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To cite this article: JC Montgomery & CA Radford (2013) Contributions of the Leigh Marine Laboratory to marine science, 1962–2012: sensory neuroethology, New Zealand Journal of Marine and Freshwater Research, 47:3, 409–425, DOI: [10.1080/00288330.2013.803985](https://doi.org/10.1080/00288330.2013.803985)

To link to this article: <http://dx.doi.org/10.1080/00288330.2013.803985>



Published online: 01 Aug 2013.



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## REVIEW ARTICLE

### Contributions of the Leigh Marine Laboratory to marine science, 1962–2012: sensory neuroethology

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*(Received 18 December 2012; accepted 23 April 2013)*

The purpose of this paper is to highlight the contributions of the Leigh Marine Laboratory to sensory neuroethology. A brief summary of the work done at Leigh, or by Leigh staff, is given across each of the main sensory modalities: chemosense, vision and octavolateralis sensory systems (electrosense, flow sensing and hearing). Within this broad overview, three particular areas have been singled out for more in-depth treatment as examples of Leigh research that have made particularly significant contributions to marine science. These three areas are: electro-sensory processing, flow sensing and hearing, in particular the role of passive acoustics in orientation and settlement.

**Keywords:** Leigh Laboratory; marine science history; sensory neuroethology; vision; chemosense; electrosense; lateral line; hearing

#### Introduction

Sensory neuroethology is the study of sensory and neural basis of an animal's interaction with its environment. One of the central strengths of neuroethology is the emphasis on natural behaviour as the most appropriate context in which to understand sensory capabilities and neural processing. It is the biological imperatives of feeding, mating and moving-about-safely-in-between-times that have driven the evolution of sensory systems and the neural algorithms that shape animal/environment interactions. As Carl Hopkins also notes: 'Neuroethologists base their studies on behavioural studies that often are done in the field' (<http://nelson.beckman.illinois.edu/neuroethology.html>). So it is not surprising that marine laboratories such as Leigh, with their emphasis on field access and field studies, provide excellent opportunities for developing the understanding of natural behaviour on which neuroethology is based (Fig. 1). In

addition, neuroethologists are quick to select study animals that exhibit particular sensory specialisations or behavioural aptitude, and the marine environment provides a rich diversity of animal types and specialities from which to choose.

The purpose of this special edition is to highlight the contributions of the Leigh Marine Laboratory to marine science over its first 50 years, 1962–2012. The structure of this specific contribution will be to provide a brief summary of the work done at Leigh, or by Leigh staff, across each of the main sensory modalities: chemosense, vision and octavolateralis sensory systems (electrosense, flow sensing and hearing). Work on sensory systems only really began at the Leigh Marine Laboratory in the 1980s, so this review concentrates on the last 25 years of the Laboratory's history. Within this broad overview, three particular areas have been singled out for more in-depth treatment as examples of Leigh research that have made particularly

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**Figure 1** Natural behaviour in the field: a two spot Demoiselle (*Chromis dispilus*) photographed on Leigh reef, showing classic rheotaxis facing into the tidal flow. Like many behaviours, rheotaxis is mediated by mix of sensory input including visual station holding and flow sensing. The direct contribution of flow sensing to rheotaxis was discovered in work done at the Leigh Marine Laboratory (Montgomery et al. 1997).

significant contributions to Marine Science. These three areas are: electrosensory processing, flow sensing and hearing, in particular the role of passive acoustics in orientation and settlement. Much of the work has been done on fish, but the work on hearing and passive acoustics has recently extended to include invertebrates. The definition of Leigh research obviously has at its foundation work done at Leigh, or by Leigh staff; however, it is not a closed set. The publication record shows a high level of interactivity between Leigh and city campus staff, strong international collaborations, and crossover interests between marine and freshwater research. The three areas selected for more in depth coverage fall within the Leigh research definition, but also profile this interactivity.

### **Chemosense (olfaction and taste)**

Olfaction and taste play crucial roles in prey detection, food selection, reproductive interac-

tions and habitat selection. There has not been a strong tradition of work in chemosensory systems at Leigh, but there is a strand of work that runs through the first and last of these behavioural categories. With the exception of some electro-olfactogram work, this strand has been a mix of field and laboratory behaviour.

A number of fish species have sensory barbels that are used in prey detection. Goatfish (*Upeneichthys porosus*), which are a common species at Leigh and in coral reef habitats, develop the barbel on settlement (McCormick 1993). They forage during the day using the taste buds on the barbels to detect small prey buried in the upper layers of sandy patches on and surrounding the reef. Goatfish are observed feeding during the day, but are also night active, indicating the potential for chemosensory systems to provide feeding opportunities under low light conditions. The nocturnal southern bastard cod *Pseudophycis barbata* has also been shown to utilise chemo- and mechanosensory

systems when hunting for prey under low light conditions (Bassett & Montgomery 2011a). This study also characterised the cruise search strategy used by this species in the context of its use of chemo and mechanosensory systems for prey detection. Search strategies have been extensively studied in relation to visual search, but this is one of the first studies to extend search efficiency considerations to non-visual search.

Tracking down an olfactory source is also an important food search behaviour, as testified by the common use of bait for line fishing, pot trapping and baited underwater video (BUV) fish census techniques. With respect to the use of bait attraction for fish census, studies rarely take account the influence of the sensory capabilities and diurnal and seasonal responsiveness of target species, or the variable influence of tidal currents and bottom topography in stimulus dispersal. In a novel study designed to extend the BUV census to nocturnal fishes, it was used with infrared lighting and compared with diver surveys to investigate fish populations in situ (Bassett & Montgomery 2011b). At night, fish abundance at the BUV was related to the olfactory capability of each species. Olfactory specialists were shown to arrive at baited underwater video drops earlier, and in greater numbers, than non-olfactory species. This pattern was reversed in non-olfactory species, which were found to dominate underwater census surveys and appear less at baited underwater video drops. The sensory capacity of a species was found to be a larger determinant for fish abundance at baited underwater video drops than was the actual density of that species. The BUV technique was also highly effective at determining the diel activity of fish species.

Tracking an olfactory source can be difficult, especially under natural conditions where the odour is being dispersed in a turbulent plume. Under these conditions, olfactory released rheotaxis, combining information from both chemo- and mechanosensory systems, becomes an effective search strategy. Experimental evidence for a direct role of the mechanosensory lateral line in olfactory search behaviour was

obtained in laboratory experiments by Baker et al. (2002), and field evidence of olfactory released rheotaxis using infra-red video recording of search behaviour in short-finned eel (*Anguilla australis*) in one of the streams at the top of Leigh harbour (Carton & Montgomery 2003).

The use of olfaction for guiding adult migration or larval movement and habitat selection during settlement is wide spread in aquatic environments (e.g. Montgomery et al. 2001). As one recent local example, Radford et al. (2012b) have shown that snapper (*Pagrus auratus*) can use olfactory cues to orient to an appropriate seagrass settlement habitat. In addition to the olfactory cues produced by specific habitat types, established populations may also provide a good 'proxy' for suitable migration and settlement destinations. However, to date, there are only two documented examples of intraspecific pheromones acting as in this way: the migratory pheromone in sea lamprey (*Petromyzon marinus*) (Li et al. 1995), and the species-specific attraction of New Zealand galaxid (banded kōkopu; *Galaxias fasciatus*) juveniles to adult pheromones (Baker & Montgomery 2001a). In lamprey, the migratory pheromone is attributed to unique bile acids released by conspecific larvae (Li et al. 1995), and though similar tests have been done with banded kōkopu, the nature of the pheromone has yet to be established (Baker et al. 2006).

Even if intraspecific migratory pheromones prove not to be widespread, galaxid species are an important component of the fish biodiversity in New Zealand coastal, estuarine and freshwater systems. So it is worth noting two potential implications of the above discovery. Firstly, that streams and rivers that lose their adult populations may no longer provide the appropriate cue for whitebait migration to recolonise those populations. Secondly, that the detrimental effects of heavy metals on olfaction may adversely affect whitebait migrations through polluted estuaries (Baker & Montgomery 2001b).

### Vision

Sunlight fuels primary productivity, and provides one of the strongest forces structuring marine communities. Despite the limitations of light transmission in seawater, vision still plays a major role in primary orientation, movement, predator–prey interactions and communication. Again, vision has not been a major ‘focus’ for neuroethology studies at Leigh but there is a body of work that clusters around the areas of visual ontogeny, and visual capabilities under conditions of low or limited light.

For most marine species, first feeding occurs a matter of days after hatching, and is visually mediated. This period of first feeding is a time of high mortality with consequences for larval survival and subsequent recruitment. For the culture of marine fish species, it also represents a critical phase of larval development for successful hatchery practice. Thus visual ontogeny has important implications for understanding the required field and hatchery conditions for larval fish feeding success. One of the primary behavioural determinants of successful first feeding is visual acuity, or the maximum distance at which a small target prey item can be seen. Visual acuity can be estimated by both morphological (retinal histology) and behavioural means. Pankhurst et al. (1993) and Pankhurst (1994) compared both methods in two different fish species and found that the behavioural methods gave much lower estimates of visual acuity especially during early ontogeny. These studies also showed that acuity at first feeding is quite poor, placing real constraints on the use of artificial feeds in hatchery practise (Langdon 2003) and on the pelagic feeding conditions for successful larval survival and growth (Zeldis et al. 2005). The aquaculture implications of this work were also followed up by Carton (2005), showing that increased water turbidity due to algae had a detrimental effect on feeding success of larval kingfish (*Seriola lalandi*).

In a serendipitous natural experiment at the Leigh Laboratory, Pankhurst (1992) observed that adults of two species of fishes (sweep,

*Scorpius lineolata*, and spotty, *Notolabrus celdotus*), recovered from dark seawater storage tanks, had proportionately larger eyes than normal fishes of similar body size. Physical constraints meant that fish could only have entered the system as larvae or small juveniles, so that they must have had an extended period of residence. Age estimation from otoliths indicated that fishes from the water tanks were all older (i.e. slower growing) than normal fishes of similar size. The interpretation of these findings was that the increase in relative eye size in tank fishes may have been the result of maintenance of ocular growth, in the face of reduced rates of somatic growth; in other words, that eye growth was on a protected trajectory and to some degree decoupled from general somatic growth. In a controlled follow-up experiment (Pankhurst & Montgomery 1994), this interpretation was confirmed and extended to show that slow somatic growth was not accompanied by correspondingly slow growth of the eyes, optic tectum or the cerebellum. Growth of these parts then is strongly age dependent and maintained at the expense or in spite of low somatic growth.

These Leigh-based studies on fish visual ontogeny, and visual function at low light levels formed the basis of additional work on Antarctic fishes (Pankhurst & Montgomery 1990) and the Antarctic marine environment. The protected growth trajectory of eye size was used to study the sensory development of the Antarctic silverfish, *Pleurogramma antarcticum*. It was shown that for the first few years of growth, feeding is visually mediated with little or no feeding during the Antarctic winter. Thereafter, there is an ontogenetic shift to year-round feeding using both visual and non-visual senses (Montgomery & Sutherland 1997). Electroretinogram and behavioural methods also developed at Leigh were used to determine the low light limits for photopic and scotopic vision of four species of sub-ice Antarctic fishes. The threshold limits were predicted to be reached at depths of 20–40 and 30–60 m, respectively, under snow and ice conditions typically found

during spring and ERG-determined spectral sensitivity curves were found to be matched to the spectral irradiance under the ice (Pankhurst & Montgomery 1989). These results were used to predict the depth limitations on visual feeding in one of the planktivorous antarctic fish *Pagothenia borchgrevinki* (Montgomery et al. 1989) and compare this with prey distributions. The conclusion was even in spring sunshine much of the available prey is below the depth of effective vision, suggesting that non-visual senses are important for feeding not only during the winter, but also in the limited light regions beneath snow and ice cover.

### Electrosense

The electrosensory system is one component of the octavolateralis sensory complex, which also includes the lateral line, hearing and balance (vestibular). Electrosense is a 'primitive' sense found in basal vertebrate lineages, but has been most studied in elasmobranch fishes (Fig. 2). Sharks and rays do not lend themselves to behavioural study, but even so, there is good field evidence for the use of electroreception in mating, prey detection and some theoretical work on its potential use in movement and migration (Montgomery & Walker 2001). Much of the Leigh based work on electroreception has addressed the issue

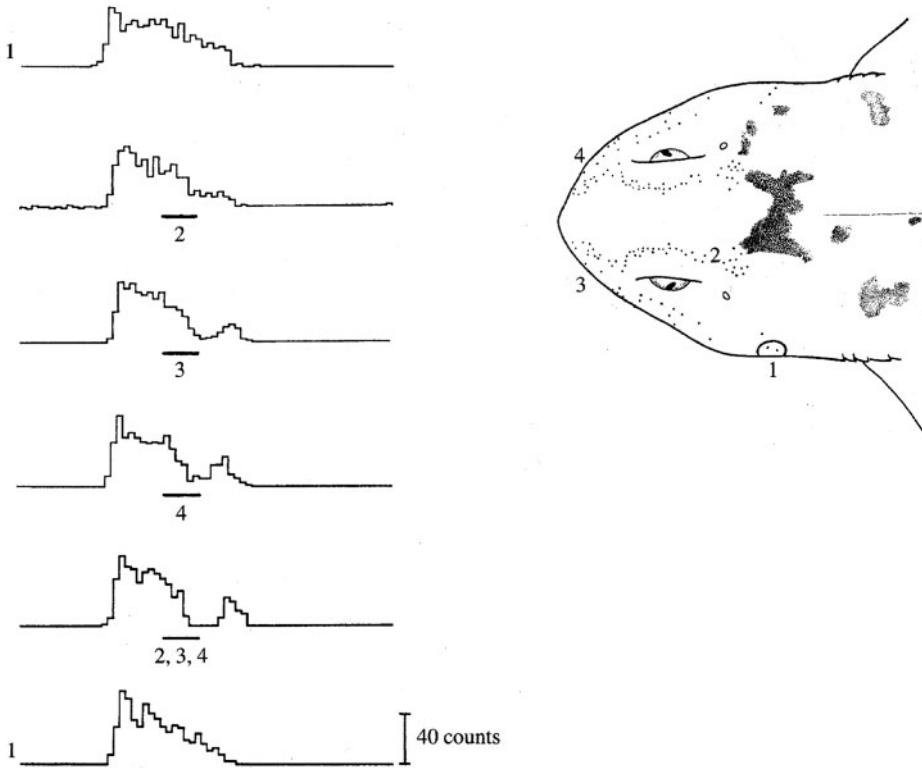


**Figure 2** The electrosense and lateral line of the skate (*Raja nasuta*). The pore openings of the electrosensory ampullae of Lorenzini are naturally pigmented in this species, so each of the black dots is a pore opening. In some cases, particularly the pores on the base of the pectoral fins, the jelly-filled canal leading away from the pore is evident. The canals of the mechanosensory lateral line have been injected with blue ink. The injection site is evident on the left side of the photograph, and the canals are more extensively filled on this side.

of how the brain can discriminate between the weak electric fields of biological interest, and the equivalent weak electric fields that the animal creates itself. This work has been the focus of long-standing collaboration between Leigh and the Marine Biological Laboratory at Woods Hole. Given the joint nature of this work, and the fact that the work has been reviewed elsewhere (Bodznick et al. 1999; Montgomery & Bodznick 1999), it is appropriate here to provide only a brief overview with particular reference to the work actually done at Leigh.

The ability to discriminate self-generated electro-sensory input from biologically important

signals turns out to be a function of the first relay nucleus in the hindbrain (Montgomery & Bodznick 1994). This area of the brain is known as the dorsal octavolateralis nucleus (DON). Sensory nerves entering this area carry the biologically important signals, but are also strongly driven by the animal's own electric fields. The extraordinary finding is that the self-generated 'noise' is effectively cancelled in the DON. Two mechanisms are at work. The first is that the neurons receiving the input from the sensory nerves receive both excitatory input from a particular part of the body surface, and balancing inhibitory inputs from other parts of the body (Fig. 3). Because the



**Figure 3** Evidence for common-mode rejection. Receptive field organisation for one of the DON neurons. Stimulus 1 is located in the excitatory receptive field and activated by a 1 Hz sine wave and a peak-to-peak intensity of  $5 \mu\text{V}$  at the skin surface. The locations of the other stimuli are indicated on the diagram of the fish's head. They were activated with a  $2\text{-}\mu\text{V}$  square wave of 100 ms duration (indicated by a solid line below histograms) timed to coincide with the excitatory portion of the response to activation. Response records are firing rate histograms of 50 stimulus presentations. Numbers below each response record indicate the active stimuli. Activation of 2, 3 or 4 results in a small inhibitory response, activation of 2, 3 and 4 together produces strong inhibition. 16 ms bins (from Bodznick & Montgomery 1992).

inputs generated by the animal's own electric field are the same for all receptors, this mechanism cancels much of the self-generated noise, but does not affect the focal electric sources from potential prey. In other words, the self-generated noise is common to all receptors, whereas the biological signals affect receptors differentially. This is a mechanism known to electronic engineers as common-mode rejection and is widely used in amplifier technologies. The second mechanism is a sophisticated adaptive filter, which learns to cancel any residual field left over after common-mode rejection. The detailed mechanism of the adaptive filter depends on the cerebellum-like structure of the DON (Montgomery et al. 2012), and in fact this line of work led to the suggestion that the cerebellum itself, which is found only in gnathostomous vertebrates, evolved from the cerebellum-like structures found in agnathans (Montgomery & Bodznick 2010).

There are two additional strands of work at Leigh that related to the study of electrosensory systems and the evolution of elasmobranch brains. The first strand addresses some of the potential practical applications of understanding electrosense. It has long been suggested that the electrosense may provide a practical way of mitigating elasmobranch by-catch in long-line fisheries. The possibility stems from the acute sensitivity of electrosense (with a demonstrated threshold sensitivity to electric field gradients of 5 nV/cm), and the fact that elasmobranchs have electrosense whereas teleost fishes do not. A recent MSc thesis (Howard 2011) examined the ability of electric fields of different configurations to deter feeding at a bait station. Although feeding deterrence could be demonstrated, the intensity and field configurations required did not lend themselves to practical implementation of this as an effective deterrence for fisheries by-catch. The possible effect of sea-floor power cables on elasmobranch movement is another area of applied interest. As marine tidal and wind power technologies develop, power cables will become more common. The potential detrimental effects of these cables is often raised in resource consent considerations,

but as yet, the behaviour of elasmobranch around these cables is not known.

The second strand extends the work on the function and evolution of the cerebellum in elasmobranchs to investigate the evolutionary diversity of shark brains. The relative development of different brain areas were studied in twenty batoid species (Lisney et al. 2008), and 80 species of sharks and holocephalans (Yopak et al. 2007; Yopak & Montgomery 2008). The general finding from this study was that principal component analysis and cluster analysis both reveal that certain species are clustered with others that share ecological traits, rather than with more closely related species from the same order. This suggests that ecological factors do play a role in defining patterns of brain organisation and there is some evidence for 'cerebrotypes' in batoids, sharks and holocephalans. Interestingly, this analysis was extended to show that several patterns of brain allometry previously observed in mammals also hold for sharks and related taxa (chondrichthyans) (Yopak et al. 2010). In each clade, the relative size of brain parts, with the notable exception of the olfactory bulbs, is highly predictable from the total brain size. Compared with total brain mass, each part scales with a characteristic slope, which is highest for the telencephalon and cerebellum. The significance of this observed pattern of brain scaling in both sharks and mammals is the implication that the fundamental brain plan that evolved in early vertebrates carried with it the propensity to permit changes in telencephalon and cerebellum size through simple changes in development times.

### **Lateral line**

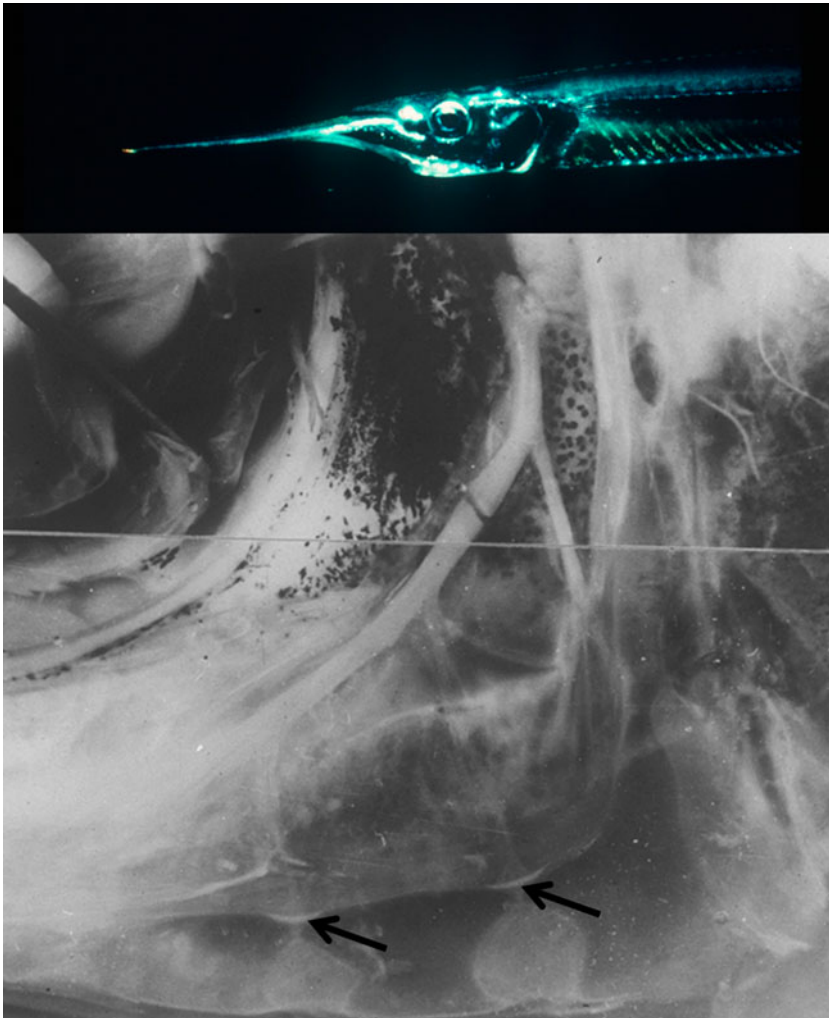
The second of the octavolateralis sensory systems for consideration is the lateral line system. There has been an extensive body of work done at the Leigh Marine Laboratory on lateral line function, particularly in the areas of prey search under low light conditions, and the use of the lateral line in primary orientation. This body of work also has strong links to studies on



New Zealand freshwater fishes many of which are nocturnal, and to species that live in other low light environments such as the deep-sea, Antarctica or caves.

The first foray into lateral line research was a serendipitous encounter with large numbers of piper (*Hyporhamphus ihi*) at the Ti Point wharf during a nocturnal field trip to collect parore (*Girella tricuspidata*). On return to the laboratory, the gut contents were analysed out

of interest and found to be nocturnal zooplankton. Inspection of the lateral line also showed that this extended down the length of the beak, albeit hidden by a retractable membrane (Fig. 4). The hypothesis arising from these observations was that piper were nocturnal planktivores, but were feeding using the lateral line rather than visually. Testing of this hypothesis became the subject of an MSc thesis, and a detailed description of the piper, its behaviour



**Figure 4** Anterior lateral line of the piper. Night photograph of a piper in the field (Leigh slide collection). Dissection of the preopercular/mandibular canal neuromasts (arrows) occur opposite constrictions in the canal (from Montgomery & Saunders 1985).

and sensory system showed that the elongate body form, swimming behaviour and lack of a specialised visual system were all consistent with this hypothesis (Montgomery & Saunders 1985).

Further field and laboratory behaviour provided additional evidence for the lateral line feeding hypothesis (Saunders & Montgomery 1985). Although piper school in large groups close to the water surface during daylight hours, at night the schools break up and individual fish can be observed swimming slowly through the water. Additional gut content analysis showed that during the day piper feed primarily on copepods and terrestrial insects trapped on the water surface; however, after dark the demersal zooplankton that enter the water column form the major dietary component. Prey selectivity was evident in that certain groups present in the plankton are not found in the stomach contents of piper, and that the size of prey taken is biased towards the larger size classes of plankton. Laboratory experiments established that piper are capable of locating prey in total darkness, and that under these conditions live prey are consumed in a higher proportion and much more quickly than dead prey. In addition, it was found that unlike visual nocturnal planktivores (MacDiarmid 1981), piper were able to feed on moon-less or overcast nights.

Further evidence for the importance of the lateral line in plankton feeding followed in Antarctic fishes. The cryopelagic *Pagothenia borchgrevinki* is the dominant planktivore in McMurdo Sound (Foster et al. 1987). Electrophysiological study of their lateral line showed that the receptors were arguably tuned to the vibration produced by their planktonic prey (Montgomery & Macdonald 1987). This line of enquiry on the role of the lateral line in the sensory ecology and evolution of Antarctic fishes continued with a joint NZ/US programme. The focus of this programme was to detail the form and function of the lateral line across the species radiation of Notothenioid fishes (Coombs & Montgomery 1992, 1994; Montgomery & Coombs 1992; Montgomery et

al. 1994). This programme culminated with the view that rather than demonstrating adaptive radiation across this group, the observation that function was essentially conserved despite considerable morphological diversity was a demonstration of disaptation and recovery in the evolution of Antarctic fish (Montgomery & Clements 2000). The idea is simply that morphological diversity in this sensory system is driven by adaptive changes to other systems (e.g. pedomorphic change to gain neutral buoyancy for the secondarily pelagic species), and that subsequent adaptive changes are required to recover original lateral line function.

Work at Leigh on the use of the lateral line in prey detection continued with a number of studies on rays (Montgomery & Skipworth 1997); dwarf scorpionfish (*Scorpaena papillosa*) (Montgomery & Hamilton 1997; Bassett et al. 2007); stargazers (*Leptoscopus macropygus* and *Genyagnus monopterygius*) (Montgomery & Coombs 1998); blue cod (*Paraperis colias*) (Carton & Montgomery 2004); triplefins (*Forsterygion* spp.) (Wellenreuther et al. 2010) and southern bastard cod (Bassett & Montgomery 2011a). Collectively these studies show that a lateral line contribution to feeding is particularly important in nocturnal fishes, and that hydrodynamic considerations are important in understanding behavioural, morphological and functional contributions to detecting biologically important signals over the top of environmental and self-generated noise (Montgomery et al. 2009). For example, behavioural and field studies with the dwarf scorpionfish show that they feed at night, and can orient and attack crabs in complete darkness using the lateral line to detect the respiratory flow fields of their prey. Laboratory behavioural experiments on this species were the first to study search strategy in a lateral line predator. They showed that they use a saltatory search strategy, stopping to detect prey with the lateral line, and then moving to the edge of the receptive field before stopping again. In addition to self-generated noise produced by swimming, electrophysiological studies on this same species have shown that breathing movements represent a significant source of self-generated

noise for the lateral line (Montgomery et al. 1996). As in the electrosensory system described above, this self-generated interference is removed in the first processing stage in the brain.

The second strand of lateral line work originating from the Leigh Marine Laboratory has been the use of the lateral line in primary orientation and swimming. Fish show strong orientation to water currents, an orientation behaviour known as rheotaxis (Fig. 1). It seems intuitively obvious that a flow sensing system such as the lateral line might play a role in rheotaxis, but prior to this work, the accepted view was that rheotaxis was mediated by visual and tactile cues. Using a simple flume it was shown that pharmacological block of the entire lateral-line system substantially increased the velocity threshold for rheotactic behaviour (Montgomery et al. 1997). The same effect was observed when only superficial neuromasts were ablated. These results provided a direct demonstration that rheotaxis can be mediated by the lateral line, and indeed by one specific receptor class of this system, the superficial neuromasts. This rather simple demonstration has had significant implications for areas as diverse as larval orientation and recruitment (Kingsford et al. 2002); olfactory search behaviour (Carton & Montgomery 2003); and the mechanics and control of fish swimming (Colgate & Lynch 2004). The discovery is also finding utility in the control of fish behaviour around turbine intakes (Schilt 2007) and even in drug discovery targeting toxicity and protection of hair cell receptors (Coffin et al. 2009).

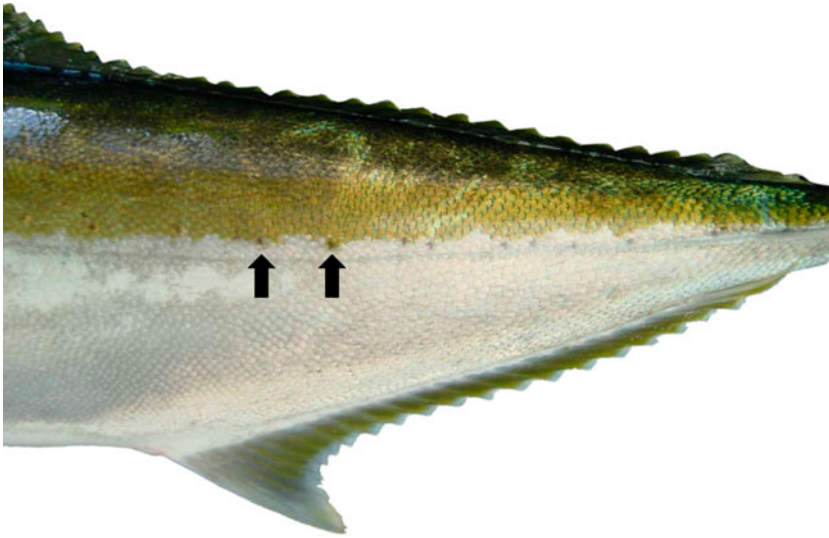
The ability of the lateral line system to monitor flow over the surface of the fish has for a long time given rise to speculation about the possible use of the lateral line for swimming efficiency (e.g. Schilt 2007). However, despite a number of attempts, biological evidence for a direct contribution of the lateral line to swimming efficiency has been elusive. Recently, a new approach to this question was taken at Leigh using a fast swimming species, the kingfish and an exercise flume designed and built in-house. The flume allowed measurement of metabolic

rate as an indicator of swimming efficiency. The swimming performance of kingfish was evaluated after unilateral disruption of trunk superficial neuromasts (Fig. 5) and showed significant impairment of swimming performance and efficiency of fish with sensory disruption (Yanase et al. 2012). These data provide the first direct evidence that an intact lateral line is important to the swimming performance and efficiency of carangiform swimmers, but the functional mechanism of this effect remains to be determined.

### Hearing

The third and final octavolateralis sensory system considered here is the sense of hearing. This review of the contribution of neuroethological research at the Leigh Marine Laboratory over the last 50 years concludes with hearing, as this is a relatively new research area for the Laboratory. Moreover, it is an area that has expanded rapidly, with over 20 publications originating from Leigh (or Leigh staff) in the last decade or so, including several reviews (Montgomery et al. 2001, 2006). The first publication from the Laboratory in this area was in 2000 (Tolimieri et al. 2000), and provided behavioural evidence for the orientation of larval fish to replayed reef sound. In effect, this publication was a significant contribution to the conceptual shift occurring at this time: marine larvae are not simply passive particles, but that their directed activity contributes to their distribution at the end of the pelagic larval stage. Swimming capability is clearly a significant determinant of the extent to which larval fish and other taxa can actively modify their dispersal distribution. Dudley et al. (2000) showed that late larval stage fish of some local species could swim surprisingly well. The best species studied (sweep *Scorpiis lineolata*), swam longer than the others, managing about 400 h on average, which equates to about 200 km, with one individual swimming for 559 h (271 km).

The pertinent idea of the conceptual shift is that late larval stage fish use the detection of ambient reef noise to orient to, and swim towards,

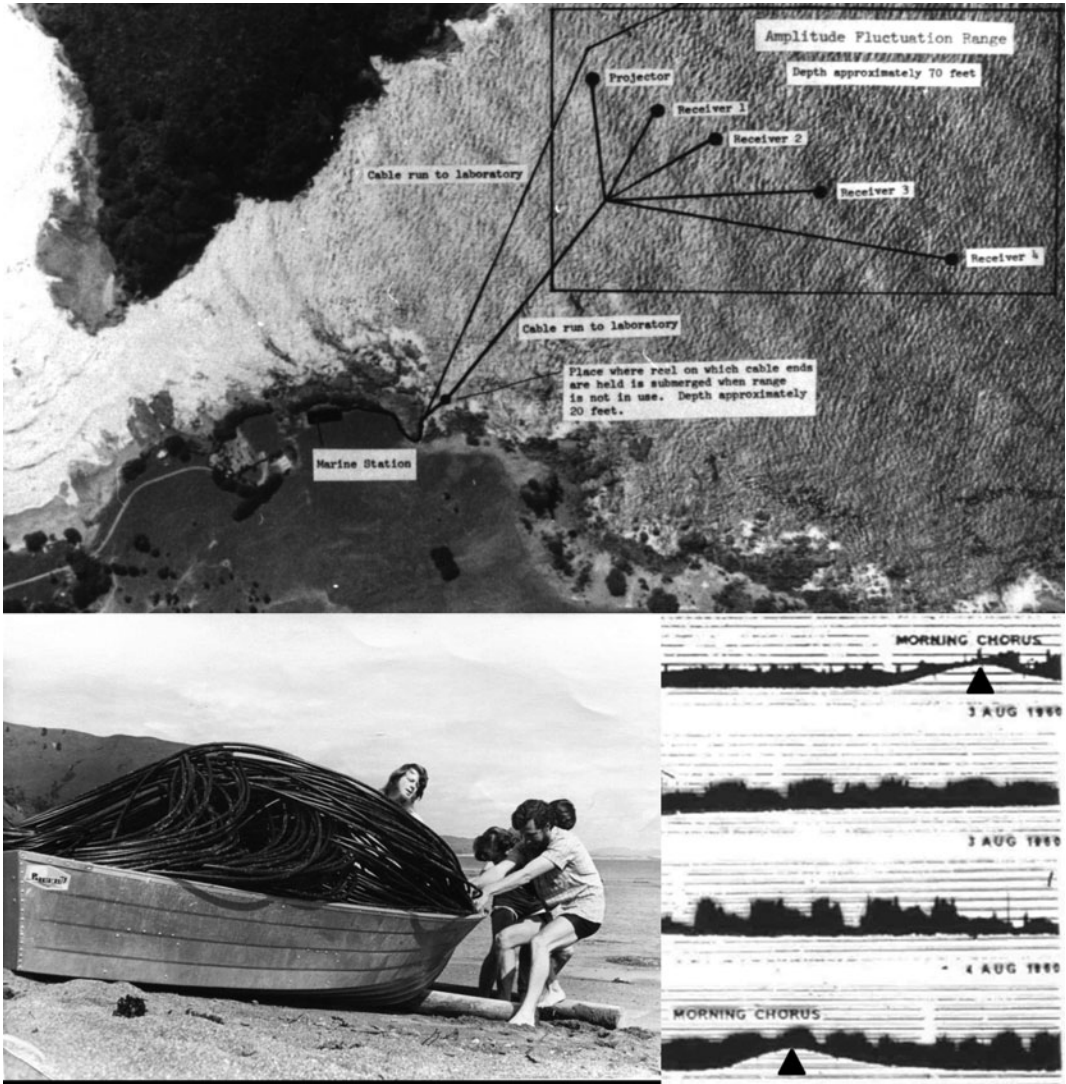


**Figure 5** Posterior trunk of the kingfish showing the lateral line canal and associated free-standing neuromasts (pigmented dots above the canal). Ablation of the free-standing neuromasts decreases swimming efficiency in this species (Yanase et al. 2012).

suitable habitat in a way that can significantly influence their settlement distribution. The early evidence supporting this idea showed that in the local Leigh area (Tolimieri et al. 2000) and on the Barrier Reef (Tolimieri et al. 2004; Simpson et al. 2005) light trap catches, and recruitment to artificial reefs was enhanced by replayed reef noise. For this effect to be accepted as biologically significant further evidence for this idea had to include characterisation of the sound sources on a reef, how that sound is propagated in the coastal area, and auditory capabilities and phonotactic (=sound orientation) responses of the pre-settlement larvae themselves. In other words, to meet the ‘test’ of ‘biological significance’ the argument has to be that reef sound within the hearing capability of the larval fish occurs far enough off-shore, and the larvae themselves-respond to it in the appropriate way as to beneficially influence their settlement. The components of this argument can then be broken down into specific research questions. What are the origins and properties of reef sound? What are the characteristics of sound propagation in the near-shore area that allow prediction of sound characteristics

at a given distance from the reef? What are the hearing capabilities of late stage larval fish? Do larvae show an appropriate phonotaxis? Each of these questions has been addressed in subsequent studies summarised below. It is relevant here to reinforce the claim made in the introduction that marine laboratories such as Leigh, with their emphasis on field access and field studies, provide excellent opportunities for developing the understanding of natural behaviour on which neuroethology is based. This claim is particularly true in the area of marine acoustics and hearing. The physics of underwater sound make it difficult, if not impossible, to address some of these research questions in tanks, or in the laboratory, so field experiments become essential. In cases where electrophysiology is required experiments can’t be undertaken in the field, meaning that the complexities of sound stimuli in tanks, and the interpretation of the results back to field relevance, are topics of hot discussion.

Characterisation of reef sound in the Leigh area has turned up some interesting results, some of which reference back to the very early days of the Leigh Laboratory and the activities and



**Figure 6** Aerial view of Goat Island and the acoustic array, cable for the array being launched from Goat Island Beach, and first acoustic records of the morning chorus (indicated by the black triangles).

interests of the Physics Department at that time. An extensive acoustic array was established early in the Laboratory history to characterise sound propagation characteristics of interest to the Navy and seismic survey methods (Fig. 6). One of the incidental findings was systematic increases in ambient sound which were dubbed the evening and morning chorus and attributed

to urchin activity (Tait 1964; Castle 1974). This finding was confirmed in a recent systematic study of ambient noise associated with the temperate reefs in the Leigh area. Ambient sound levels vary, not only diurnally, but also by month and season. They were highest during the new summer moon and the lowest during the full moon in winter. Bandpass filtering (700–2000 Hz and

2–15 kHz), combined with counts of the snaps produced by shrimps, and data from other studies showed, that the majority of the sound intensity increases could be attributed to two organisms: the sea urchin (*Evechinus chloroticus*) and the snapping shrimp (*Alpheus novaezealandiae*) (Radford et al. 2008a). Laboratory recordings were also used to confirm that the contribution of urchins was due to their ovoid calcareous skeleton, or ‘test’, acting as a Helmholtz resonator (Radford et al. 2008b). Given that the distribution of urchin and shrimps is habitat dependent, it is perhaps not surprising that the nature of the ambient sound also varies spatially (Radford et al. 2010).

Having established the essential characteristics of the reef sound (intensity, spectral composition, temporal and spatial variation) the question then becomes how well does this sound carry out into the pelagic zone where the larval fish are? One of the critiques of the likely potential for reef sound to be biologically meaningful was based on a propagation model of a point-source and spherical or cylindrical spreading (Mann et al. 2007). The restricted effective distance of reef sound predicted using this model did not take account of the distributed nature of the reef source. Radford et al. (2011) used field measurements and modelling to show that the spatially extended sound source of a reef creates a surrounding zone, which extends for a distance offshore equal to the length of the reef, within which there is almost no loss in the sound level. Beyond this zone, the sound level decreases with cylindrical spreading plus any seafloor attenuation. The importance of this ‘reef effect’ is that the sound from a reef would be detectable at a much greater distance from the reef than would be estimated from a spot measurement near the reef or by theoretical models of sound spreading from a point source.

Characterisation of the sensory stimulus available for larval fish to detect and orient to a reef is essential, but estimates of the possible effective range of reef sound also depend on reliable estimates of the hearing capabilities of pre-settlement larvae, and ultimately only field behaviour can tell us that these larvae respond to

that stimulus with appropriate orientation behaviour. Estimates of hearing threshold are obtained by physiological or behavioural means. As indicated above, both of these means are subject to the complexities of defining the physical stimulus in tanks. In addition, fish hearing is complicated by the fact that many fish are thought to only be capable of responding to the particle motion component of underwater sound, whereas others have specialised structures to enable them to detect the acoustic pressure. Add to this the paucity of data on late stage larval fishes, as opposed to adults, and it is clear that there is still much to do to adequately define appropriate hearing thresholds and hence determine the acoustic range of the reefs. Development of an auditory evoked potential (AEP) capability at the Leigh Laboratory, and a novel particle motion stimulus method are recent steps towards addressing the issues above (Radford et al. 2012a). This same AEP technique has been used to begin to characterise the development of hearing over the larval life history period, initially using hāpuku (*Polyprion oxygeneios*), a species with an extended larval duration (Caiger et al. 2013). It has also been used to show that background noise can detrimentally affect hearing thresholds (Caiger et al. 2012), so care needs to be taken to provide appropriate conditions for housing fish for later experimental evaluation of hearing thresholds.

The discussion so far focuses on settlement orientation of larval fishes; however, there were indications early on in this work that there may be a similar story for reef invertebrates (Jeffs et al. 2003). The results for invertebrates took an interesting turn when it was discovered that sound may not be just an orientation cue, but directly trigger or accelerate metamorphosis in crab larvae (Stanley et al. 2010). The response occurs at biologically realistic sound levels (Stanley et al. 2011) and to sounds appropriate to preferred habitat (Stanley et al. 2012). Overall, these results indicate that sounds emanating from specific underwater habitats may play a significant role in determining spatial patterns of recruitment in coastal crab species.

**Concluding remarks**

Fifty years is not a bad pedigree for a marine laboratory, given that the oldest established marine laboratories internationally (Naples, Woods Hole and Plymouth) are only a little over twice that age. The term 'neuroethology' is more recent, effectively dating from the formation of the International Society for Neuroethology in 1986. However, despite not being called neuroethology, this activity has been an important line of work at many marine laboratories, including the oldest laboratories named above. Perhaps the standout examples are early work on the neuronal structure of the brain at Naples, and the squid axon work at Plymouth and Woods Hole. In many respects, this early marine neuroscience takes advantage of the diversity of marine animals to make fundamental discoveries on the structure and function of the nervous system with direct application to medical science. Some of the work reviewed in this paper, in particular the structure and function of the cerebellum-like DON in sharks, or hair-cell based rheotaxis, may have potential medical application. However, the main context of these studies is comparative neuroethology. The studies reviewed above contribute to a better understanding the diversity and evolution of sensory systems and the vertebrate brain. However, the field behaviour impetus of neuroethology also means that these studies are of direct relevance to ecology. Predator/prey interactions, reproductive communication, dispersal, settlement and migration are all vital biological activities with a strong neuroethology interface. At the more applied level, fish neuroethology will likely prove to be important in a very wide range of endeavour, including: optimising hatchery methods; population recovery through migratory pheromone manipulation for galaxid species; mitigating obstacles to migration; possible control of settlement and biofouling; and setting noise standards for marine environment. Neuroethology studies at the Leigh Marine Laboratory have made a small, but significant, contribution to the

enormous progress that has been made in the last 50 years. The connection of the Laboratory to surrounding ecosystems, and the diversity of local species, provides an essential platform for a continuing contribution to this progress.

**References**

- Baker CF, Montgomery JC 2001a. Species-specific attraction of migratory banded kokopu juveniles to adult pheromones. *Journal of Fish Biology* 58: 1221–1229.
- Baker CF, Montgomery JC 2001b. Sensory deficits induced by cadmium in banded kokopu (*Galaxias fasciatus*) juveniles. *Environmental Biology of Fishes* 62: 455–464.
- Baker CF, Montgomery JC, Dennis TE 2002. The sensory basis of olfactory search behaviour in the banded kokopu (*Galaxias fasciatus*). *Journal of Comparative Physiology* 188A: 553–560.
- Baker CF, Carton AG, Fine JM, Sorensen PW 2006. Can bile acids function as a migratory pheromone in banded kokopu, *Galaxias fasciatus* (Gray)? *Ecology of Freshwater Fish* 15: 275–283.
- Bassett DK, Montgomery JC 2011a. The feeding response of *Pseudophycas barbata* to multisensory prey cues in a low light environment. *Journal of Fish Biology* 79: 526–532.
- Bassett DK, Montgomery JC 2011b. Investigating nocturnal fish populations in situ using baited underwater video: with special reference to their olfactory capabilities. *Journal of Experimental Marine Biology and Ecology* 409: 194–199.
- Bassett D, Carton AG, Montgomery JC 2007. Saltatory search in a lateral line predator. *Journal of Fish Biology* 70: 1148–1160.
- Bodznick D, Montgomery JC 1992. Suppression of ventilatory refferance in the elasmobranch electrosensory system: medullary neuron receptive fields support a common mode rejection mechanism. *Journal of Experimental Biology* 171: 127–137.
- Bodznick D, Montgomery JC, Carey M 1999. Adaptive mechanisms in the elasmobranch hindbrain. *Journal of Experimental Biology* 202: 1357–1364.
- Caiger PE, Montgomery JC, Bruce M, Lu J, Radford CA 2013. A proposed mechanism for the observed ontogenetic improvement in the hearing ability of hapuka (*Polypriion oxygeneios*). *Journal of Comparative Physiology A*: Apr 25. [Epub ahead of print].
- Caiger PE, Montgomery JC, Radford CA 2012. Chronic low-intensity noise exposure affects the hearing thresholds of juvenile snapper. *Marine Ecology Progress Series* 466: 225–232.

- Carton AG 2005. The impact of light intensity and algal-induced turbidity on first-feeding *Seriola lalandi* larvae. *Aquaculture Research* 36: 1588–1594.
- Carton AG, Montgomery JC 2003. Evidence of rheotactic component in the odour search behaviour of freshwater eels. *Journal of Fish Biology* 62: 501–516.
- Carton AG, Montgomery JC 2004. A comparison of lateral line morphology of blue cod and torrent-fish: two sandperches of the family Pinguipedidae. *Environmental Biology of Fishes*. 70: 123–131.
- Castle MJ 1974. A study of ambient sea noise. PhD thesis, University of Auckland.
- Coffin AB, Reinhart KE, Owens KN, Raible DW, Rubel EW 2009. Extracellular divalent cations modulate aminoglycoside-induced hair cell death in the zebrafish lateral line. *Hearing Research* 253: 42–51.
- Colgate JE, Lynch KM 2004. Mechanics and control of swimming: A review. *IEEE Journal of Oceanic Engineering*, 29: 660–673.
- Coombs S, Montgomery JC 1992. Fibers innervating different parts of the lateral line system of the Antarctic notothenioid, *Trematomus bernacchii*, have similar neural responses, despite large variation in the peripheral morphology. *Brain Behaviour and Evolution* 40: 217–233.
- Coombs S, Montgomery JC 1994. Structure and function of superficial neuromasts in the Antarctic fish, *Trematomus bernacchii*. *Brain, Behaviour and Evolution* 44: 287–298.
- Dudley B, Tolimieri N, Montgomery JC 2000. Swimming ability of late-stage fish larvae from New Zealand Waters. *Marine and Freshwater Research* 51: 783–7.
- Foster BA, Cargill JM, Montgomery JC 1987. Planktivory in *Pagothenia borchgrevinki* (Nototheniidae) in McMurdo Sound Antarctica. *Polar Biology* 8: 49–54.
- Howard S 2011. Elasmobranch electrosensory biology and bycatch reduction. MSc Thesis. Auckland, University of Auckland.
- Jeffs A, Tolimieri N, Montgomery JC 2003. Crabs on cue for the coast; the use of underwater sound for orientation by pelagic crab stages. *Marine and Freshwater Research* 54: 841–845.
- Kingsford MJ, Leis JM, Shanks A, Lindeman KC, Morgan SG, Pineda J 2002. Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science* 70(Supplement 1): 309–340.
- Langdon C 2003. Microparticle types for delivering nutrients to marine fish larvae. *Aquaculture* 227: 259–275.
- Li WM, Sorensen PW, Gallaher DD 1995. The olfactory system of migratory adult sea lamprey (*Petromyzon marinus*) is specifically and acutely sensitive to unique bile-acids released by conspecific larvae. *Journal of General Physiology* 105: 569–587.
- Lisney TJ, Yopak K E, Montgomery JC, Collin SP 2008. Variation in brain organization and cerebellar foliation in chondrichthyans: batoids. *Brain Behavior and Evolution* 72: 262–282.
- McCormick, MI 1993. Development and changes at settlement in the barbel structure of the reef fish, *Upeneus tragula* (mullidae). *Environmental Biology of Fishes* 37: 269–282.
- MacDiarmid AB 1981. Factors influencing the distribution and abundance of two temperate planktivorous reef fish *Pempheris adspersa* and *Scorpius violaceus*. MSc thesis, University of Auckland, New Zealand.
- Mann DA, Casper BM, Boyle KS, Tricas TC 2007. On the attraction of larval fishes to reef sound. *Marine Ecology Progress Series* 338: 307–310.
- Montgomery JC, Bodznick D 1994. An adaptive filter cancels self-induced noise in the electrosensory and lateral line mechanosensory systems of fish. *Neuroscience Letters* 174: 145–148.
- Montgomery JC, Bodznick D 1999. Signals and noise in the elasmobranch electrosensory system. *Journal of Experimental Biology* 202: 1349–1355.
- Montgomery JC, Bodznick D 2010. Functional origins of the vertebrate cerebellum from a sensory processing antecedent. *Current Zoology* 56: 277–284.
- Montgomery JC, Clements K 2000. Disaptation and recovery in the evolution of Antarctic fish. *Trends in Ecology and Evolution* 15: 267–271.
- Montgomery JC, Coombs S 1992. Physiological characterization of lateral line function in the Antarctic fish, *Trematomus bernacchii*. *Brain Behaviour and Evolution* 40: 209–216.
- Montgomery JC, Coombs S 1998. Peripheral encoding of moving sources by the lateral line system of a sit-and-wait predator. *Journal of Experimental Biology* 201: 91–102.
- Montgomery JC, Hamilton AR 1997. The sensory biology of prey capture in the dwarf scorpion fish (*Scorpaena papillosus*). *Marine and Freshwater Behaviour and Physiology* 30: 209–223.
- Montgomery JC, Macdonald JA 1987. Sensory tuning of lateral line receptors in antarctic fish to the movements of planktonic prey. *Science* 235: 195–196.
- Montgomery JC, Saunders AJ 1985. Functional morphology of the piper *Hyporhamphus ihi* with reference to the role of the lateral line in feeding. *Proceedings of the Royal Society of London B* 224: 197–208.



- Montgomery JC, Skipworth E 1997. Detection of weak water jets by the short-tailed stingray *Dasyatis brevicaudatus* (Pisces: dasyatidae). *Copeia* 1997: 881–883.
- Montgomery JC, Sutherland KBW 1997. Sensory development of the Antarctic silverfish *Pleurogramma antarcticum*: a test for the ontogenetic shift hypothesis. *Polar Biology* 18: 112–115.
- Montgomery JC, Walker M 2001. Orientation and navigation in elasmobranchs: which way forward? *Environmental Biology of Fishes* 60: 109–116.
- Montgomery JC, Pankhurst NW, Foster BA 1989. Limitations on visual feeding in the planktivorous antarctic fish *Pagothenia borchgrevinki*. *Experientia* 45: 395–397.
- Montgomery JC, Coombs S, Janssen J 1994. Form and function relationships in lateral-line systems—comparative data from 6 species of Antarctic notothenioid fish. *Brain, Behaviour and Evolution* 44: 299–306.
- Montgomery JC, Bodznick D, Halstead MBD 1996. Hindbrain signal processing in the lateral line system of the dwarf scorpionfish, *Scorpeana papillosus*. *Journal of Experimental Biology* 199: 893–899.
- Montgomery JC, Baker CF, Carton AG 1997. The lateral line can mediate rheotaxis in fish. *Nature* 389: 960–963.
- Montgomery JC, Tolimieri N, Haine O 2001. Active habitat selection by pre-settlement reef fishes. *Fish and Fisheries* 2: 261–277.
- Montgomery JC, Jeffs A, Simpson SD, Meekan M, Tindle C 2006. Sound as an orientation cue for the pelagic larvae of reef fish and decapod crustaceans. *Advances in Marine Biology* 51: 143–196.
- Montgomery JC, Windsor SP, Bassett DK. 2009. The behavior and physiology of mechanoreception: separating signal and noise. *Integrative Zoology* 4: 3–12.
- Montgomery JC, Bodznick D, Yopak KE 2012. The cerebellum and cerebellum-like structures of cartilaginous fishes. *Brain Behavior and Evolution* 80: 152–165.
- Pankhurst NW 1992. Ocular morphology of the sweep *Scorpius lineolatus* and the spotty *Notolabrus celidotus* (Pisces: Teleostei) grown in low intensity light. *Brain Behavior and Evolution* 39: 116–123.
- Pankhurst PM 1994. Age-related-changes in the visual-acuity of larvae of New Zealand snapper, *Pagrus auratus*. *Journal of the Marine Biological Association of the United Kingdom* 74: 337–349.
- Pankhurst NW, Montgomery JC 1989. Visual function in four Antarctic nototheniid fishes. *J Exp Biol* 142: 311–324.
- Pankhurst NW, Montgomery JC 1990. Ontogeny of vision in the Antarctic fish *Pagothenia borchgrevinki* (Nototheniidae). *Polar Biology* 10: 419–422.
- Pankhurst NW, Montgomery JC 1994. Uncoupling of visual and somatic growth in the rainbow-trout *Oncorhynchus mykiss*. *Brain Behavior and Evolution* 44: 149–155.
- Pankhurst PM, Pankhurst NW, Montgomery JC 1993. Comparison of behavioral and morphological measures of visual-acuity during ontogeny in a teleost fish, *Forsterygion varium*, Tripterygiidae (Forster, 1801). *Brain Behavior and Evolution* 42: 178–188.
- Radford CA, Jeffs AG, Tindle CT, Montgomery JC 2008a. Temporal patterns in ambient noise of biological origin from a shallow water temperate reef. *Oecologia* 156: 921–929.
- Radford C, Jeffs A, Tindle C, Montgomery JC 2008b. Resonating sea urchin skeletons create coastal choruses. *Marine Ecology Progress Series* 362: 37–43.
- Radford CA, Stanley JA, Tindle CT, Montgomery JC, Jeffs AG 2010. Localised coastal habitats have distinct underwater sound signatures. *Marine Ecology Progress Series* 401: 21–29.
- Radford CA, Tindle CT, Montgomery JC, Jeffs AG 2011. Modelling a reef as an extended sound source increases the predicted range at which reef noise may be heard by fish larvae. *Marine Ecology Progress Series* 438: 167–174.
- Radford CA, Montgomery JC, Caiger P, Higgs DM 2012a. Pressure and particle motion detection thresholds in fish: a re-examination of salient auditory cues in teleosts. *Journal of Experimental Biology* 215: 3429–3435.
- Radford CA, Sim-Smith CJ, Jeffs AG 2012b. Can larval snapper, *Pagrus auratus*, smell their new home? *Marine and Freshwater Research* 63: 898–904.
- Saunders AJ, Montgomery JC 1985. Field and laboratory studies of the feeding behaviour of the piper *Hyporhamphus ihi* with reference to the role of the lateral line in feeding. *Proceedings of the Royal Society London B* 224: 209–221.
- Simpson SD, Meekan M, Montgomery JC, McCauley R, Jeffs A 2005. Homeward sound. *Science* 308: 221.
- Schilt CR 2007. Developing fish passage and protection at hydropower dams. *Applied Animal Behaviour Science* 104: 295–325.
- Stanley J, Radford C, Jeffs A 2010. Induction of settlement in crab megalopae by ambient under-

- water reef sound. *Behavioural Ecology* 21: 113–120.
- Stanley JA, Radford CA, Jeffs AG 2011. Behavioural response thresholds in New Zealand crab megalopae to ambient underwater sound. *PLoS ONE* 6(12): e28572.
- Stanley JA, Radford CA, Jeffs AG 2012. Location, location, location—finding a suitable home in amongst the noise. *Proceedings of the Royal Society B—Biological Sciences* 279: 3622–3621.
- Tait RI 1964. The evening chorus: a biological noise investigation. NRL Report, Naval Research Laboratory, HMNZ Dockyard, Auckland.
- Tolimieri N, Haine O, Jeffs A, Mccauley R, Montgomery JC 2004. Directional orientation of pomacentrid larvae to ambient reef sound. *Coral Reefs* 23: 184–191.
- Tolimieri N, Jeffs A, Montgomery JC (2000). Ambient sound as a cue for navigation: reef fish larvae are attracted to reef sound in the field. *Marine Ecology Progress Series* 207: 219–224.
- Wellenreuther M, Michelle Brock M, Montgomery JC, Clements KD 2010. Comparative morphology of the mechanosensory lateral line system in a clade of New Zealand triplefin fishes. *Brain Behavior and Evolution* 75: 292–308.
- Yanase K, Herbert NA, Montgomery JC 2012. Disrupted flow sensing impairs hydrodynamic performance and increases the metabolic cost of swimming in the yellowtail kingfish, *Seriola lalandi*. *Journal of Experimental Biology* 215: 3944–3954.
- Yopak KE, Montgomery JC 2008. Brain organization and specialization in deep-sea chondrichthyans. *Brain Behavior and Evolution* 71: 287–304.
- Yopak KE, Lisney TJ, Collin SP, Montgomery JC 2007. Variation in brain organization and cerebellar foliation in chondrichthyans: sharks and holocephalans. *Brain Behavior and Evolution* 69: 280–300.
- Yopak KE, Lisney TJ, Darlington RB, Collin SP, Montgomery JC, Finlay BL 2010. A conserved pattern of brain scaling from sharks to primates. *Proceedings of the National Academy of Science* 107: 12946–12951.
- Zeldis JR, Oldman J, Ballara SL, Richards LA 2005. Physical fluxes, pelagic ecosystem structure, and larval fish survival in Hauraki Gulf, New Zealand. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 593–610.