– http://www.soc.soton.ac.uk/OTHERS/CSMS
European Geophysical Society (EGS)
– http://www.mpae.gwdg.de/EGS/EGS.html
Global Ocean Ecosystem Dynamics (GLOBEC)
– http://www1.npm.ac.uk/globec
International Association for Meteorology and Atmospheric Sciences (IAMAS) – http://iamas.org
International Association for the Physical Sciences of the Oceans (IAPSO)
– http://www.olympus.net/IAPSO
International Council for the Exploration of the Sea (ICES) – http://www.ices.dk
International Council for Science (ICSU)
– http://www.icsu.org
International Geosphere-Biosphere Program (IGBP)
– http://www.igbp.kva.se
Intergovernmental Oceanographic Commission (IOC) – http://ioc.unesco.org/iocweb
Joint Global Ocean Flux (JGOFS)
– http://ads.smr.uib.no/jgofs/jgofs.htm
Baltic Marine Environment Protection Commission (HELCOM) – http://www.helcom.fi/oldhc.html
North Pacific Marine Science Organization (PICES)
– http://pices.ios.bc.ca
Ocean Drilling Program (ODP)
– http://www-odp.tamu.edu
OSPAR Commission for the Protection of the Marine Environment of the North-East Atlantic
– http://www.ospar.org
Scientific Committee on Antarctic Research (SCAR)
– http://www.scar.org
Scientific Committee on Oceanic Research (SCOR)
– http://www.jhu.edu/ ~ scor
The Oceanography Society (TOS)
- http://tos.org
Tropical Ocean – Global Atmosphere Coupled Ocean/Atmosphere Response Experiment (TOGA)
– http://trmm.gsfc.nasa.gov/trmm_office/field_campaigns/toga_coare/toga_coare.html
United Nations (UN) – http://www.un.org
United Nations Environment Program (UNEP)
– http://www.unep.ch/index.html
United Nations Educational, Scientific and Cultural Organization (UNESCO)
– http://www.unesco.org
World Bank, Global Environmental Facility (GEF)
– http://www.gefweb.org
World Meteorological Organization (WMO)
– http://www.wmo.ch
World Ocean Circulation Experiment (WOCE)
– http://www.soc.soton.ac.uk/OTHERS/woceipo/ipo.html

INTERTIDAL FISHES

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doi:10.1006/rwos.2001.0017

Introduction and Classification of Intertidal Fishes

The intertidal zone is the most temporally and spatially variable of all marine habitats. It ranges from sand and mud flats to rocky reefs and allows the development of a wide variety of plant and animal communities. The members of these communities are subject to the many and frequent changes imposed by wave action and the ebb and flow of the tide. Consequently, animals living permanently in the intertidal zone have evolved a variety of anatomical, physiological and behavioral adaptations that enable them to survive in this challenging habitat. The greater motility of fishes compared with most other intertidal animals allows them greater flexibility in combating these stresses and they adopt one of two basic strategies. The first is to remain in the zone at low tide. This strategy used by the 'residents', requires the availability of some form of shelter to alleviate the dangers of exposure to air and to predators. 'Visitors' or 'transients', that is species not adapted to cope with large changes in environmental conditions, only enter the intertidal zone when it is submerged and leave as the tide ebbs. The extent to which particular species employ either of these strategies varies widely. Many species found in the intertidal zone spend most of their lives there and are integral parts of the intertidal ecosystem. At the other extreme, others simply use the intertidal zone at high tide as an extension of their normal subtidal living space. In between these extremes are species that spend seasons of the year or parts of their life history in the intertidal zone and use it principally as a nursery or spawning ground. The different behavior patterns used by residents and visitors mean that few fishes are accidentally stranded by the outgoing tide.

Habitats, Abundance and Systematics

Fishes can be found in almost all intertidal habitats and in all nonpolar regions. Most shelter is found on rocky shores in the form of weed, pools, crevices and spaces beneath boulders and it is on rocky shores that resident intertidal fishes are usually most numerous. If, however, fishes are capable of constructing their own shelter in the form of burrows in the sediment, as in the tropical mudskippers (Gobiidae), they may be abundant in such habitats. Visiting species may also be extremely numerous on occasions and are particularly common in habitats such as sandy beaches, mudflats and saltmarshes. Few fishes occupy gravel beaches although species like the Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*, Osmeridae) and some pufferfishes (Tetraodontidae) may spawn on such beaches. Estimating abundance in terms of numbers per unit area can be difficult because of the cryptic nature of the fishes and the patchiness of the habitat. The difficulty is particularly acute on rocky shores where fishes may be highly concentrated in areas such as rock pools but absent elsewhere. Nevertheless, fish densities can be relatively high, particularly at the time of recruitment from the plankton, and on occasions may exceed 10 individuals per m^2.

Over 700 species of fishes from 110 families have so far been recorded in the intertidal zone worldwide. This figure represents less than 3% of known fish species but is certainly an underestimate because it is based only on species recorded on rocky shores. Species on soft sediment shores are not included and many areas of the world have yet to be studied in detail. The final count is therefore likely to be much higher. Intertidal fish faunas are frequently dominated by members of a few families (**Table 1**). Generally speaking, more species are found in the tropics than in temperate zones and each area of the world tends to have its own characteristic fauna. The Atlantic coast of South Africa, for example, is characterized by large numbers of clinid species, New Zealand by triplefins, the northeast Pacific by sculpins and pricklebacks (Stichaeidae) and many other areas by blennies, gobies and clingfishes.

Table 1 Analysis of 47 worldwide collections of rocky shore intertidal fishes to show the 10 families with the largest number of species. Based on Prochazka *et al.* in Horn *et al.* (1999). Note that abundance of species does not necessarily imply that families are also numerically abundant

Family	*Common name*	*Number of species*
Blenniidae	Blennies and rockskippers	55
Gobiidae	Gobies and mudskippers	54
Labridae	Wrasses	44
Clinidae	Clinids, kelpfishes, klipfishes	33
Pomacentridae	Damselfishes	30
Tripterygiidae	Triplefin blennies	30
Cottidae	Sculpins	26
Labrisomidae	Labrisomids	26
Scorpaenidae	Scorpionfishes	25
Gobiesocidae	Clingfishes	24

Characteristics of Intertidal Fishes as Adaptations to Intertidal Life

Resident intertidal fishes are probably descended from subtidal ancestors and have few, if any, characters that are truly unique. They are thus representatives of families that have convergently evolved morphological, behavioral and physiological traits that enable them to survive in shallow turbulent habitats. The distribution of many resident intertidal species also extends below low water mark but they mainly differ from their fully subtidal relatives in the degree to which they can withstand exposure to air and are capable of terrestrial locomotion. Nevertheless, a few species can be considered truly intertidal in their distribution because they never occur below low water mark. Examples are the mudskippers of the genus *Periophthalmus* and blennies of the genera *Alticus* and *Coryphoblennius*.

Morphology

All the common families of intertidal fishes possess the characteristic morphological features of fishes adapted for benthic life in turbulent waters. They are cryptically colored, are rarely more than 15 cm long and are negatively buoyant because they lack a swimbladder or possess one that is reduced in volume. Four basic body shapes can be recognized: elongate, dorsoventrally flattened (depressed), smoothly cylindrical (terete), or laterally compressed (**Figure 1**). In many species the fins are modified to act as attachment devices to prevent dislodgement by turbulence or to assist movement over rough surfaces. In most blennies, the rays of the paired and ventral fins are hooked at their distal ends and may be covered with a thick cuticle to minimize wear. In the gobies and clingfishes, the pelvic fins are fused to form suction cups and allow the fish to attach themselves firmly to the substratum. There seem to be few 'typical' sensory adaptations to intertidal life although many species have reduced olfactory and lateral line systems. These sensory systems would be of limited use for species living in turbulent waters or in those that frequently emerge from the water.

Behavior

Intertidal fishes also show characteristic behavior that enables them to cope with the rigors of intertidal life. Their modified fins and relatively high

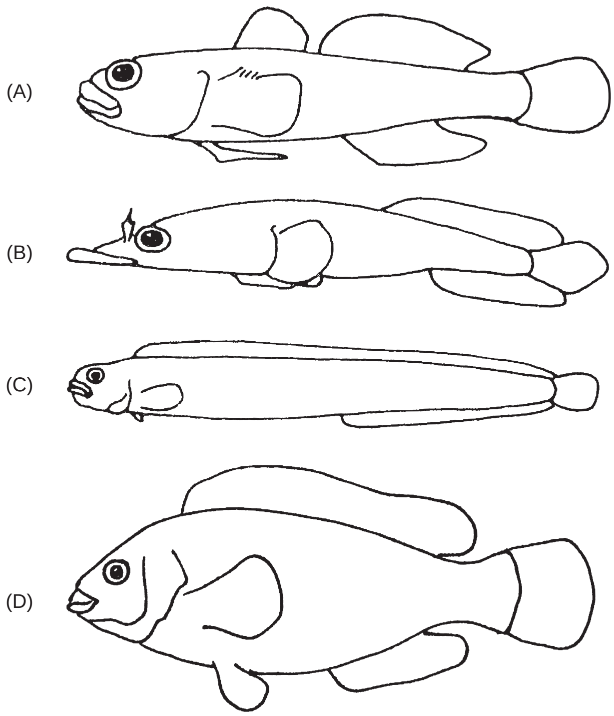

Figure 1 Sketches of four intertidal fish species to demonstrate the basic body shapes. (A) Terete (*Gobius paganellus*, Gobiidae); (B) dorsoventrally flattened (*Lepadogaster lepadogaster*, Gobiesocidae); (C) elongate (*Pholis gunnellus*, Pholidae); (D) laterally compressed (*Symphodus melops*, Labridae).

density allow them to remain on or close to the bottom with the minimum of effort and to resist displacement by surge. Most are also thigmotactic, a behavior that keeps as much of their body touching the substratum as possible and ensures that they come to rest in contact with solid objects when inactive. Their mode of locomotion also reflects this bottom-dwelling lifestyle. Few excursions are made into open water and those species with large pectoral fins use them as much as the tail for forward movement and swim in a series of short hops. Clingfishes and gobies can progress slowly over horizontal and vertical surfaces using their sucker. Elongate forms, which usually have reduced paired fins, creep along the bottom using sinuous movements of their body or alternate lateral flexions of the tail. Strong lateral flips of the tail are also used by some blennies and gobies that can jump between rock pools at low tide and by the semiterrestrial mudskippers in their characteristic 'skipping' movements over the surface of the mud. When progressing more slowly mudskippers use the muscular pectoral fins as 'crutches' to move over the substratum.

Resident species are generally active at a particular state of the tide, although these tidally phased movements can be modulated by the day/night cycle so that some species may only be active, for example, on high tides that occur during the night. Visitors present a more complicated picture because, although their movements are also basically of tidal frequency, they are modulated by a wider range of cycles of lower frequency. Individuals may migrate intertidally on each tide, on every other tide depending on whether they are diurnal or nocturnal, or only on day or night spring tides. They may enter the zone as juveniles in spring or summer, stay there for several months, during which time they are tidally active, and then leave when conditions become unsuitable in winter or as they grow and mature.

The distances over which fishes move in the course of their intertidal movements are dependent on several factors. At one end of the scale are relatively gradual but ultimately extensive shifts in position related to the seasons. At the other end are local, short-term, tidally related foraging excursions. Residents tend to be very restricted in their movements and are often territorial, whereas visitors regularly enter and leave the intertidal zone and may cover considerable distances in each tide. Body size also determines the scale of movement. Residents are small and have limited powers of locomotion whereas visitors usually possess good locomotory abilities and can travel greater distances more rapidly.

The small size and poor swimming abilities of resident species partially account for the restricted extent of their movements but there is good evidence that some species also possess good homing abilities. Most evidence comes from experiments in which individuals are experimentally displaced short distances from their 'home' pools and subsequently reappear in these pools a short time later. Experiments with the goby *Bathygobius soporator* suggest that this species acquires a knowledge of its surroundings by swimming over them at high tide. It can remember this knowledge for several weeks and use its knowledge to return to its pool of origin. Homing is also known in some species of blennies and sculpins and is presumably based on the use of visual clues in the environment. Displacement experiments with the sculpin *Oligocottus maculosus*, however, suggest that this species at least may also use olfactory clues to find its way back to its home pool.

The energy expended in these movements at the various temporal and spatial scales described suggest that they play an important part in the ecology of both resident and visiting species alike. Several functions have been proposed for these movement patterns of which the most obvious is feeding. Visitors move into the intertidal zone on the rising tide to take advantage of the food resources that are only accessible at high water and move out again as the tide ebbs. Residents, on the other hand, simply move out of their low-tide refuge, forage while the tide is high, and return to the refuge before low tide. Following the flooding tide into the intertidal zone may have the added benefit of providing protection from larger predators in deeper water. Movements at both short and long time scales may also be in response to changing environmental conditions. Visitors avoid being stranded above low water mark at low tide because of the lack of refuges or because they are not adapted for the low tide conditions that may arise in possible refuges such as rock pools. Longer term seasonal movements into deeper water can be viewed as responses to changes in such physical factors as temperature, salinity and turbulence. Finally, several species whose distribution is basically subtidal move into the intertidal zone to spawn (see Life histories and reproduction below).

In order to synchronize their behavior with the constantly changing environment fishes must be able to detect and respond to the cues produced by these changes. The cues that fish actually use in timing and directing their tidally synchronized movements are mostly unknown. Synchronization could be achieved by a direct response to change. The flooding of a tide pool or the changing pressure associated with the rising tide, for example, could be used to signal the start of activity. In addition, behavior may be synchronized with the external environment by reference to an internal timing mechanism. The possession of such a 'biological clock' that is phased with, but operates independently of, external conditions is a feature common to all intertidal fishes in which it has been investigated. In the laboratory the presence of the 'clock' can be demonstrated by recording the activity of fish in the absence of external cues. Under these conditions fish show a rhythm of swimming activity in which periods of activity alternate with periods of rest (**Figure 2**). In most cases the period of greatest activity appears at the time of predicted high tide on the shore from which the fish originated. These 'circatidal' activity rhythms, so called because in constant conditions the period of the rhythm only approximates the average period of the natural tidal cycle (12.4 h), can persist in the laboratory for several days without reinforcement by external cues. After this time activity becomes random but in the blenny *Lipophrys pholis* the rhythm can be restarted (entrained) by exposing fish to experimental cycles of wave action or hydrostatic pressure or by replacing them in the sea. The probable function of this circatidal 'clock' is that it enables a fish to anticipate future changes in tidal state and regulate its activity and physiology accordingly. If activity is prevented in the wild, by storms for example, then the persistent nature of the clock allows fish to resume activity that is appropriate to the tidal state at the next opportunity.

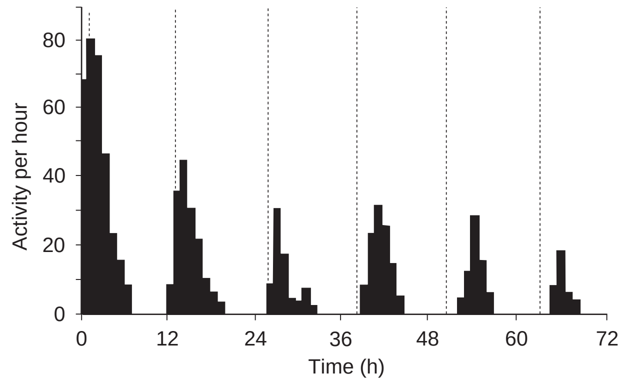

Figure 2 The 'circatidal' activity pattern shown by the blenny *Lipohrys pholis* in constant laboratory conditions. Peaks of activity correspond initially to the predicted times of high tide (dotted lines) but gradually occur later because the 'biological clock' has a period greater than that of the natural tidal cycle (12.4 h). In the sea the clock would be continually synchronized by local tidal conditions.

Physiology

The ebbing tide exposes the intertidal zone to air and so the location of a fish is critical to its survival. Over the low tide period resident fish face not only the danger of exposure to air but also to marked changes in other physical and chemical conditions. On rocky shores, pools act as low-tide refuges but even here temperature, salinity, pH and oxygen content of the water can change markedly for the few hours that the pool is isolated from the sea. Consequently, many resident species are usually more tolerant of changes in these factors than subtidal species. Exposure to air could result in desiccation but, surprisingly, resident intertidal fishes show no major physiological or anatomical adaptations for resisting desiccation. Instead, desiccation is minimized by behavior patterns that ensure fish hide in pools, or in wet areas under stones and clumps of weed at low tide. Nevertheless, many species can survive out of water in moist conditions for many hours and tolerate water losses of more than 20% of their body weight, equivalent to that of some amphibians (**Figure 3**). The ability to tolerate water loss is generally correlated with position on the shore; those fish that occupy higher levels are the most resistant. Prolonged emersion could also present fish with problems of nitrogen excretion and osmoregulation but those species that have

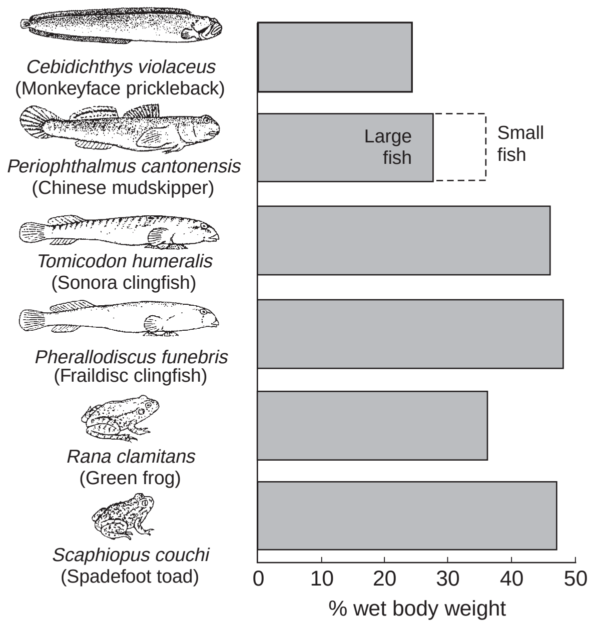

Figure 3 Tolerance of water loss as a percentage of wet body weight in four intertidal fishes compared with two amphibians. (Reproduced with permission from Horn and Gibson, 1988.)

been investigated seem to be able to cope with any changes in their internal medium caused by the absence of water surrounding them.

A further consequence of emersion is the change in the availability of oxygen. Although air contains a greater percentage of oxygen than water its density is much lower causing the gill filaments to collapse and reducing the area of the primary respiratory surface. Unlike some freshwater fishes, intertidal fishes that leave the water or inhabit regions where the water is likely to become hypoxic have no specialized air-breathing organs but maximize aerial gas exchange in other ways. Some species have reduced secondary gill lamellae, thickened gill epithelia and their gills are stiffened with cartilaginous rods. Such features reduce the likelihood of gill collapse when the fish is out of water. The skin is also used as an efficient respiratory surface because it is in contact with air and is close to surface blood vessels. In order to be effective, however, the skin must be kept moist and fish that are active out of water frequently roll on their sides or return to the sea to wet the skin. It is probable that some species use vascularized linings of the mouth, opercular cavities, and, possibly, the esophagus as respiratory surfaces.

The ability to respire in air is currently known for at least 60 species from 12 families and many of these voluntarily leave the water. Fish capable of respiring out of water have been classified into three main types. 'Skippers' are commonly seen out of water and actively feed, display and defend territories on land. They are typified by the tropical and subtropical mudskippers (Gobiidae) and rockskippers (Blenniidae). The second much less terrestrially active group, the 'tidepool emergers', crawl or jump out of tide pools mainly in response to hypoxia. Species from several families show this behavior but it has been best studied in the sculpins. The third group, the 'remainers', comprises many species that sit out the low-tide period emersed beneath rocks and in crevices or weed clumps. Some may be guarding egg masses and they are not active out of water unless disturbed.

Feeding Ecology and Predation Impact

Intertidal fishes are no more specialized or generalized in their diets and feeding ecology than subtidal fishes. Most are carnivorous or omnivorous and a few are herbivores. Herbivores appear to be less common in higher latitudes but a satisfactory explanation of this phenomenon is still awaited. In some cases the diet changes with size so that the youngest stages are carnivorous but larger amounts of algae are included in the diet as the fish grow. The small size of most resident fishes also means that their diet is composed of small items such as copepods and amphipods. In common with many other small fishes, they may also feed on parts of larger animals such as the cirri of barnacles or the siphons of bivalve molluscs, a form of browsing that does not destroy the prey. The extent to which intertidal fishes have an impact on the abundance of their prey and on the structure of intertidal communities is not clear. In some areas no impact has been detected whereas in others fish may have a marked effect, particularly on the size and species composition of intertidal algae. Those species that only enter the intertidal zone to feed contribute to the export of energy from this area into deeper water.

Life Histories and Reproduction

The majority of resident intertidal fishes rarely live longer than two to three years although some temperate gobies and blennies have a maximum life span of up to 10 years. Maturity is achieved in the first or second year of life and the females of longer-lived species may spawn several times a year for each year thereafter. Representatives of 25 teleost families are known to spawn in the intertidal zone. Of these, residents and visitors make up about equal proportions. Intertidal spawning has both costs and benefits. For resident species, intertidal spawning reduces the likelihood of dispersal of the offspring from the adult habitat. It also obviates the need for movement to distant spawning grounds; a process that would be energetically costly for small-bodied demersal fishes with limited powers of locomotion and would at the same time expose them to greater risks of predation. These advantages do not apply to subtidal species many of which are good swimmers and whose adult habitat is offshore. For these species, the benefits are considered to be reduced egg predation rates and possibly faster development if the eggs become emersed. In both residents and visitors alike eggs spawned intertidally may be subject to the costs of increased mortality caused by desiccation and temperature stress. In addition, visitors may be vulnerable to avian and terrestrial predators during the spawning process.

The rugose topography of rocky shores and the cryptic sites chosen for spawning has led to the development of complex mating behavior in many species, particularly the blennies and gobies. In these species, courtship displays by the male include elements of mate attraction and a demonstration of the location of the chosen spawning site. Observing these displays is difficult in most groups but field observations have been made on several Mediterranean blennies that live in holes in rock walls and on mudskippers that perform their mating behavior out of water on the surface of the mud.

All species spawn relatively few (range approximately 10^2–10^5) large eggs (~ 1 mm diameter) that are laid on or buried in the substratum. Large eggs produce large larvae which may reduce dispersal from shallow water by minimizing the amount of time spent in the planktonic stage. On hard substrata the eggs are laid under stones, in holes and crevices and in or under weed. They may be attached individually to the substratum surface in a single layer (blennies, gobies, clingfishes) or in a clump (sculpins). In the gunnels and pricklebacks the eggs adhere to each other in balls but not to the surface. In soft sediments the eggs may be buried by the female as in the grunions (Atherinidae), or laid in burrows as in the mudskippers and some gobies. Killifishes (*Fundulus*) lay their eggs in salt-marsh vegetation.

In temperate latitudes spawning usually takes place in the spring and early summer, but spawning rhythms of shorter frequency may be superimposed on this annual seasonality. Subtidal species such as the grunions, capelin and pufferfishes that use the intertidal zone as a spawning ground mostly take advantage of spring tides to deposit their eggs in the sediment high on the shore, usually at night. During the reproductive season such fish, therefore, spawn at fortnightly intervals at the times of the new and full moons. The larvae develop over the intervening weeks and hatch when the eggs are next immersed.

Buried eggs are left unattended but eggs laid in layers, clumps or balls are always cared for by the parent. The sex of the individual that undertakes this parental care varies between species. In some it is the male, in others the female and in yet others both sexes participate. In some members of the families Embiotocidae, Clinidae and Zoarcidae fertilization is internal and the young are produced live. Parental care by oviparous species takes a variety of forms but all have the function of increasing egg survival rates and removal of the guardian parent greatly increases mortality. Most species guard the eggs against predators but some also clean and fan the eggs to maintain a good supply of oxygen and reduce the possibility of attack by pathogens.

Development time of the larvae depends on species and temperature but when fully formed the eggs hatch to release free-swimming planktonic larvae. In only one case, the plainfin midshipman (*Porichthys notatus*, Batrachoididae) does the male parent also care for the larvae, which in this species remain attached to the substratum near the nest site. The factors stimulating hatching are mostly unknown although it has been suggested that wave shock and temperature change associated with the rising tide may be involved. Until recently it was assumed that the hatched larvae were dispersed randomly by currents and turbulence. It has been shown, however, that at least some species minimize this dispersion by forming schools close to the bottom and are rarely found offshore (**Figure 4**). On completion of the larval phase the larvae metamorphose into the

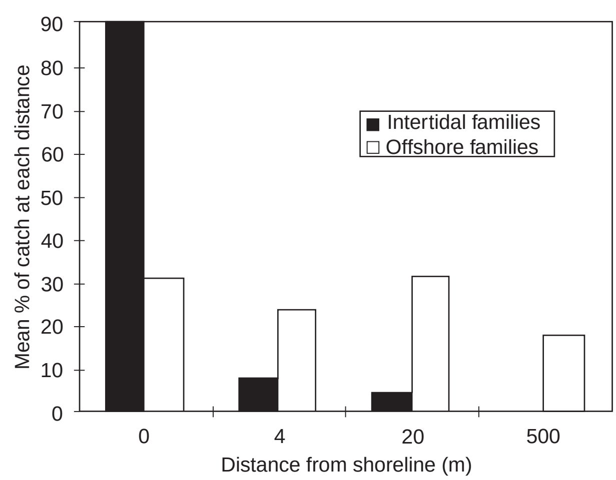

Figure 4 Comparison of the distribution of fish larvae from four intertidal and five offshore families caught in plankton nets at four distances from the shoreline in Vancouver harbour, British Columbia. (Based on data in Marliave JB (1986) *Transactions of the American Fisheries Society* 115: 149–154.)

benthic juvenile phase and settle on the bottom. The clues used by settling larvae to select the appropriate substratum are poorly known but there is some evidence to suggest that individuals can discriminate between substratum types and settle on their preferred type.

See also

Fish Ecophysiology. Fish Larvae. Mangroves. Rocky Shores. Salt Marshes and Mud Flats. Sandy Beaches, Biology of.

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INTRA-AMERICAS SEA

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doi:10.1006/rwos.2001.0380

Introduction

The Intra-Americas Sea (IAS) is a semi-enclosed salt-water body of the tropical and subtropical western Atlantic Ocean that comprises the Caribbean Sea, the Gulf of Mexico, the Straits of Florida, the Bahamas, the Guianas, and the adjacent waters. Biogeographically, the IAS includes the estuarine, coastal, shelf, and pelagic waters from the mouth of the Amazon River at the equator off Brazil, to Bermuda and westward to the shores of North, Central, and South America. Geographically, the boundaries may be set approximately as $\phi = 0^\circ$ to 32°N latitude, and $\lambda = 50$–98°W longitude. **Figure 1** summarizes the geographical setting.

Early oceanographic explorations of the region were by European scientists who chose to name the IAS (the Caribbean Sea in particular) the 'American Mediterranean'. While superficially this terminology describes the IAS as a similar semi-enclosed sea where evaporation (E) exceeds precipitation (P) plus river runoff (R), $E > P + R$, the Mediterranean Sea is markedly different in character from its western Atlantic counterpart. Also, the IAS was broken into smaller components, and little attention was paid to the Caribbean Sea and by Gulf of Mexico oceanographers and vice versa. Conversely, the Straits of Florida and the water currents of the Gulf Stream system are perhaps the most widely studied oceanographic features on Earth.

With the coming of significant international cooperation between scientists from throughout all the Americas, the IAS began to be appreciated as a unified body of water distinctly different from the early and mid-twentieth century European perspective. An inclusive term was needed to integrate not only the oceanography of the region, but its meteorology and maritime socioeconomic connectivity as well. Thus the term Intra-Americas Sea was developed from the multilingual and multicultural heritage shared by its people.

Regional Overview

Pre-Columbian indigenous peoples of the Intra-Americas Sea certainly knew of the oceanic currents and atmospheric winds. Caribes from the south, Tainos in the middle Antilles, Arawaks from the north, Mayas and Olmecs to the west, all moved freely from island to island to continent, presumably with some knowledge of the currents and winds we have named Caribbean Current, Trade Winds, Gulf Stream, Hurricane, and Guianas Current. European explorers and conquistadors relearned this information, not from the IAS's inhabitants, but from hardship after experiencing what was so well known already. James A. Mitchner's 1989 novel *Caribbean* imagines so well what science could have learned directly.

As regards the geological setting, the IAS encompasses three tectonic plates: the North American Plate, the Caribbean Plate, and the South American Plate (the Cocos and Nazca Plates mark Pacific tectonic boundaries but are not significantly involved in the air–sea regime discussed herein). About 3 Ma the Caribbean Plate drifting from west to east closed the gap between North and South America, creating Panama and deflecting oceanic flow northward. Central America and the eastern Caribbean margin are volcanically active today.