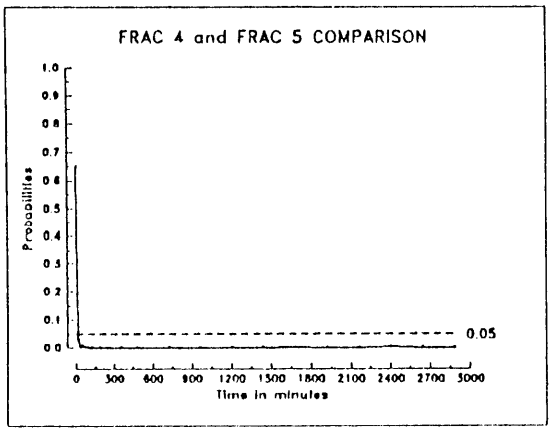


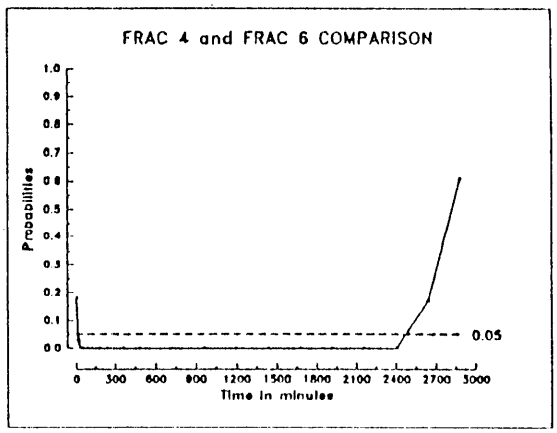


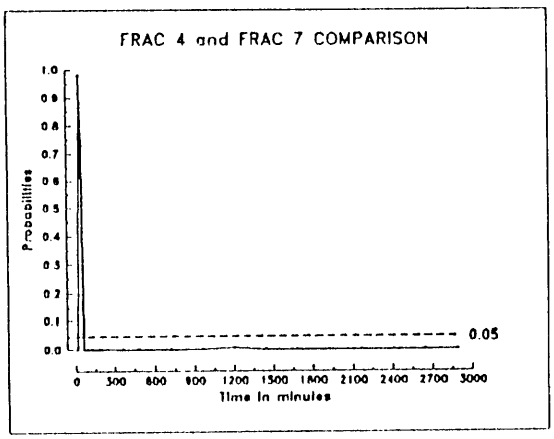
Profiles of probability comparisons for the venom fractions continued.

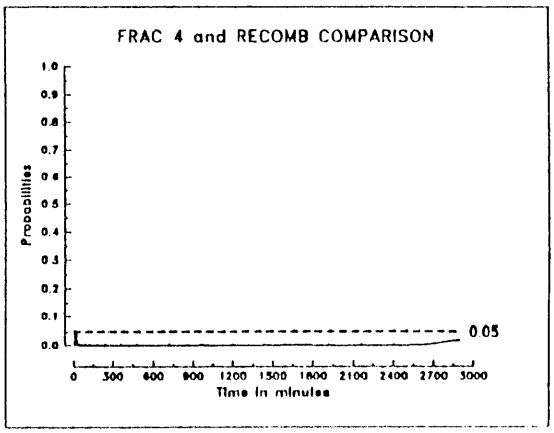












Profiles of probability comparisons for the venom fractions continued.