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Sub-Antarctic and High Antarctic Notothenioid Fishes: Ecology and Adaptational Biology Revealed by the ICEFISH 2004 Cruise of RVIB *Nathaniel B. Palmer*

BY H. WILLIAM DETRICH III, BRADLEY A. BUCKLEY, DANIEL F. DOOLITTLE, CHRISTOPHER D. JONES, AND SUSANNE J. LOCKHART

ABSTRACT. The goal of the ICEFISH 2004 cruise, which was conducted on board RVIB *Nathaniel B. Palmer* and traversed the transitional zones linking the South Atlantic to the Southern Ocean, was to compare the evolution, ecology, adaptational biology, community structure, and population dynamics of Antarctic notothenioid fishes relative to the cool/temperate notothenioids of the sub-Antarctic. To place this work in a comprehensive ecological context, cruise participants surveyed the benthos and geology of the biogeographic provinces and island shelves on either side of the Antarctic Polar Front (or Antarctic Convergence). Genome-enabled comparison of the responses of cold-living and temperate notothenioids to heat stress confirmed the sensitivity of the former to a warming Southern Ocean. Successful implementation of the international and interdisciplinary ICEFISH research cruise provides a model for future exploration of the sub-Antarctic sectors of the Indian and Pacific Oceans.

INTRODUCTION

On May 17, 2004, the Research Vessel Ice-breaker *Nathaniel B. Palmer* set sail from Punta Arenas, Chile, to conduct the ICEFISH cruise (the acronym stands for International Collaborative Expedition to collect and study Fish Indigenous to Sub-antarctic Habitats).

Much of the cruise area, particularly those regions inside the Antarctic Polar Front (APF; Figure 1), are inadequately sampled for fish and benthos because they are remote and trawling is difficult (Arntz et al., 2005). ICEFISH provided our international, multidisciplinary team the rare opportunity to compare

high- and sub-Antarctic notothenioid fishes as we transitioned between these distinct oceanographic regimes.

The ICEFISH cruise generated large-spatial-scale benthic and geologic data sets that enhance our understanding of the biogeographic provinces and island shelf areas of the regions surveyed. The ICEFISH cruise track (Figure 1) shows the range of water masses and frontal regions sampled. The Burdwood Banks, the Falkland Islands/Islas Malvinas, and Tristan da Cunha are outside the APF, whereas the other islands are within this front.

Tristan da Cunha was included in the cruise profile because the warmest living notothenioid known, the Tristan klipfish, *Bovichtus diacanthus* (10–27°C), resides in its waters. Sampling of *B. diacanthus* enabled us to compare the genetically encoded responses of cold-living and temperate notothenioids to acute heat stress. This assessment rises to a practical urgency because oceanic warming associated with climate change will threaten the habitat range of the cold-adapted notothenioids, in turn perturbing the ecology of the South Atlantic and Southern Oceans.

RESULTS AND DISCUSSION

Fish Observations on Burdwood Banks and around the Falkland Islands/Islas Malvinas

North of the APF near South America, we caught the sub-Antarctic notothenioids *Patagonotothen elegans*, *P. guntheri*, *P. ramsayi*, *Cottoperca gobio*, and *Dissostichus eleginoides* on the Burdwood Banks. Similar notothenioid species were captured at the Falkland Islands/Islas Malvinas, as well as *P. tessellata* and the Falklands Mullet, *Eleginops maclovinus*.

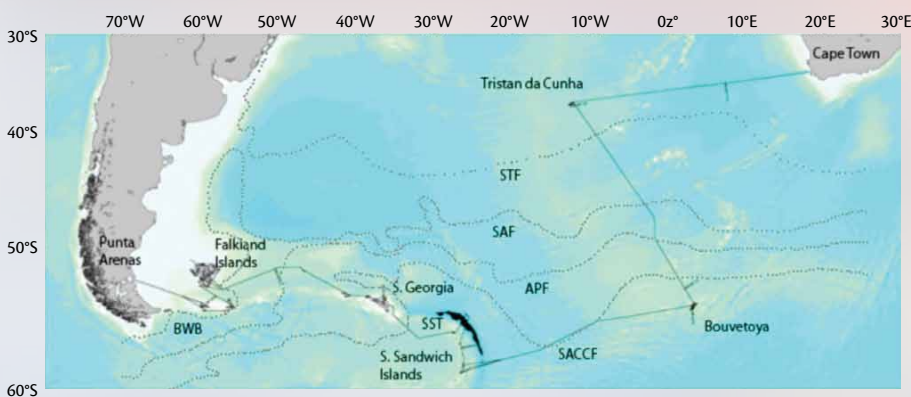


Figure 1. ICEFISH trackline (solid line) in the southern Atlantic Ocean and the Atlantic sector of the Southern Ocean. Historical positions of major oceanographic frontal features are shown with dotted lines: Southern Antarctic Circumpolar Current Front (SACCF), Antarctic Polar Front (APF, or the Antarctic Convergence), Sub-Antarctic Front (SAF), and Sub-Tropical Front (STF). BWB = Burdwood Banks. SST = South Sandwich Trench. Modified from Detrich et al. (2005) and Doolittle et al. (2008)

Two specimens of the remarkable Pike icefish, *Champscephalus esox* (Figure 2) were collected near the Falkland Islands/Islands Malvinas. Icefishes, the most derived notothenioid family, are unique among vertebrates because they fail to make red blood cells and the oxygen transport protein hemoglobin (Ruud, 1954; Near et al., 2006). They rely on oxygen physically dissolved in their “white” blood to support respiratory metabolism. Ruud proposed that the evolutionary loss of red cells and hemoglobin could only occur in the well-aerated and very cold waters of the Southern Ocean (O_2 near saturation, temperature range -1.9°C to $+2^\circ\text{C}$; Ruud, 1954). Yet the Pike icefish, unlike the other 15 species of its family, lives north of the APF, where water temperatures are $\sim 5^\circ\text{C}$ higher. We hypothesize that *C. esox* thrives in the South Atlantic because it evolved circulatory adaptations to its warmer habitat, a proposal that can be tested using genomic technologies.

Fish Observations South of the APF

The total number of finfish specimens recorded within the APF during the ICEFISH cruise trawl deployments was 9,105 specimens of 29 species (see Jones et al., 2008). The benthic composition of 31 hauls (38 metric tons) was analyzed and sorted into 52 taxonomic groups. We collected sediment samples at 22 locations among the island groups to characterize seafloor composition.

Finfish within the APF contained faunal elements from both the low and high Antarctic regions. Since most of the Scotia Arc is situated south of the Convergence (Figure 1) and within the Antarctic Circumpolar Current, it is a center of dispersal for Antarctic and sub-Antarctic marine organisms (Andriashev, 1965; DeWitt, 1971; Arntz et al., 2005).

At Shag Rocks, the dominant finfish species in our trawls was *P. guntheri* (95%), as was true at stations north of the APF; *Champscephalus gunnari* and *Lepidonotothen nudifrons* were also caught. In striking contrast, *L. nudifrons* dominated the catch at nearby South Georgia, and *P. guntheri* was absent. Other species captured at South Georgia were *L. larseni*, *Gobionotothen gibberifrons*, and *Muraenolepis microps*. Benthic browsers and prey for several finfish species, *L. nudifrons* and *G. gibberifrons* provide a direct



Figure 2. RVIB *Nathaniel B. Palmer* at anchor in Cumberland East Bay, South Georgia. The ICEFISH (International Collaborative Expedition to collect and study Fish Indigenous to Sub-antarctic Habitats) cruise was conducted aboard the *Palmer* from May 17 to July 17, 2004. The vessel departed from Punta Arenas, Chile, fished at the Burdwood Banks, Falkland Islands/Islands Malvinas, Shag Rocks/South Georgia, the South Sandwich Islands and Trench, Bouvetøya Island, and Tristan da Cunha, and completed the expedition at Cape Town, South Africa (see Figure 1 for cruise track). Thirty-one scientists from eight nations, including 10 graduate students and undergraduates from six countries, collected fish and invertebrate fauna during the 62-day cruise (visit <http://www.icefish.neu.edu>). The inset sub-Antarctic Pike icefish, *Champscephalus esox* (standard length 26 cm), was caught near the Falkland Islands/Islands Malvinas.

link between the benthic communities and large piscivorous finfish species.

Along the South Sandwich Island (SSI) chain, 14 species of finfish were captured, dominated by *L. larseni*. The composition and diversity of finfish species at the SSIs resembled those at South Georgia, but *L. squamifrons* and *G. marionensis* were caught for the first time. We also captured *Harpagifer spinosus*, the first observance and collection of this species outside the Kerguelen and Crozet Islands (Hureau et al., 1980). One station on the abyssal flank (5,350 m) of the South Sandwich Trench yielded seven specimens of the macrourid *Coryphaenoides flicauda*. This record is likely the first south of the APF in the Atlantic sector of the Southern Ocean, and it extends the known depth range of the species by ~ 300 m (Iwamoto, 1990).

Sampling around Bouvetøya Island yielded 11 species of finfish, which were also dominated by *L. larseni*. Surprisingly, *L. nudifrons* was absent.

These observations document a distinct shift

in the composition and diversity of finfish species from the eastern sectors of the Southern Ocean to Bouvetøya, with a major increase in the catch of rattails and *L. squamifrons* and the disappearance of species of the genus *Gobionotothen* (cf. Gon and Heemstra, 1990).

Benthic Observations South of the APF

Local benthic invertebrate composition was often disproportionately represented by single species of one or a few phyla. The lowest phyletic diversity was recorded at the northernmost station at Shag Rocks. Off the northwest coast of South Georgia, *Sterechinus* echinoids predominated with little competition from other phyla. Further east along the northern coast of South Georgia, sponge communities, particularly volcano glass sponges (likely *Rossella* spp.), dominated the benthic habitats; they were less prominent at deeper, more southerly locations. At the SSIs, invertebrate species transitioned from a sub-Antarctic to an Antarctic faunal assemblage from the northernmost to the southernmost stations

(Lockhart and Jones, 2008). At Bouvetøya, the major phylum at most stations was Echinodermata, but some taxa (e.g., cidaroid urchins common to other Antarctic and sub-Antarctic shelf habitats) were absent. Nevertheless, stations off Bouvetøya's north-eastern coast yielded the greatest diversity of benthic invertebrate phyla, in contrast to the low diversity of fish species.

Seafloor Classification and Chemical Analysis South of the APF

We used acoustic classification of seafloor sediments, coupled to Smith-MacIntyre bottom grabs for ground truthing and chemical analysis, to collect data at spatial and temporal frequencies that realistically portray the ecological functioning of the Antarctic benthos and its associated nekton. Table 1 presents the sediment classifications and chemical analyses. South Georgia deep shelf sediments consisted of ~ 50:50 proportions of mixed sand/gravel and mud, those of the SSIs were dominated by sands and gravels, and sands (42.2%) and sandy silts (14.6%) predominated at Bouvetøya. Organic matter concentrations were lowest for the volcanic sediments of the SSIs. The high abundance of CaCO₃ at Bouvetøya can be attributed to serpulid worm tubes, which were abundant in our trawls; only traces of CaCO₃ were detected at South Georgia and the SSIs.

We infer that primary productivity and benthopelagic coupling are greater at South Georgia and Bouvetøya relative to the SSIs.

Heat-Shock Physiology of Sub- and High Antarctic Fish Species

The heat shock response (HSR) is an evolutionarily conserved cellular reaction to acute heat exposure (see Buckley and Somero, 2009). HSR involves induction of molecular chaperones, termed heat shock proteins (Hsps), which assist refolding of proteins whose conformations have been perturbed by elevated temperature. Proteins that cannot be rescued are subjected to ubiquitin-mediated protein degradation (UPD) by the proteasome. These two processes—protein protection by chaperones and ubiquitin-mediated protein breakdown—work in tandem to maintain protein homeostasis during proteotoxic heat stress.

Our sampling of *Notothenia coriiceps* at Bouvetøya Island and *B. diacanthus* at Tristanda Cunha provided the opportunity to compare the HSRs and UPDs of cold-living and temperate notothenioids. Both fishes evolved from the temperate, most recent common ancestor of the Notothenioidei, but *N. coriiceps* subsequently evolved a cold-adapted physiology whereas *B. diacanthus* retained a temperate physiology (Eastman, 2000).

After subjecting specimens to physiologically

relevant thermal challenges and maintaining others at normal body temperatures (see legend to Figure 3), we analyzed changes in HSR and UPD gene expression in *B. diacanthus* and *N. coriiceps* by hybridizing total gill tissue cDNAs from heat shock and control specimens to a cDNA microarray derived from the goby fish, *Gillichthys mirabilis*. Figure 3 (left panel) shows that mRNAs corresponding to each size class of Hsp cDNA on the array were up-regulated \geq twofold (relative to control values), the threshold for statistical significance, by heat shock in the gill tissue of *B. diacanthus*. Genes involved in the UPD pathway (labeled Ubiquitin) were also induced. In contrast, *N. coriiceps* specimens challenged by heat shock did not induce expression of genes of the HSR or UPD pathways (Figure 3, right panel). Although the sample sizes are small, our data indicate that the temperate notothenioid *B. diacanthus* possesses a robust HSR and UPD, whereas its cold-adapted relative, *N. coriiceps*, has lost these protective capacities. The absence of functional HSR and UPD pathways in this and other high Antarctic notothenioids (Hofmann et al., 2005) undoubtedly makes them sensitive to rising oceanic temperatures and may lead to their local extinction in warming regions of the Southern Ocean.

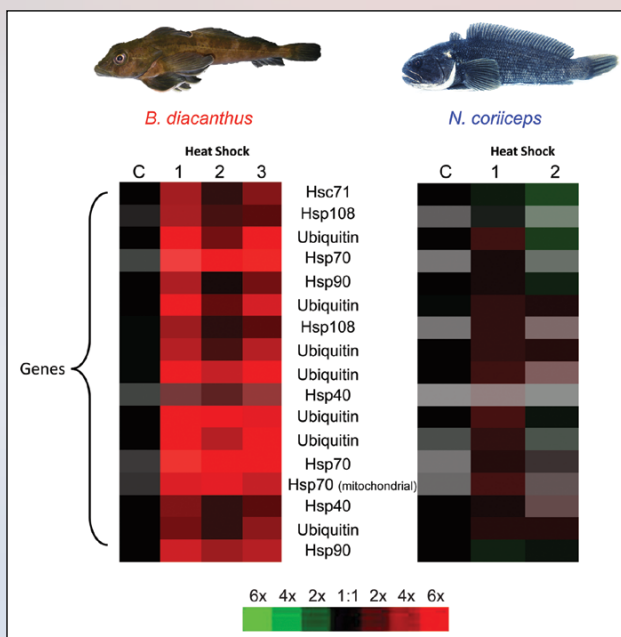


Figure 3. Heat shock response/ubiquitin-mediated protein degradation (HSR/UPD) pathway gene expression profiles in gill tissues from *B. diacanthus* and from *N. coriiceps* measured by microarray analysis. The left and right panels show heat maps of microarrays hybridized to gill cDNAs from control (C) and heat-shocked (1, 2, 3) *B. diacanthus* and from control (C) and heat-shocked (1, 2) *N. coriiceps*, respectively. Red and green denote genes that were induced or repressed relative to control values, respectively, and grey and black indicate genes whose expressions changed minimally or not at all. Color intensity is proportional to fold induction or repression (see scale); values exceeding ± 2 are statistically significant. Images of *B. diacanthus* (standard length ~ 12 cm) and *N. coriiceps* (SL ~ 35 cm) are shown. Methods: *N. coriiceps*, maintained in seawater aquaria at -1°C , were exposed to an increase of 10°C (-1°C to 9°C) over a three-day period. *B. diacanthus*, maintained in seawater aquaria at 16°C , were subjected to a 10°C increase in temperature (16 – 26°C) over a 10-hour interval. Control specimens were maintained at their respective starting temperatures. HSR and UPD gene expression profiles were examined by use of a cDNA microarray derived from *G. mirabilis* (Buckley and Somero, 2009).

Table 1. Seafloor classification and chemical analysis.

Location	Sediment Class (%)				Organic Matter (%)	CaCO ₃ (%)
	Sands	Gravels	Mixed S/G	Mud		
South Georgia	n/a	n/a	46.5	53.5	1.6–3.5	0.0–0.7
S. Sandwiches	59.2	13.3	n/a	27.6	0.3–1.5	0.1–0.7
Bouvetøya	56.8	15.7	n/a	27.4	0.7–3.8	0.1–5.9

n/a = not applicable

CONCLUSIONS/ FUTURE DIRECTIONS

The influence of development, species composition, and abundance of benthic communities, as well as geological composition, and structure of the seafloor on spatial demographics of demersal finfish communities warrants further study (Jones and Lockhart, 2011). Size composition, maturity stage, and dietary patterns for several species of finfish collected during the course of the ICEFISH cruise should be examined and compared to benthic community structure and seabed composition to reveal the relationships of finfish to other components of the Antarctic ecosystem. Finally, oceanic warming, which is pronounced near the Antarctic Peninsula, makes imperative an understanding of the capacity of the notothenioid fishes of the Southern Ocean to resist or adapt to such change.

CRUISE SPECIMEN DATA, METADATA, AND TECHNICAL REPORT

Station records, museum specimen collections, and other cruise information are available on the ICEFISH 2004 cruise website (<http://www.icefish.neu.edu>). Metadata and a cruise technical report are available from the Marine Geoscience Data System (<http://www.marine-geo.org/tools/search/entry.php?id=NBPO404>).

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